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On the cover:

Luffa aegyptiaca Mill., illustrated in Köhler's Medizinal-Pflanzen in naturgetreuen Abbildungen mit kurz erläuterndem Texte: Atlas zur Pharmacopoea germanica, austriaca, belgica, danica, helvetica, hungarica, rossica, suecica, Neerlandica, British pharmacopoeia, zum Codex medicamentarius, sowie zur Pharmacopoeia of the United States of America. Vol. 4, Plate 99.
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Contents

Tunisian Cucurbits: A Reservoir of Genetic Diversity for Sustainable Agriculture

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The members of the Curcurbiteae family, known as cucurbits, encompass a vast group of around 130 genera and 800 species (Chomicki et al. 2019). These versatile plants can be cultivated in warmer regions across the globe. In Tunisia, watermelon (*Citrullus lanatus* (Thunb.) Matsum. and Nakai), melon (*Cucumis melo* L. var. *reticulatus*, var. *inodorus*, and var. *cantalupensis*), snake melon (*C. melo* L. var. *flexuosus*), pumpkins (*Cucurbita pepo*, *C. maxima*, and *C. moschata*), sponge gourd (*Luffa cylindrica*) and bottle gourd (*Lagenaria siceraria*) represent the most commonly grown cucurbits. The landraces within these cucurbit species serve as a vital source of genetic diversity, offering substantial value to plant breeders.

Tunisia boasts a rich repository of cucurbit landraces (Figure 1) that have been subject to extensive phenotyping for agro-morphological and quality traits. Studies have been conducted on various Tunisian cucurbit landraces, including melon (Chikh-Rouhou et al. 2023a; Chikh-Rouhou et al. 2021a), watermelon (Chikh-Rouhou and Garcés-Claver, 2021), pumpkins (Chikh-Rouhou et al. 2023b; 2023c), and bottle gourd (Chikh-Rouhou and Garcés-Claver, 2023). These studies revealed a high level of diversity for the evaluated characteristics with the identification of several sources of resistance and promising fruit quality traits. These findings underscore the significance of Tunisian cucurbits as a genetic resource with the potential to bolster traditional agriculture, particularly in the face of climate change.

In addition to agro-morphological and quality traits, research has examined the rhizosphere microbiome composition associated with Tunisian cucurbit landraces, including melon (Aydi-Ben Abdallah et al. 2021), watermelon (Aydi-Ben Abdallah et al. 2023), and pumpkins (Aydi-Ben Abdallah et al. 2024). These studies demonstrated that the composition of the soil microbial community has been shaped by cucurbit landraces, i.e. the differences in the composition of the soil microbial community resulted in differences in yield components and fruit quality. Indeed, symbiotic interactions between the cucurbit plants and their microbial counterparts in the soil were detected for some agronomic traits.

Studies have also examined the resistance of Tunisian cucurbit landraces to fungal diseases (Table 1) including powdery mildew (Chikh-Rouhou et al. 2022, Kacem and Chikh-Rouhou, 2022, Chikh-Rouhou et al. 2020), fusarium wilt (Chikh-Rouhou et al. 2021b; 2018; 2013), and to pests such as the aphid (Chikh-Rouhou et al. 2019). In these studies, several Tunisian landraces exhibited resistance to one or two fungal diseases based on their genetic makeup. These investigations contributed to a greater understanding of the value of Tunisian cucurbit landraces and highlight their adaptability and resilience.

A preliminary evaluation for a low watering regime (drought stress) was conducted at the experimental field of the Regional Research Centre on Horticulture and Organic Agriculture (CRRHAB) and the results were promising for the pumpkin accessions (Unpublished). The information gained from this study could prove valuable in efforts to select landraces capable of thriving in diverse and stressful agroclimatic conditions. The use of climate-resilient crops is emerging as a highly effective and sustainable practice contributing to crop productivity resilience.

The genetic diversity identified within these landraces calls for the development of a strategy for their conservation and utilization in breeding programs. Such initiatives are crucial for the safeguarding of these plant materials as a valuable gene pool, but also to utilize them as a means to fortify traditional agricultural methods. Planning for the sustainable management and propagation of these genetic resources is essential to address the challenges posed by climate change while maintaining agricultural productivity.

In conclusion, Tunisian cucurbits offer a wealth of genetic diversity. This has far-reaching implications for the sustainability of agriculture under evolving climate conditions. This resource-rich germplasm is a testament to nature's adaptability and resilience, and strategic efforts for its conservation and utilization are essential for the future of agriculture in Tunisia and beyond.

Acknowledgements

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Figure 1. Diversity of some cucurbits (watermelon, pumpkin and melon) collected at the Regional Research Centre on Horticulture and Organic Agriculture (CRRHAB), Tunisia

Table 1. Resistance to biotic stress identified in Tunisian cucurbit landraces.

	FOM* Resistance	**FON* Resistance**	**Resistance to *Aphis gossypii*[c]**	**Powdery mildew resistance[d]**
Melon landraces[a]	Maazoun Ch.M		Chamem (Ananas type)	Dziri
	Maazoun M. Chaker			Sarachika
	Maazoun Mahdia			Rupa
	FL			Chamem
	Dziri			Asli
	Lobneni			
	Horchay			
	Stambouli			
	Chamem (Ananas Type)			
Watermelon landraces[b]	-	Arbi Sahline	-	-
		Arbi Mahdia		
		Arbi Echamekh		
Pumpkin landraces[b]	-	-	-	Arbi Ch.M Arbi
Lagenaria[b]	In all collected accessions	In all collected accessions	-	-

* FOM resistance: *Fusarium oxysporum* f. sp *melonis* ; FON resistance: *Fusarium oxysporum* f. sp *niveum*
[a] Chikh-Rouhou et al. 2021b
[b] Data not yet published
[c] Chikh-Rouhou et al. 2019
[d] Chikh-Rouhou et al. 2022; Kacem and Chikh-Rouhou, 2022

Cucumis bisexualis, Buried in the Taxonomic Wastebasket *C. melo* subsp. *agrestis*, is the Correct Name for Mapao Egg, Hermaphrodite Line Y101, and Weedy Melon UT1, and Helps Focus on Trait Evolution and Domestication of *C. melo*

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This is a continuation of efforts to clarify the taxonomy of *Cucumis*, which despite receiving a lot of attention from plant breeders and molecular-developmental biologists is lacking modern taxonomic treatments (Renner et al., 2007; Sebastian et al., 2010; Schaefer and Renner, 2021). The only complete treatment of the genus, Kirkbride's (1993) monograph, is greatly outdated, covering only 32 of the 65 species currently recognized in *Cucumis* (https://cucurbit.de/calycophysum/cucumis/). Five more species are in the process of being described (H. Schaefer, Technical University of Munich, pers. comm. 22 Jan. 2024).

Kirkbride had a rather broad concept of *Cucumis melo,* a taxon name under which he synonymized 522 names published by earlier workers, creating what might be called a taxonomic wastebasket. To gain some control over the mass of variation, he subdivided the thousands of collections into two clusters, subspecies *melo* and subspecies *agrestis,* based on ovary pubescence. As shown with molecular characters, these two clusters are unnatural, with accessions instead clustering by geographic origin and not ovary pubescence or their wild/cultivated origin (Endl et al., 2018).

Among the hundreds of names that Kirkbride (1993) synonymized under subspecies *agrestis* is *Cucumis bisexualis* A.-M. Lu & G.C. Wang published in 1984. The type collection consists of two plants collected in June 1979 by Gui-Chen Wang #01 and labelled as "Introduced from Ningyang County, Shandong Province, now cultivated in vegetable fields in Beijing. Growing alongside fields." The two plants are mounted on two sheets with identical labels in Chinese and with annotation labels indicating that Charles Jeffery identified the material as *Cucumis melo* var. *agrestis* on 3 Apr. 1980 (one of the two annotation slips is in his own handwriting) and that An-Min Lu and Zhi-Yun Zhang identified the material as *Cucumis bisexualis* A.-M. Lu & G.C. Wang on 8 May 1983. The sheets have been digitized by the Beijing herbarium with the unique identifiers PE01178335 and PE01178336. Neither is annotated as the holotype, but PE01178335 bears a cellophane envelope with two black-and-white photos of fruit cross sections (Fig. 1), which are also visible through the cellophane. This specimen is presumably the holotype.

The original species description is in Latin and states that the species differs from *Cucumis melo* by its consistently bisexual flowers and smaller fruits, 3-3.5 cm long and 2-3 cm in diameter. The first author of the description, Professor Lu An-Min (1939–) from the Beijing Institute of Botany, worked on the Cucurbitaceae for the *Flora of China* (Lu and Zhang, 1986), which therefore includes *C. bisexualis* as a distinct species. In the mid-1980s, Lu visited Charles Jeffrey (1934 - 2022), the best western expert on the cucurbits, then working at the Kew herbarium (Renner and Hind, 2022). Lu and Jeffrey collaborated for many years on the English-language treatment of the Chinese Cucurbitaceae (Lu and Jeffrey, 2011) in which they synonymized *C. bisexualis* under *C. melo* subsp. *melo*, a surprising decision given that Lu himself had described the species as distinct from *C. melo* and given that Jeffrey in 1980 had annotated the Beijing type collection as var. *agrestis*.

Cucumis bisexualis is of interest biologically because of its bisexual flowers and in terms of the light it may shed on the history of domestication of melons. While the two type collections were made in 1979 alongside agricultural fields in Beijing, their labels state that the species was introduced from Ningyang County, which is located about 530 km south of Beijing. The natural range of *C. bisexualis* is not entirely clear but the species is widespread in the Yellow River delta, where its seeds germinate in low-salinity conditions (Zhang et al., 2011). Other studies that have accepted the taxon as a good species have focused on the coumarin-rich fruits, which go by the common name 'mapao egg' or 'muskmelon egg' (Ma et al., 2018, 2020). These studies state that the species is mainly distributes in the eastern Chinese provinces Henan, Shandong, Anhui, and Jiangsu.

Archaeobotanical and molecular evidence suggests that melon domestication occurred independently in Northeast

Africa, in India, and perhaps a third time in the lower Yangtze region of China (Fuller, 2006, 2012; Renner and Schaefer, 2011; Fuller et al., 2014; Endl et al., 2018). The archaeobotanical evidence consist of the seeds, which prove the presences of melons at a particular site and time, and the increase of seed size during the domestication process, since seed size correlates allometrically with fruit size and the seeds themselves might also have been used as a snack or for oil extraction. Figure 2 shows the seeds of modern *C. bisexualis* next to seeds of domesticated *C. melo* and seeds of the wild African *C. melo* subsp. *meloides*, one of the many names misplaced in the wastebasket "*agrestis*." It is clear that *C. bisexualis* has much smaller seeds than wild "*agrestis."*

Small seed size is the reason that at least some of the many *Cucumis* seeds reported from archaeobotanical sites in China (dating to 6000-4000 BP) have been identified as *Cucumis bisexualis* (Zheng and Chen, 2006). Molecular data are needed to confirm such morphology-based identifications of ancient seeds and also to assess a possible role of *C. bisexualis* in the domestication of *C. melo* in China.

Cucumis bisexualis provides an excellent opportunity to study the control of fruit flesh thickness and stamen and pistil development in *Cucumis* (Fig. 3). Two mapao melon accessions, both classified as var. *agrestis*, are maintained by the National Mid-Term Genebank for Watermelon and Melon, China as 'x207' and '1114wd'. Liu et al. (2020) re-sequenced their genomes and suggested that mapao melon might be a feral form of cultivated melon, which would imply a dramatic reversal in seed size (Fig. 1) as well as the evolution of bisexual flowers from the monecious condition.

The first reference genome of mapao melon was produced by Lyu et al. (2023), using HiFi long reads and high-throughput chromosome conformation capture (Hi-C) technologies. Lyu and colleagues discovered a super long sequence absence on Chromosome 4 in mapao compared to eight other forms of *C. melo* for which genome assemblies are currently available, including two Chinese germplasms classified as "*agrestis"* ('HS' and 'IVF77').

Two other studies have focused on the genetic control of the male and female organs in *C. bisexualis* flowers. The first of these, by Wang et al. (2022), applied genome re-sequencing to the hermaphrodite line Y101 obtained from the Laboratory of Cucurbits Germplasm Innovation and Genetic Improvement, Northwest A & F University, Yangling, Shaanxi, China, where unsurprisingly it is classified as "*agrestis*." The paper's photos of the flowers, as well as the description of the thin-skinned small fruits, unambiguously identify Y101 as *C. bisexualis*. The second study, by Nashiki et al. (2023), applied re-sequencing to 'Japanese weedy melon (UT1)' collected from an island in the Seto Inland Sea, which the authors classify as "*agrestis*." The plants bear exclusively bisexual flowers on the main stem and lateral branches, and the paper's color photo of the plant habit and flowers (Fig. 3b) clearly shows *C. bisexualis*. A polymorphism discovered in UT1 was consistent with that of the bisexual line Y101 (Wang et al., 2022), further confirming the identity of Y101 and UT1.

In conclusion, *Cucumis bisexualis*, described by Lu An-Min in 1984 is the correct, and by chance also informative, name – the species' flowers are indeed always bisexual – for mapao egg, hermaphrodite line Y101, and weedy melon UT1. Using this name would help bring together insights on trait evolution and domestication of *C. melo.*

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Figure 1. The type specimen of *Cucumis bisexualis* deposited in the Beijing herbarium (acronym PE), China.

Figure 2. Seeds of *Cucumis bisexualis* in cellophane next to seeds of (A) domesticated *Cucumis melo* and (B) *Cucumis melo* subsp. *meloides* from Africa ("agrestis"). Photo credits: A) P. Renner, Jan. 2023; B) H. Schaefer, Feb. 2023

Figure 3. Fruits and habit of *Cucumis bisexualis*. (A) Fruits on the hand of Luo Shi-Xiao; (B) habit and flower of Japanese weedy melo UT1. Photo credits: A) S-X. Luo, 6 Nov. 2022; B) Kindly provided by Yosuke Yoshioka.

Interspecific Hybridizations in *Citrullus* – Notes

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Introduction

Citrullus is a relatively small genus that includes only seven known species. The phylogenetic relationships among these species have been well established (Chomicki and Renner, 2015). Based on its relationship to the cultivated watermelon (Renner, 2019) it might be assumed that *C. lanatus* var. *cordophanus* would hybridize readily with commercial watermelon cultivars and breeding lines. In a similar manner, it is generally known that *C. amarus* (citron) and *C. mucosospermus* (egusi), the two species most closely related to *C. lanatus*, can be hybridized with *C. lanatus* and produce fertile progeny. In fact, a pollenizer (SP-6) with multiple disease resistance was developed through the crosses of these three species (Brusca and Zhang, 2012). This places both *C. amarus* and *C. mucosospermus* firmly in the secondary genepool (as defined by Harlan and de Wet, 1971).

Citrullus colocynthis, a species distantly related to *C. lanatus*, also hybridizes with *C. lanatus* and produces fertile progeny (Levi et al., 2002). In a cross of RCAT055816 x PI537300 (*C. amarus* x *C. colocynthis*), the F_1 was essentially sterile. However, X. Zhang and colleagues have developed unique lines with very small fruit size and very thin rind using *C. colocynthis* (PI537300) as a pollen donor. These findings suggest that *C. colocynthis* might also be considered to be a member of the secondary genepool.

These earlier reports indicate that several of watermelon's wild relatives, both closely related and distantly related, can be hybridized with *C. lanatus*. However, little information, with few exceptions (de Winter, 1990; Jarret et al., 2017), has been presented on the ability to hybridize several of watermelon's other crop wild relatives (CWRs) with *C. lanatus,* or among themselves. These other desert-dwelling species offer potential opportunities for the introgression of desirable traits (Simmons et al., 2019) into the cultivated watermelon, either directly or indirectly. These species include *C. ecirhosus*, *C. rehmii* and *C. naudinianus*.

This brief note is offered to provide information obtained over several years of working with these less well investigated species. The work is hardly complete, and it is hoped that further studies will be undertaken.

Materials and Methods

All plant materials were obtained from the S-009 genebank in Griffin, GA as described previously (Jarret et al., 2017) and grown in the greenhouse or field on the GA Experiment Station. Unless noted otherwise, the excised embryos of hybrid seeds were germinated in vitro, or entire seeds were germinated in Petri dishes on moist paper towel after cracking the seed coat with a small vise-grip (Jarret et al., 2017). The success of hybridizations was evaluated based on the phenotypic characteristics of the resultant progeny, or in the case of crosses with *C. naudinianus*, via molecular analysis.

Molecular Analysis. Genomic DNA isolation involved use of the plant DNA isolation kit (QIAGEN cat# 69104). PCR reactions consisted of 50 ng genomic DNA, 0.20 µM mixed forward and reverse primers, 1X Buffer (10 mM Tris-HCl pH 8.2, 50 mM KCl, Triton 0.1%, BSA 1 mg/ml), 1.5 mM $MgCl_2$, 0.2 mM dNTPs and 1 U *Taq* polymerase (Promega) in 10-µL reaction volumes. Amplification was performed in a GeneAmp PCR 9700 System thermal cycler (Applied Biosystems) programmed to 94°C for 2 min followed by 35 cycles of 94°C for 30 s, 50-65°C for 30 s, 72°C for 1 min, then 72°C for 10 min. Amplified products were separated on a high-throughput DNA fragment analyzer (AdvanCE FS; Advanced Analytical Technologies, Ames, IA) and diluted in a 1:11 ratio depending on the concentrations of products; the dilution and the

injection voltage were adjusted to prevent overloading the PCR product on the fragment analyzer. PCR product of 2 µl was pipetted directly into the wells of the sample plate containing 22 µl 1X TE dilution buffer. Alternatively, to prevent evaporation a drop of mineral oil was overlaid on each sample. The samples were size-separated by use of a 96-capillary automated system with capillaries 80 cm long. Polymer and other required reagents were from the DNF-900 dsDNA reagent kit (Advance Analytical Technologies). The DNF-900 dsDNA reagent kit can effectively separate amplicon ranges between 35 and 500 bp and resolve 1-bp differences between alleles. Following the capillary electrophoresis, the data were processed by use of PRO Size 2.0, software (Advance Analytical Technologies). The data were normalized to the 35-bp lower marker and 500-bp upper marker and calibrated to the 75- to 400-bp range.

Results and Discussion

Crosses with *C. lanatus* cv. Sugar Baby as Male Parent

***C. ecirrhosus* x cv. Sugar Baby.** *C. ecirrhosus* is native to the Namib Desert. This species is a perennial and F_1 hybrids with *C. ecirrhosus* generally exhibited a perennial growth habit. Unlike most other *Citrullus* species, *C. ecirrhosus* (and its hybrids with *C. lanatus*) could be readily propagated via vine cuttings (Simmons et al., 2019). This species produces a caudex (Fig. 1), an organ utilized for water storage (Rowley, 1978; Romero, 2022).

The cross *C. ecirrhosus* x cv. Sugar Baby was made with relative ease. However, limited attempts to cross *C. ecirrhosus* with 2 other cultivars of *C. lanatus* (i.e. cvs. Charleston Gray and Bush Jubilee) met with less success indicating a genotypic effect on crossability. The F_1 plants of *C. ecirrhosus* x cv. Sugar Baby were vigorous. In 2020, a single F_1 plant was propagated to produce 12 rooted cuttings that were placed in the field to produce fruit/seed on the GA Experiment Station. Plants were allowed to open pollinate. Fruit set on the earliest flowers was low but improved as the season progressed and the plants increased in size. The total yield of fruit from these plants was substantial (Fig. 2). Seed yields averaged 85 seed/fruit in fruit that averaged 8-10" in diameter. Fruit rinds were uniformly dark green and smooth. Fruit flesh was moderately firm and whitish-yellow. Fruit were often irregular in shape, but were generally near round. F_2 seed germination averaged 55%.

***C. rehmii* x cv. Sugar Baby.** The fruit of *C. rehmii* have a unique rind that is patterned and springy (not hard) bearing some resemblance to the rind of *Cucumis melo* but of a different color and texture. This species is an annual, also native to the Namib Desert (De Winter, 1990), and is sometimes referred to as the Namib melon. Its distribution is sympatric with that of *C. lanatus* and *C. ecirrhosus* (De Winter 1990).

Successful crosses of *C. rehmii* x cv. Sugar Baby were readily made in the greenhouse. The viability of F_1 seed was ~ 45%. In 2022, a small population (10 F_1 plants) was grown in the field on the GA Experiment Station. F_1 plants were near normal in fertility as judged by late season fruit set. The fruit harvested from these F_1 plants were similar in size and general appearance (coloration) to the fruit harvested from the F_1 plants of the *C. lanatus* x *C. ecirrhosus* population described earlier (Fig. 3). However, the fruit were often smaller, irregular in shape and with a waxy coating and a thin rind. Fruit flesh was off-white to pale yellow and spongy. Ten randomly selected mature fruit yielded 55-105 F_2 seed each. Our accession of *Citrullus rehmii* hybridized readily with cv. Charleston Gray.

***C. colocynthis* x cv. Sugar Baby.** The ability to produce fertile F_1 progeny from the cross *C. lanatus* x *C. colocynthis* has been previously reported (Levi et al., 2017). Hence, it will not be discussed except to note that a series of 6 hybridizations with *C. colocynthis* as the male parent resulted in an average of 22 seed/fruit and the reciprocal an average of 9 seed/fruit.

***C. naudinianus* x cv. Sugar Baby.** *C. naudinianus* is the species most distantly related to the cultivated *C. lanatus* and is the *Citrullus* species most closely related to *C. colocynthis. C. naudinianus* is a perennial, dioecious, and until recently was classified as *Acanthosicyos naudinianus*. Based on the known systematic relationships of *Citrullus* spp. (Chomicki and Renner, 2015), and the extremely limited availability of *C. naudinianus* flowers (see *C. colocynthis* x *C. naudininanus*), we elected to utilize most *C. naudinianus* female flowers to perpetuate the line or to cross with that species most likely (based on taxonomic relationships) to produce viable seed, that species being *C. colocynthis*. Hence, no hybridizations with cv. Sugar Baby were attempted.

Crosses with cv. Sugar Baby as Female Parent

cv. Sugar Baby x *C. ecirrhosus.* This cross was also made with relative ease. The F_1 plants of cv. Sugar Baby x *C. ecirrhosus* were vigorous and also readily propagated by vine cuttings. In 2021, 10 cuttings were clonally propagated from a randomly selected F_1 plant and grown on the GA Experiment Station as described earlier for the reciprocal cross. Fruit set, fruit size, fruit shape and coloration of the fruit harvested from these F_1 plants were similar to those harvested from the *C. ecirrhosus* x cv. Sugar Baby hybrid population. Seed yields averaged 95 seed/fruit (10 fruit sample) in fruit averaging 9-11" in diameter. In this cross, as in the reciprocal, plants exhibited a perennial growth habit.

cv. Sugar Baby x *C. rehmii*. This cross was made with relative ease. Ten F_1 fruit yielded an average of 95 seed/fruit. Germination of these has yet to be tested. *C. rehmi* crossed readily with *C. lanatus* cv. Charleston Gray.

Hybridizations with *C. naudinianus*

C. colocynthis* x *C. naudininaus. Plants of *C. naudinianus* are large with vines readily reaching 10 meters and longer. The size of this plant prevented our maintaining more than a single male and female plant in the greenhouse. While the male plant produced sufficient flowers for limited use as a pollen source, the female plant produced only 6 flowers over the course of several months. The paucity of female flowers effectively precluded efforts to hybridize this species as pollen recipient and so the few female flowers that were available were used to maintain the accession (PI 596694).

Over the course of several years, we noted that PI 596694 was susceptible to gummy stem blight (causal agent *Stagonosporopsis* spp.) but the plants did not succumb to the disease over that time period. Cankers were periodically observed along the older portions of the vines near the crowns of the plants. Fungicides served to control the pathogen. Plants derived from newly formed storage organs initially appeared to be free of the pathogen but have not been tested.

This cross (*C. colocynthis* x *C. naudinianus*) can be made with some difficulty. Ten hybridizations yielded 357 seeds of which 165 were fully developed (Fig. 4). Five randomly selected seeds from a single cross were successfully germinated *in vitro*. The F_1 plants exhibited a growth habit that was intermediate between the two parents and they produced a small tap root.

C. rehmii* x *C. naudinianus. The cross of *C. rehmii* x *C. naudinianus* was accomplished resulting in F_1 plants that were moderately vigorous. Eight hybridizations produced 112 seed, 66% of which were fully developed. The vines of F_1 plants branched (Fig. 5 -middle) at nearly every node. Leaves were scabrid as is typical of *C. naudinianus*. This hybrid produced carrot-like storage roots (Fig. 5 upper) that were smaller and of a different shape than typical *C. naudinianus* storage organ. Plants of this hybrid produced multiple (two or sometimes three) male flower buds/node with all, except one bud, eventually aborting and the remaining bud sometimes developing to maturity. A single plant of this hybrid combination produced hermaphroditic-like flowers with a fully developed pistil, partially developed ovary and partially or near fully-developed anthers – Fig. 5 - lower).

C. ecirrhosus* x *C. naudinianus. *C. ecirrhosus* was hybridized with *C. naudinianus* with moderate difficulty (based on the number of apparently viable seed produced). The reciprocal cross was also successful resulting in 64 fully developed seed. Structures believed to be rudimentary aerial roots were sometimes observed on the hybrid plants (Fig. 6).

Miscellaneous Crosses

C. rehmii* x *C. ecirrhosus. This cross was readily accomplished with plentiful fully-developed viable F_1 seed (average ~95) present in mature fruit (Fig. 7 – upper).

C. ecirrhosus* x *C. rehmii. The reciprocal of the previous cross yielded fewer than three seed (typically none) per mature fruit. Most fruit contained only empty seed coats (Fig. 7 - lower).

C. rehmii* x *C. mucosospermus. The cross *C. rehmii* x *C. mucosospermus* and its reciprocal were made without difficulty. Fruit averaged 30 -70 seed each.

C. rehmii* x *C. amarus. It is well known that *C. amarus* (citron melon) intercrosses with *C. lanatus*. However, the cross compatibility of *C. amarus* with other more distant species has not been reported. F_1 plants of *C. rehmii* x *C. amarus* (and the reciprocal cross) are vigorous with rather thin vines that are moderately branched. The F_1 fruit of greenhouse grown plants were roundish in shape and about the size of large *C. rehmii* with intermediate coloration (Fig. 8 - lower). The F_1 plants set fruit readily when selfed. A total of three hybridizations resulted in an average of ~95 seed/fruit. All were fully developed (Fig. 8 - upper).

C. rehmii* x *C. colocynthsis. This cross was readily accomplished with abundant fully-developed (60-150) viable F_1 seed present in a mature fruit (Fig. 9).

Conclusions

Of the six known CWR of watermelon, five (*C. amarus*, *C. mucosospermus*, *C. ecirrhosus*, *C. rehmii* and *C. colocynthis*) can be hybridized with *C. lanatus* to produce fertile F_1 progeny capable of generating an F_2 population. In the course of this work, genotypic effects on the success of individual hybridization partners were observed. Some crosses such as *C. rehmii* x *C. ecirrhosus* exhibited a strong uni-directional effect and were successful only when one species was used as the female parent. In general, the interspecific hybrid plants were vigorous and displayed, as expected, phenotypic characteristics that were intermediate to the two parents.

Although no evidence was found to indicate fertility in the single *C. naudinianus* interspecific hybrid plant available for observation (due to greenhouse space limitations), that obstacle might be overcome by inducing tetraploidy (Bae et al., 2020), a process known to sometimes restore the fertility of interspecific hybrids (Oates et al., 2012), or by producing a greater number of hybrid plants. Due to the limited number of male parent plants and genotypes available for evaluation in this work (1), any attempt to meaningfully predict the ease of hybridization of *C. naudinianus* with other *Citrullus* species based on the present study, or the resultant fertility of hybrid offspring so produced, would be premature.

Whether or not watermelon's CWRs, with their many adaptive and disease resistance traits, are ultimately more

fully utilized to improve the crop via conventional or marker-assisted breeding strategies, remains to be seen. One or more of the existing CWR might be used as a bridging species to access the genome of a more distantly related species. Crosses of *C. amarus* x *C. ecirrhosus* x *C. mucosospermus* have been used to develop lines for high femaleness and superior disease resistance for use as rootstock for commercial watermelon production (X. Zhang - personal communication, Fig. 10). Information obtained from the study of the CWR might also be expected to contribute to gene editing efforts (Feng et al., 2023). In order to realize the greater use of these CWRs, a significant investment in resources, and a realistic (possibly long-term) time frame, may be required.

Recently, large amounts of genetic data on watermelon and its CWR have become available as a result of multiple genomic, pangenomic and super-pangenomic studies (Guo et al., 2013; Jarret et al., 2021; Nie et al., 2023; Sun et al., 2023; Wu et al., 2023). These provide a guide for potentially circumventing some of the obstacles that typically limit the introgression of desirable traits from CWR to the cultivated crop. This outpouring of *Citrullus* spp. genomic data will facilitate future utilization of the CWR and curtail or ameliorate some of the constraints to their broader use.

As a final note, the genepool assignments mentioned earlier are somewhat tentative as estimates of crossability among *Citrullus* species can be highly genotype dependent.

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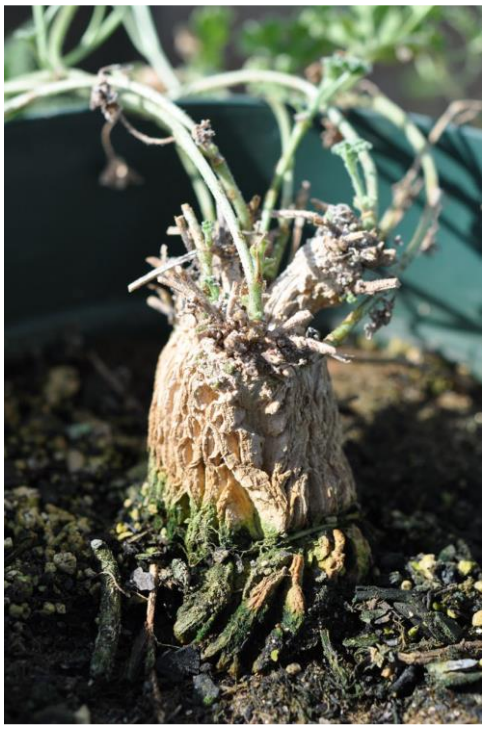

Figure 1. Caudex on 2-year-old *C. ecirrhosus*.

Figure 2. Some of the fruit harvested from 12 plants of a *C. ecirrhosus* x cv. Sugar Baby F_1 hybrid in 2020 (Griffin, GA).

Figure 3. Mature fruit harvested from selfed *C. rehmii* x cv. Sugar Baby F_1 plant grown in the field.

Figure 4. Mature fruit of *C. colocynthis* x *C. naudininaus* F_1 hybrid.

Figure 5. Upper: Carrot-like tap/storage root of a *C. rehmii* x *C. naudinianus* F_1 plant. Middle: Vine branching pattern of a *C. rehmii* x *C. naudinianus* F_1 plant. Lower. Hermaphroditic-like flower on a *C. rehmii* x *C. naudinianus* F_1 hybrid.

Figure 6. Aerial roots on *C. ecirrhosus* x *C. naudinianus* F_1 hybrid.

Figure 7. Mature F_1 fruit of *C. rehmii* x *C. ecirrhosus* (upper) and *C. ecirrhosus* x *C. rehmii* (lower).

Figure 8. Upper: Interior of a mature fruit of a *C. rehmii* x C. *amarus* F_1 hybrid fruit. Lower: Exterior of a *C. rehmii* (left) and a mature *C. rehmii* x C. *amarus* F_1 hybrid fruit.

Figure 9. Mature fruit of *C. colocynthis* (left), *C. rehmii* (right) and their F_1 hybrid (middle).

Figure 10. Lines with strong plant (to be used as rootstock), high femaleness derived from the crosses *C. amarus* x *C. ecirrhosus* x *C. mucosospermus*.

2024 Watermelon Gene List

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Introduction

Watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai) is a major cucurbit crop that accounts for 6.2% of the world area devoted to vegetable crops (FAO, 2022). Watermelon is grown for its fleshy, juicy, and sweet fruit. Mostly eaten fresh, it provides a delicious and refreshing dessert, especially in hot weather. The watermelon has high lycopene content in the red-fleshed cultivars: 60% more than tomato. Lycopene has been classified as useful in the human diet for prevention of heart attacks and certain types of cancer (Perkins-Veazie et al., 2001).

Watermelon is native to northeast Africa where it was domesticated as a source of water, a staple food crop, and an animal feed. It was cultivated in Africa and the Middle East for more than 4000 years, then introduced to China around 900 AD, and finally brought to the New World in the 1500s. There are 2.9 million ha of watermelon grown in the world, with China and the Middle Eastern countries the major consumers. China is the largest watermelon producer, with 60.5% of the total production. The other major watermelon producing countries are Turkey, India, Brazil, Algeria, Russian, Pakistan and the United States (FAO, 2022). In the United States, watermelon is used fresh as a dessert, or in salads. U.S. production is concentrated in Florida, California, Texas, and Georgia (USDA, 2020), increasing from 1.2 M tons in 1980 to 3.9 M tons in 2002, with a farm value of $329 million (USDA, 2002).

Watermelon is a useful crop species for genetic research because of its small genome size, and the many available gene mutants. The genome size of watermelon is 425 million base pairs (Guo et al., 2013). DNA sequence analysis revealed high conservation useful for comparative genomic analysis with other plant species, as well as within the Cucurbitaceae (Pasha 1998). Like some of the other cultivated cucurbits, watermelon has much genetic variability in seed and fruit traits. Genetic investigations have been made for some of those, including seed color, seed size, fruit shape, rind color, rind pattern, and flesh color.

This is an update to the gene list for watermelon. The watermelon genes were originally organized and summarized by Poole (1944). The list and updates of genes for watermelon have been expanded and published by Robinson et al. (1976), the Cucurbit Gene List Committee (1979, 1982, and 1987), Henderson (1991 and 1992), Rhodes and Zhang (1995), Guner and Wehner (2003), and Wehner (2007 and 2012). This current gene list provides an update of the known genes of watermelon, with 236 total mutants grouped into (a) seed and seedling mutants, vine mutants, flower mutants, fruit mutants, and resistance mutants (Table 1), (b) protein (isozyme) mutants (Table 2), and (c) DNA (RFLP, RAPD, InDel and SNP) markers and cloned genes (Table 3).

Researchers are encouraged to send reports of new genes, as well as seed samples of lines containing the gene mutant to the watermelon gene curator (Cecilia McGregor), or to the assistant curator (Todd C. Wehner). Please inform us of omissions or errors in the gene list. Scientists should consult the list as well as the rules of gene nomenclature for the Cucurbitaceae (Cucurbit Gene List Committee, 1982; Robinson et al., 1976) before choosing a gene name and symbol. Please choose a gene name and symbol with the fewest characters that describes the recessive mutant and avoid use of duplicate gene names and symbols. The rules of gene nomenclature were adopted in order to provide guidelines for naming and symbolizing genes. Scientists are urged to contact members of the gene list committee regarding rules and gene symbols. The watermelon gene curators of the Cucurbit Genetics Cooperative are collecting seeds of the type lines for use by interested researchers and would like to receive seed samples of any of the lines listed.

This gene list has been modified from previous lists in the following ways: 1) the description of the phenotypes of several of the gene mutants has been expanded, 2) the descriptions for phenotypes of interacting gene loci have been added, 3) some type-lines that carry each allele of each gene locus have been added, 4) the function genes that control important trait have been updated, 5) genes that have not previously been

described have been added: *Rbf*; *cgmm*; *csm*; *dw-4*; g^{W}; g^{N}; *la*; *Ms-4*; *ob*; *pa*; *Tr*; *psf*; *sf*; *So*; T^{1}; *tm*; *Wbn*; *w-yl*; Y^{Car}; Y^{Pg}.

Watermelon Gene Lists

Poole, 1944: 15 genes total
Robinson et al., 1976: 10 genes added, 25 genes total
Robinson et al., 1979: 3 genes added, 28 genes total
Robinson et al., 1982: 2 genes added, 30 genes total
Henderson, 1987: 3 genes added, 33 genes total
Henderson, 1991: 3 genes added, 36 genes total (plus 52 molecular markers)
Rhodes and Zhang, 1995: 3 genes added, 39 genes total (plus 109 molecular markers)
Rhodes and Dane, 1999: 5 genes added, 44 genes total (plus 111 molecular markers)
Guner and Wehner, 2003: 8 genes added, 52 genes total
Wehner, 2007: 8 genes added, 60 genes total
Wehner, 2012: 2 genes added, 62 genes total
Xu et al., 2024 (the list presented here): 20 genes added, 82 genes total

Gene Mutants

Seed and seedling genes

Watermelon seed coat colors include black, brown, tan, white, green, and red. Seeds may have pink or black tips, or black rims (a dark band around the seed periphery). There are reports of other seed coat colors that include one background color with a different foreground color, that makes the seed coat color difficult to classify. Other factors that make it difficult to classify seed coat color include different shades of a single color. Two observers may classify a single phenotype as different colors or give the same name to two different phenotypes. That makes it difficult to review previous studies.

Research on watermelon seed coat color began in the 1930s. Kanda (1931) reported the first genetic study of watermelon seed characters including 13 crosses. He described 6 ground colors (white, yellowish white, reddish brown, reddish orange, black, and yellowish green) and 5 patterns (black spot on the seed tip, black dots, black rim, yellow margin on the periphery of both flat sides, or solid color) and proposed 7 pairs of genes controlling these characters. However, due to the ambiguity of naming the seed coat colors, it is difficult to compare seed coat colors between Kanda and other studies. As a result, the classification of Kanda has not been adopted widely.

McKay (1936) studied the inheritance of tan, green and red seed coat colors in different types (preserving and stock) of citron, and demonstrated that both tan and green are monogenic dominant over red. The genotypes for tan and red were later assigned by Poole et al. (1941) as *RR tt WW* for tan, and *rr tt WW* for red. The genotype *rr TT WW* was inferred for green (McKay, 1936; Poole, 1944).

Porter (1937) investigated crosses between black-, tan- and white-seeded lines, and reported either two loci or multiple alleles at one locus controlling seed coat color. Black was dominant over clump, tan, and white. The white seed color in 'Pride of Muscatine' referred to in the paper is formally named "white with tan tip" (Wehner, 2008). This demonstrates the ambiguity of classification of seed coat colors as mentioned above. It is difficult to confirm the results due to this ambiguity when the type lines are no longer available. The white-seeded cultivars used by Porter might have been real white or white with tan tip. Other crosses were studied by Porter only in the F1 generation, which showed the dominance of black over white, red over white, black over green, and green over red. The green over red dominance is consistent with a previous report (McKay, 1936). Additionally, Porter also found no linkage among rind toughness, flesh color, or skin color.

Weetman crossed 'Long Iowa Belle' (described as light tan with peripheral black banded seeds) with 'Japan 4' (described as medium brown, black-dotted seeds) and found the latter was a single dominant allele. These two coat colors were later referred to as clump and black, respectively (Poole et al., 1941). The cross between 'Japan 6' (the seed color is described as reddish brown, or tan as referred by Poole) and 'Long Iowa Belle' showed a 9:3:3:1 segregation ratio in F2, indicating dominant alleles at two loci (Weetman, 1937).

Poole et al. (1941) studied the inheritance of several color types including black, tan, red, clump, white tan-tip, and white pink-tip and found that these phenotypes can be explained by a 3-locus model. The black seed-color is found to be dominant over other colors, consistent with previous reports. Poole et al. proposed three genes *r*, *t* and *w* that interact to determine the seed color. From their crossing experiments, Poole et al. assigned the genotypes *RR TT WW* for black seeds, *RR tt WW* for tan, *RR TT ww* for clump, *RR tt ww* for white tan-tip, *rr tt WW* for red, and *rr tt ww* for white pink-tip. They did not observe genotypes *rr TT WW* and *rr TT ww* in their experiments. From earlier studies and the above genotypes, it can be inferred that *rr TT WW* should correspond to green seed color (McKay, 1936; Poole, 1944).

In addition, there is a fourth gene, *d*, suggested by Poole for the stippled surface with numerous black dots (usually with a visible tannish or reddish undercoat). The *d* gene is a modifying locus for black seed color, and only acts in the *RR TT WW* genotype, making *RR TT WW DD* is black, *RR TT WW dd* is dotted black (Poole, 1941).

Shimotsuma (1963) reported that brown seed color was dominant to white in crosses of 3 wild lines of watermelon. Sharma and Choudhury (1982) showed fuscous black is one

gene dominant over white seed coat color. However, it is not clear how the brown, fuscous black and white colors correspond to current color classifications. Additional research is needed to clarify this and other inheritance studies of seed coat colors.

Tannish (*T^1*) found in the cross dotted black (from 'Charleston Gray') × red (from PI 189225) seed coat color is a novel locus or a different allele of the *T* locus, and no individuals with green seed color were observed (Paudel et al., 2019a). *T^1* produces the seed coat color of light shade of brown with yellowish tinge, similar to khaki, which is different from the range of brown color used to describe tan seed coat color by Poole (1941). The *R*, *T^1*, *W* and *D* loci were mapped on chromosomes 3, 5, 6, and 8, respectively (Paudel et al., 2019a). *ClPPO* (*Cla97C03G057100*) encoding polyphenol oxidase (PPO) was reported as a dominant candidate gene for black seed coat (maybe *RRTTWWDD*), involving in the oxidation step of the melanin biosynthesis. There is a single nucleotide insertion in the coding region of *ClPPO*, resulting in a frameshift mutation and leading to early termination of translation, which may be the cause for the formation of light-yellow seeds. In addition, *ClPPO* specifically showed significantly high level of transcript and PPO activity in black seed coat (Li et al., 2020a).

The genes *s* and *l* for short and long seed length (sometimes called small and large seed size) control seed size, with *s* epistatic to *l* (Poole et al., 1941). The genotype *LL SS* gives medium size, *ll SS* gives long, and *LL ss* or *ll ss* gives short seeds. The *Ti* gene for *Tiny seed* was reported by Tanaka et al. (1995). Tiny seed from 'Sweet Princess' was dominant over medium-size seed and controlled by a single dominant gene. The small seed gene behaved in a manner different from Poole's medium-size seed cultivar, where short was recessive to medium-size seeds. Tanaka et al. (1995) suggested that the *Ti* gene was different from the *s* and *l* genes. Unfortunately, the origin of short- and long-seed genes was not described in Poole's paper. *Tomato seed* is shorter and narrower than the short seeded genotype, *ll ss*, with a width x length of 2.6 x 4.2 mm. The trait is controlled by the *ts* gene (Zhang, 1996; Zhang et al., 1994a) with genotype *LL ss tsts*. The interaction of the four genes for seed size (*l*, *s*, *Ti* and *ts*) needs to be investigated further. However, the original type-lines for the *s* and *l* genes are not available.

Many QTLs related to seed size have been reported (Li et al., 2018b; Kim et al., 2015; Maragal et al., 2022; Osae et al., 2021). Recently, a 13.96 Kb deletion on chromosome 2 was found to be related with the tomato seed trait that was controlled by a single recessive gene in the cross 'B38' (medium seed) and 'B166' (tomato seed). There are only two candidate genes in this region, *Cla97C02G045390* and *Cla97C02G045400*, which encode an Acyl-CoA Nacyltransferases (NAT) superfamily protein and a BAG family molecular chaperone regulator 1-like, respectively. Compared with *tomato seed*, these two genes were always highly expressed in medium seeds, suggesting it may be important genes for controlling seed size (Li et al., 2021). However, it is unknown whether this site is the same as *ts*. Gong et al. (2022b) conducted an association analysis between seed size traits and SNP data. The two genes involved in abscisic metabolism, *Cla97C05G104360* and *Cla97C05G104380*, showed relatively higher gene expression in the three smaller-seeded materials ('XiangXiaoGua', 'SuXianXiaoZi' and 'XiaoHongYu'), which may negatively regulate ABA content in seeds and affect seed size (Gong et al., 2022b). Wang et al. (2021) have shown that *ClBG1* (*Cla97C08G153160*) is a key function gene regulating seed size, which encodes β-glucosidase 40 to catalyze the hydrolysis of ABA-glucose ester to release free ABA. After gene knockout, seed size and weight were significantly reduced, which was mainly attributed to decreased cell number resulting from decreased ABA levels. In addition, seed germination was promoted in the *clbg1* mutant due to decreased ABA content.

Cracked seed coat cr (El-Hafez et al., 1981) is inherited as a single gene that is recessive to smooth seed coat. There is no seed available of the type line, 'Leeby', but there are other lines available having a seed cracking trait that may be allelic, such as PI 593350. *Pale leaf* (*pl*) is a spontaneous chlorophyll mutant with light green foliage that can be observed as early as the cotyledon stage (Yang, 2006).

The *egusi seed* trait is controlled by the single recessive gene *eg* in PI 490383w, PI 560006, PI 560023, PI 169233, and PI 186490, which have thin seed coats, thick seed edges, and fleshy and thin pericarp covering the seeds (Gusmini et al., 2004; Prothro et al., 2012; Paudel et al., 2019b). However, the seeds are difficult to distinguish from the smooth (noncracked) seeds of the normal type after washing and drying. Li et al (2023) suggested that the thin seed coat trait was controlled by a suppressor gene together with the *eg* gene in egusi watermelon.

Egusi seeds are rich in oil and protein. Four main quantitative trait loci (M-QTL) for seed oil percentage (SOP) were identified by Prothro with the eg locus contributing 84% of the explained phenotypic variation (Prothro et al., 2012). A high correlation between seed size, kernel percentage (KP) and SOP has been observed in watermelon and were co-mapped in linkage group 2. However, KP showed a positive correlation with SOP in both egusi and normal seed types whereas seed size traits showed negative correlations with SOP (Prothro et al., 2012; Meru and McGregor, 2013). Recently, the *eg* locus was mapped to an overlapping region on watermelon chromosome 6 (Luan et al., 2019). The

candidate region was further reduced to 15.7 Kb, harboring only one gene, *Cla97C06G116000*, encoding epidermal patterning factor-like 4 protein that is a group of cysteine-rich secreted peptides that regulate a range of developmental processes. However, further research is needed on this result (Li et al., 2023).

Vine genes

Several genes control leaf or foliage traits of watermelon. *Nonlobed leaf* (*nl*) has sinuate leaves rather than the lobed leaf type of the typical watermelon (Mohr, 1953). According to nomenclature rules, the trait should be named directly for the mutant trait (*sinuate leaves*, *sn*), rather than for the absence of the normal trait (nonlobed, *nl*). A dominant gene designated as *ClLL1* (*Cla97C04G076510*, homologous to *AtLMI1*) has been reported to control sinuate leaves in dessert watermelon, which encodes a homeobox-leucine zipper-like protein. The integrity of LZ motif, damaged due to a 24 bp deletion in the conserved domain, may be responsible for the generation of sinuate leaves (Wei et al., 2017).

Seedling leaf variegation slv (Provvidenti, 1994) causes a variegation resembling virus infection on seedlings. It is linked or pleiotropic with *Ctr* for cool temperature resistance. The *yellow leaf* (*Yl*) gene results in yellow leaves and is incompletely dominant to green leaves (Warid and Abd-El-Hafez, 1976). *Delayed green* (*dg*) (Rhodes, 1986) causes pale green cotyledons and leaves for the first few nodes, with later leaves developing the normal green color. *Inhibitor of delayed green* (*i-dg*) makes leaves normal green even when they have the *dgdg* genotype (Rhodes, 1986).

The delayed green leaf phenotype of 'Houlv' lines is similar to that controlled by *dg* from 'Pale 90', but their allele identity is unknown. A major QTL for the 'Houlv' trait was mapped on chromosome 3. The candidate gene (*ClCG03G010030*) encodes a FtsH extracellular protease family protein, involved in early chloroplast development. A SNP mutation (G/A) was identified in the 'Houlv' parent, which caused a missense mutation. A higher expression was observed in the green leaf plants than that in delayed green leaf plants at early leaf development (Kidanemariam, 2020).

The *juvenile albino ja* gene (Zhang et al., 1996b) causes reduced chlorophyll in seedling tissues, as well as leaf margins and fruit rind when plants are grown under short day conditions. The dominant gene *Spotted cotyledons Sp* (Poole, 1944) causes round yellow spots to form on cotyledons, leaves and fruit, resulting in the fruit pattern called moon and stars. For more information on *Sp*, see the fruit gene section below. *Lethal albino* is controlled by the recessive gene *la.* The cotyledons of the mutant do not turn green properly to synthesize nutrients and the plant will die within a week or so. Plants that can turn green and growth normally are heterozygote for *la* gene (*Lala*) (Ma and Zhang, 1999). The yellow leaf trait of *whole growth period leaf yellowing watermelon* mutant is controlled by a recessive gene *w-yl*, which is insensitive to temperature and light intensity. The chloroplast volume, the number of thylakoids and the number of grana lamellae in the leaves of mutant are smaller, which leads to a significant reduction in chlorophyll and chlorophyll precursors content. The genetic map showed that the candidate gene of *w-yl* was mapped to 2.217 Mb region on chromosome 2, and *Cla97C02G036040*, *Cla97C02G036050* and *Cla97C02G036060* may be the key factors leading to yellowing of leaves (Zhu et al., 2022).

So far, five dwarf genes of watermelon have been identified that affect stem length and plant habit: *dw-1* (Mohr, 1956; Mohr and Sandhu, 1975) and *dw-1s* (Dyutin and Afanas'eva, 1987) are allelic, and *dw-1*, *dw-2* (Liu and Loy, 1972), *dw-3* (Huang et al., 1998), and *dw-4* (Yang and Li, 2009) are non-allelic. *Dwarf-1* plants have short internodes due to fewer and shorter cells than the normal plant type. Plants with *dw-1s* have vine length intermediate between normal and dwarf, and the hypocotyls were somewhat longer than normal vine and considerably longer than dwarf. The *dw-1s* is recessive to normal plant type. Plants with *dw-2* have short internodes due to fewer cells than the normal type, and plants with *dw-3* have leaves with fewer lobes than the normal leaf. Plants with *dw-4* have fewer branches (about 4-6), flat leaves and normal flower organs, which are controlled by a recessive gene (Yang and Li, 2009).

Currently, four candidate loci for dwarf traits have been identified. C*la97C09G179710*, as a candidate gene for *dw-1*, was mapped on the long arm of chromosome 9 and encoded an ATP-binding cassette transporter (ABC transporter) protein. The 1-bp deletion in exons of this gene co-segregated with the dwarf trait in some natural population, resulting in a frameshift mutation and a truncated protein (Zhu et al., 2019). The *ClGA3ox* (*Cla97C09G164590*) encodes a gibberellin 3β-hydroxylase functions as the best possible candidate gene for dwarf trait of 'N21' line. The fourth polymorphism site (a G to A transition) at the 3' AG splice receptor site of the intron leads to a 13 bp deletion in the coding sequence of *ClGA3ox* in dwarf line 'N21' and thus results in a truncated protein lacking the conserved domain for binding of 2-oxoglutarate (Wei et al., 2019). In a recent study, *ClGA3ox* may play an important role in controlling the hypocotyl length of watermelon (Wang, 2022). The *dsh* line, a gibberellin (GA)-deficient mutant, is a bush with a short vine, short internodes, thin stems, numerous branches, and small leaves, flowers, and fruits, close to the known *dw-2* phenotype. *ClGA20ox* (*Cla97C07G143880*) encoding a gibberellin 20-oxidase-like protein is the primary gene controlling dwarfism in the *dsh* line. The transcriptional regulation may be mediated by two SNPs in the promoter of

ClGA20ox, resulting in compromised GA biosynthesis and internode extension. *ClaGA20ox* RNAi plants generally exhibited dwarfism, with short stems and internodes as well as small leaves and fruit (Dong et al., 2018; 2021b). The GA receptor gene *Cla97C09G178830* is the candidate gene of 'ZXG01061', a dwarf mutant of short internode and GA3 insensitive, and the frameshift mutations and low expression level may lead to loss-of-function changes and GA3 transmission dysfunction, resulting in a dwarf phenotype (Liu et al., 2022a). In addition, exogenous GA can recover the dwarfing phenotype of 'N21' and the *dsh* line, rather than 'ZXG01061', and the allelic relationships between these candidate genes and *dw-1*, *dw-2*, *dw-3*, and *dw-4* are worth further verification.

The *golden yellow* mutant is controlled by the single recessive gene *go*, where the stem and older leaves are golden yellow (Barham, 1956). The type line for *go* is 'Royal Golden'. One benefit of the *go* gene is that the fruit become golden yellow as they mature, so it might be useful as an indicator of mature fruit. The gene *tl* (formerly called *branchless*, *bl*) results in *tendrilless* branches after the 5th or 6th node (Lin et al., 1992; Rhodes et al., 1999; Zhang et al., 1996a). Also, plants have half the number of branches of the normal plant type, vegetative meristems gradually become floral, tendrils and vegetative buds are replaced by flowers (with a large percentage being perfect), and growth becomes determinate. Recently, Dou et al. (2022) found that the branchless trait of 'WCZ' is controlled by a recessive gene *ClTFL1* (*Cla97C04G076830*) that encodes the TERMINAL FLOWER 1 protein. The *ClTFL1* has a SNP in the fourth exon, resulting in a mutation from alanine to glutamate at the end of protein, showing complete co-segregation with branchless plants. However, the allelic relationship between *ClTFL1* and *tl* is unknown. In addition, the branchless, tendrilless, and determinate inflorescence traits in watermelon are co-segregating (Yi et al., 2022).

Flower genes

Three genetic loci determine the floral sex type of watermelon. The *andromonoecious* gene *a* (Rosa, 1928) controls monoecious (*AA*) vs. andromonoecious (*aa*) sex expression in watermelon. Andromonoecious plants have both staminate and perfect flowers, and appear to be the wild type. *Light green flower color* is controlled by the single recessive gene, *gf* (Kwon and Dane, 1999). A gynoecious mutant was discovered in 1996, and is controlled by a single recessive gene, *gy* (Jiang and Lin, 2007). The gynoecious type may be useful for hybrid production, or for cultivars having concentrated fruit set. A recessive gene, *trimonoecious* (*tm*), controls the sex expression of trimonoecious watermelon that have staminate, pistillate and perfect flowers. The *a* allele is epistatic to the *tm* allele. The following phenotype-genotype relationships are proposed for each of the sex determination in watermelon: monoecious, *A_Gy_Tm*; trimonoecious, *A_Gy_tmtm*; andromonoecious, *aaGy_Tm_* or *aaGy_tmtm*; gynoecious, *A_gygyTm_*; gynomonoecious, *A_gygytmtm*; and hermaphroditic, *aagygyTm_* or *aagygytmtm*. The *A* is from 'XHB' (*AAGyGyTmTm*), *gy* is from 'XHBGM' (*AAgygyTmTm*) and *a* is from 'SL3H' and 'AKKZW' (*aaGyGytmtm*) (Ji et al., 2015).

Map-based cloning of the *A* gene showed *CitACS4* (*Cla97C03G066110*) encodes for 1-aminocyclopropane-1-carboxylate synthase 4. *CitACS4* is likely to be involved in the biosynthesis of the ethylene required for stamen arrest during the development of female flowers. A SNP mutation in a conserved domain leads to the decrease in enzyme activity and the production of ethylene in pistillate floral buds, promoting the conversion of female into hermaphrodite flowers, and therefore of monoecy into andromonoecy (Boualem et al., 2016; Ji et al., 2016, Manzano et al., 2016). The *gy* gene, *ClWIP1* (*Cla97C02G049440*), was identified in the cross 'XHB' (monoecious wild type) and 'XHBHM' (a spontaneous gynoecious mutant), which encodes a putative C2H2 zinc finger transcription factor, expressed specifically in carpel primordia and is related to the abortion of carpel primordia in early floral development. Chromosome translocation results in the loss of function of *ClWIP1*, and the production of a gynoecious line (Zhang et al., 2020a). The partially andromonoecious trait (producing male, female, bisexual, and hermaphrodite flowers within the same plant) produced by a recessive gene *pa* (partial andromonoecy), with *ClCG01G020800* of a 38 bp frameshift deletion as the candidate gene that was different from *CitACS4*. This gene encodes a chitinase-like protein that is widely involved in floral organ development in Arabidopsis and rice and can regulate ethylene biosynthesis and signaling pathways (Aguado et al., 2020).

Six genes for male sterility have been reported. *Glabrous male sterile* (*gms*) is unique, with sterility associated with glabrous foliage (Ray and Sherman, 1988; Watts, 1962, 1967). A second male sterile *ms-1* (Zhang and Wang, 1990) produces plants with small, shrunken anthers and aborted pollen. A third male sterile mutant appeared simultaneously with dwarfism, and the dwarf gene was different from the three known dwarf genes. It was named male sterile dwarf (*ms-dw*) by Huang et al. (1998). All male sterile genes reduce female fertility as well. These mutants have been used in hybrid production, but have not been as successful as hoped, since they often have low seed yield. A new, spontaneous male sterile mutant (*ms-2*) with high normal seed set has been identified and will be more useful for hybrid production (Dyutin and Sokolov, 1990). A male sterile mutant having unique foliage characteristics (*ms-3*) was reported by Bang et

al. (2006). Deng et al. (2022) reported a single dominant male sterile mutant (*Ms-4*) through EMS mutagenesis.

Recently, several candidate genes for male sterile have been identified. *ClPEX1* (*Cla97C06G112900*) encoding pollen-specific leucine-rich repeat protein is identified as a candidate gene for *ms-1*, which is significantly less expressed in the pollen of male-sterile G17AB plants. *ClPEX1* RNAi fruits exhibited a markedly inhibited seed set and were much smaller than the fruits of the male-fertile watermelon plants (Dong et al., 2021). A spontaneous male-sterile watermelon mutant, '*Se18*', was reported to have abnormal tapetum development, which resulted in completely aborted pollen grains. The causal gene *ClATM1* (*Cla97C06G117840*) encodes a basic helix-loop-helix (bHLH) transcription factor with a 10-bp deletion and produces a truncated protein without the bHLH interaction and functional (BIF) domain in '*Se18*' plants. *ClATM1* is specifically expressed in the tapetum layer and in microsporocytes during stages 6-8a of anther development (Zhang et al., 2021). The male sterility trait of *Ms-4* was controlled by the candidate gene *ClMS1* (*Cla97C09G181360*), which is caused by a base change from G to A of the coding region. *ClMS1* was predicted to encode a heat shock 70 kDa protein 4, an interesting and highly conserved protein, and the insertion of an HSP70 antisense gene fragment in tobacco and rice has been confirmed to lead to pollen abortion and male sterility (Deng et al., 2022). Further research should seek to decipher the functional mechanism underlying *ClPEX1* and *ClMS1*. Watermelons with few or no seeds are mainly triploid, which has many disadvantages due to unbalanced genome content. A spontaneous mutant line 148 was identified, which can set seeds normally when self-pollinated. The homozygous translocation in '148' can produce normal seeds, but a heterozygous translocation on the 2.09 Mb of chromosome 6 results in abnormalities in meiotic prophase I, producing significantly fewer seeds when hybridized (Tian et al., 2021).

Control of flowering time was oligogenic with a major, stable, colocalized QTL (Qdff3-1) on chromosome 3 responsible for nearly 50% of the phenotypic variation observed for days to first male flower and days to first female flower (McGregor et al., 2014). This region includes a *ClFT* (*Cla97C03G060990*) and a *ClPP2C* (*Cla97C03G061230*) gene. The protein encoded by the *FT* gene is a flowering hormone that can be transported over a long distance and has key functions on the process of flower bud formation. *PP2C* is a distinct family of Ser/Thr protein phosphatase that can positively regulate the transcription level of integrons and floral meristem specific genes in Arabidopsis (Gimode et al., 2019). In addition to the major QTL on chromosome 3, two other QTL were identified for days to first male flower (chromosomes 2 and 3) and days to first female flower (chromosomes 3 and 11) and one for the female-male flower interval on chromosome 2 (McGregor et al., 2014).

Fruit genes

Watermelon fruit shape makes a continuum from round to oval to oblong to elongate. Fruit shape is controlled by a single, incompletely dominant gene, resulting in fruit that are elongate (*OO*), oval (*Oo*), or spherical (*oo*) (Poole and Grimball, 1945; Weetman, 1937). In a recent study, another series of alleles at the *ob* locus is proposed for the fruit shape: allele Ob^E for elongate fruit, which is the most dominant; allele Ob^R (not the same as the o gene for round) for the round fruit, and allele ob for *oblong fruit* (not the oval fruit), which is the most recessive (Lou and Wehner. 2016).

Many QTL for fruit shape distributed across all 11 chromosomes have been identified based on map-based cloning (Pan et al., 2020). *ClSUN* (*Cla97C03G066390*), a major gene for fruit shape, belongs to IQD protein family, which is associated with cytoskeleton arrays and Ca2+-CaM signaling modules. There was a significant correlation between fruit shape and *ClSUN* allelic (*ClSUN25-26-27a*) variation (Dou et al., 2018b; Legendre et al., 2020). Another major QTL for fruit shape was mapped on chromosome 2 (Sandlin et al., 2012; Cheng et al., 2016). Carpel number is related to fruit shape variation. The *trimerous* (*Tr)* carpel was a dominant trait to pentamerous (*tr*) carpel*, w*hich was mapped in the 244 Kb region of chromosome 7. *Cla97C07G143260* is annotated as receptor-like protein kinase 2 with eight non-synonymous SNPs in trimerous and pentamerous carpel, making it the most likely candidate gene for carpel number (Qiu et al., 2022).

A single gene controls *furrowed fruit surface f* (Poole, 1944) that is recessive to smooth (*F*). The type line for furrowed was not given by Poole, but cultivars such as Stone Mountain and Black Diamond have a furrowed fruit surface, in contrast to cultivars such as Mickylee with a smooth fruit surface. A single gene, *Rbf* (*Rind bloom formation*), is reported to control bloom formation in the fruit surface, which is dominant to *rbf* (bloomless). The main component of watermelon bloom is *Ca*, while most of the bloom components of other plants, such as cucumber and pumpkin, are composed of silicon. Research by Lee et al. (2022) indicated three nonsynonymous SNPs in *Cla97C01G020050* encoding a CSC1-like protein that cosegregated with *Rbf*. The CSC1-like protein is an osmosensitive Ca-permeable cation channel in eukaryotes, which causes temporary changes in the number of Ca ions by osmotic stress. *Rbf* is from 'FD061129' and *rbf* is from 'SIT55616RN' (Lee et al., 2022).

Explosive rind (*e*) causes the fruit rind to burst or split when cut (Porter, 1937), and has been used to make fruit easily crushed by harvest crews for pollenizer cultivars such as SP- 1 that have small fruit not intended for harvest. Tough

rind (*E*) is an important fruit trait to give cultivars shipping ability. Rind toughness appears to be independent of rind thickness; the inheritance of rind thickness has not been reported. Research discovered that rind hardness was positively correlated with fruit cracking resistance (explosive rind), but the allelic relationship between the two is unknown. A major QTL for rind hardness was mapped on chromosome 10, and the candidate gene *ClERF4* (*Cla97C10G187120*) encoding ethylene-responsive factor 4 was involved in the xylem biosynthesis and cell wall modification. Compared to 'P-a' (high rind hardness), low hardness 'P-b' had an 11-bp deletion as well as a neighboring SNP, which resulted in a frame-shift deletion and earlier termination and then caused two types of transcriptions, leading to two types of protein sequences. In addition, the resultant KASP genotyping analysis of 104 germplasm accessions supported candidate *ClERF4* as a causative gene responsible for rind hardness and thus conferring cracking resistance (Liao et al., 2020).

The flesh firmness of watermelon affects taste. Flesh that is too soft (*soft flesh, sf*) has no resistance to storage and a short shelf life, while increasingly hard flesh (*SF*) results in reduced juice and poor flavor. Watermelon flesh firmness is an important indicator to measure the fruit quality, which is a typical quantitative trait. *Cla97C06G118630* (Aux/IAA) encoding auxin-responsive protein was mapped as a *sf* candidate gene. The expression of Aux/IAA decreased with fruit developmental stages and a reduction in fruit flesh firmness was observed. Moreover, Aux/IAA and *ERF1* (ethylene-responsive factor 1) may synergistically regulate ABA dynamics, leading to changes in flesh firmness (Anees et al., 2023).

A single recessive gene, *suppressor of bitterness*, *su* (Chambliss et al., 1968), eliminates bitterness in fruit of *C. lanatus*, and is allelic to the dominant gene (*Su*) for bitter flavor in the fruit of the colocynth (*C. colocynthis*). The candidate gene *Cla011508* (*Cla97C01G003400*) for fruit bitterness encodes bHLH transcription factor family, which is homologous with *CsBl* and *CsBt* controlling bitter formation in cucumber and is involved in cucurbitacin's C biosynthetic pathway. The bitter taste of fruit is likely to be caused by the early termination of the translation locus and low expression of gene *Cla011508*, which is conservative in some germplasm resources (Li et al., 2018a; Gong et al., 2022a).

Sourness (*So*) is caused by the accumulation of organic acids in the fruit flesh. A major QTL for sour flesh trait was mapped on chromosome 6 by constructing a near isogenic line. Two candidate genes, *Cla97C06G113740* and *Cla97C06G113810*, have β-Galactosidase activity or polygalactosidase activity, catalytic and hydrolytic activities. In watermelon materials with varying degrees of sourness, the generation of sourness may be due to differences in gene expression levels, then the accumulation of organic acids by regulating the metabolic process of carbohydrates (Gao, 2018).

Modern dessert watermelons have been selected over many years for high sugar and low acid quality, whereas wild watermelons native to Africa are often not sweet, or are bitter (Liu et al., 2013). A complex multigenic inheritance pattern controls the sugar content of watermelon flesh. Many QTLs for sugar content in flesh are identified in different segregating populations (Sandlin et al., 2012; Cheng et al., 2016). Recently, a recombinant inbred line was constructed using east Asian cultivated watermelon '97103' with high sugar and unsweetened wild type watermelon PI 296341-FR from southern Africa. The molecular mechanisms of hydrolysis, sugar translocation and accumulation of watermelon raffinose family oligosaccharides (RFOs) were further elucidated by QTL localization and functional gene validation. The study found that sugar content was affected by the mutation of *ClAGA2* (alkaline alpha-galactosidase, *Cla97C04G070460*) that was a key enzyme in the hydrolysis of RFOs in the vascular bundle. Two SNPs within the promoter affect the recruitment of the transcription factor CINF-YC2 (nuclear transcription factor Y subunit C) to regulate CIAGA2 expression (Ren et al., 2021). The sugar transporter protein *ClVST1* (*Cla97C02G031010*), identified in the sugar content QTL locus *Qsuc2-1*, functions as an unloading sugar in the sink phloem, which can dynamically distribute the unloading of sugar from leaf to fruit (Ren et al., 2020). *ClTST2* (*Cla97C00G000440*), a putative tonoplast sugar transporter gene, was identified as the QTL locus *Qsuc2-2* for sugar content. *ClTST2* is one of the important genes determining sugar accumulation in vesicles, and increased expression is a selection event during domestication (Ren et al., 2018). In addition, membrane-localized *ClSWEET3* (*Cla97C01G000640*), a glucose and fructose transporter protein, is a key gene upregulated in the sugar transport during watermelon fruit development (Ren et al., 2021).

Several genes control flesh color in watermelon, producing scarlet red, coral red, orange, salmon yellow, canary yellow, or white. Genes conditioning flesh colors are *B* (Shimotsuma, 1963), *C* (Poole, 1944), *i-C* (Henderson et al., 1998), *Wf* (Shimotsuma, 1963), *y* (Porter, 1937) and y^0 (Henderson, 1989; Henderson et al., 1998). Canary yellow (*C*) is dominant to other colored flesh (*c*). Coral red flesh (Y^{Crl}) is dominant to salmon yellow (*y*). Orange flesh (y^0) is a member of a multiple allelic system at that locus, where Y^{Crl} (coral red flesh) is dominant to both y^0 (orange flesh) and *y* (salmon yellow), and y^0 (orange flesh) is dominant to *y* (salmon yellow).

In a separate study, two loci with epistatic interaction controlled white, yellow, and red flesh. Yellow flesh (*B*) is dominant to red flesh. The gene *Wf* is epistatic to *B*, so

genotypes *WfWf BB* or *WfWf bb* were white fleshed, *wfwf BB* was yellow fleshed, and *wfwf bb* was red fleshed. Canary yellow flesh is dominant to coral red, and *i-C* inhibitory to *C*, resulting in red flesh. In the absence of *i-C*, *C* is epistatic to *Y*.

A single dominant gene, scarlet red produces the scarlet red flesh color (Y^{Scr}) of 'Dixielee' and 'Red-N-Sweet' instead of the lighter, coral red (Y^{Crl}) flesh color of 'Angeleno Black Seeded' (Gusmini and Wehner, 2006). Scarlet red flesh (Y^{Scr}) is dominant to coral red flesh (Y^{Crl}), orange flesh (y^{o}) and salmon yellow flesh (y). The gene Y^{Scr} is from 'Dixielee' and 'Red-N-Sweet', Y^{Crl} is from 'Angeleno' (black seeded), y^{o} is from 'Tendersweet Orange Flesh', and y is from 'Golden Honey'. A unique orange flesh gene (Y^{Car}, orange accumulating β-carotene) has a small amount of lycopene and is rich in β-carotene. Y^{Car} is co-dominant to *C* (canary yellow), Y^{Scr} (scarlet red), Y^{Crl} (coral red) and Y^{O} (orange accumulating pro-lycopene). However, the segregation of a F2:3 population deviated significantly from the co-dominant single gene model, suggesting that epistasis may be involved (Tadmor et al., 2005; Branham et al., 2017a). A novel gene, Y^{Pg} (pale green flesh), was reported to accumulate chlorophyll in fruit flesh, producing a pale green phenotype. Pale green flesh color may be quantitatively regulated by a major effective gene, and the yellow flesh (*C*) gene is incompletely dominant to pale green flesh (Y^{Pg}) (Pei et al., 2021). Y^{Car} is from 'NY0016'; Y^{Pg} is from 'ZXG1555'.

Although flesh color is shown to be controlled by single genes, the fruit in a segregating generation from a cross between two different inbreds is often confusing. Often there are different flesh colors in different areas of the same fruit. One possible hypothesis to explain the presence of the abnormal types is that the expression of the pigment is caused by several different genes, one for each area of the fruit. Thus, the mixed colorations would have been caused by recombination of these genes. It may be useful to have a separate rating of the color of different parts of the flesh to determine whether there are genes controlling the color of each part: the endocarp between the carpel walls and the mesocarp (white rind); the flesh within the carpels, originating from the stylar column; and the carpel walls.

So far, a lot of QTL or functional genes for flesh color have been found. Two QTLs for red flesh color were first reported by Hashizume et al. (2003) on groups 2 and 8. Y^{scr} (scarlet red flesh) was mapped to a 40 Kb region on chromosome 6 in the cross 'ZXG01478' (Y^{Crl}) and '14CB11' (Y^{scr}). Of the five putative genes in this region, four encoded glycine-rich cell wall structural proteins, which implied that a new regulatory mechanism might occur between scarlet red and coral red flesh (Shang et al., 2016; Li et al., 2020b). A key gene, *ClLCYB* (lycopene β-cyclase, *Cla97C04G070940*), may determine canary yellow (C) and red flesh; a zero-distance molecular marker was developed to distinguish different alleles of the *ClLCYB* gene (Bang et al., 2007). Down-regulation of *CILCYB* caused the flesh color to change from pale yellow to red, and *CILCYB* overexpression in the red flesh line caused the flesh color to change to orange. In addition, the changes of two amino acids of *CILCYB* domestication selection led to reduction of protein stability, the accumulation of the substrate lycopene, and formation of the red flesh (Zhang et al., 2020b). In the cross 'ZXG1555' (pale green flesh) and 'COS' (pale yellow flesh), the candidate gene of Y^{Pg}, *Cla97C10G185970*, was annotated as plastid lipid-associated protein and was involved in photoprotection of photosystem II. Two SNPs in the coding region could be used to distinguish green and non-green flesh and may play a key role in regulating chlorophyll accumulation and green flesh coloration (Pei et al., 2021).

The unique *photosensitive flesh* (*psf*) mutant accumulating ζ-carotene was developed in red flesh line '302' through EMS mutagenesis. The initial yellow color of this mutant can be photobleached under intense sunlight. The *psf* was controlled by a recessive gene ClZISO (Cla97C07G142750), which encoded 15-cis-ζ-carotene isomerase to catalyze the transformation 9, 15, 9' -tri-cis-ζ-carotene into 9, 9' -di-cis-ζ-carotene. The truncated ClZISOmu protein produced by G-A transversion in *psf* lost this catalytic function, and light treatment can partially compensate the activity of ClZISOmu isomerase via photoisomerization in vitro and in vivo (Zhang et al., 2022). A major QTL for Y^{car} on chromosome 1 was mapped, associated with β-carotene accumulation (Branham et al., 2017a). Further fine mapping narrowed this region to 39.08 Kb including a candidate gene *ClPSY1* (*Cla97C01G008760*) encoding phytoene synthase, which catalyzes the conversion of two molecules of GGPP to phytoene to produce the first carotenoid. Nonsynonymous SNP mutations in the first exon of *ClPSY1* co-segregated with Ycar trait among individuals in the genetic population. In addition, several base mutations in the *ClPSY1* promoter are likely to cause change in flesh color from orange to pale yellow (Liu et al., 2022b). The natural mutations in *ClCRTISO* (*Cla97C10G200950*) of Y^{O} or *y* gene might regulate the accumulation of pro-lycopene in orange-fleshed watermelon cultivars. A SNP (T>C1976) detected in *ClCRTISO* of salmon yellow (*y*, from 'Golden Honey') and orange-P (Y^{O}, from 'Orangeglo') cultivars was close to the FAD-binding domain at the C terminus, which may be associated with significantly reduced lycopene synthesis, possibly by affecting the binding of *ClCRTISO* to FAD and thereby attenuating the catalytic efficiency of *ClCRTISO* and accumulating pro-lycopene (Jin et al., 2019).

Fruit rind pattern genes

The gene *Sp* (*Spotted*) produces spotted fruit, making interesting effects as found on cultivars such as 'Moon and Stars' (Poole, 1944). The type line for the *Sp* gene is 'Moon and Stars'. There are several cultivars having the term 'Moon and Stars' in their name, apparently having different genetic background plus the *Sp* gene, so that should be taken into account when doing genetic studies. The *Sp* trait is difficult to recognize on the fruit when the fruit are solid light green in color, but is easy to observe on solid medium green, solid dark green, gray, or striped fruit (Gusmini and Wehner, 2006). Golden yellow was inherited as a single recessive gene *go* (Barham, 1956) derived from 'Royal Golden' watermelon. The immature fruit had a dark green rind which becomes more golden yellow as the fruit matures. The stem and older leaves also become golden yellow, and the flesh color changes from pink to red. The clear stripe margin is found to be controlled by a single gene that is recessive over blurred stripe margin. The gene *csm* for the *clear stripe margin* in the cultivar 'Red-N-Sweet' is recessive to the blurred stripe margin (*Csm*) in cultivars 'Crimson Sweet', 'Allsweet', and 'Tendersweet Orange Flesh' (Lou and Wehner. 2016).

An unusual stripe pattern is found on 'Navajo Sweet' called *intermittent stripes*, with gene symbol *ins* (Gusmini and Wehner, 2006). The recessive genotype produces narrow dark stripes at the peduncle end of the fruit that become irregular in the middle and nearly absent at the blossom end of the fruit. Stripes on normal fruit, such as 'Crimson Sweet' are fairly uniform from peduncle to blossom end. The yellow belly, or ground spot, on 'Black Diamond Yellow Belly' is controlled by a single dominant gene, *Yb*. The recessive genotype, 'Black Diamond' has a ground spot that is white (Gusmini and Wehner, 2006).

Weetman (1937) proposed that three alleles at a single locus determined rind pattern. The allelic series was renamed to *G*, g^s, and *g* by Poole (1944), since *g* was used to name the recessive trait 'green', rather than *D* for the dominant trait 'dark green'. The g^s gene produces a striped rind, but the stripe width (narrow, medium, and wide stripe patterns) has not been explained as yet. Porter (1937) found that dark green was completely dominant to light green (yellowish white, in his description) in two crosses involving two different dark green cultivars ('Angeleno' and 'California Klondike'). He reported incomplete dominance of dark green in the cross 'California Klondike' x 'Thurmond Gray', the latter cultivar being described as yellowish green. Thus, gray rind pattern should be described further as either yellowish green ('Thurmond Gray') or yellowish white ('Snowball'). Rind color is controlled by a two-gene system, with *G-1G-1G-2G-2* producing the solid dark green of 'Mountain Hoosier' and 'Early Arizona', and *g-1g-1g-2g-2* producing the light green of 'Minilee' (Kumar and Wehner, 2011). The double recessive produces light green; otherwise the rind is solid dark green (with 15 solid dark green:1 light green in the F_2).

A more complete series of alleles at the *g* locus of five alleles is proposed by Lou and Wehner (2016) to explain the inheritance of fruit rind pattern and color: *G* (solid medium or dark green), g^W (wide stripe), g^M (medium stripe), g^N (narrow stripe), and *g* (solid light green or gray). Their dominance is $G > g^W > g^M > g^N > g$. The following type-lines are proposed: *GG* for solid medium or dark green of 'Peacock Shipper', 'Black Diamond', as well as 'California Klondike'; g^Wg^W for wide stripe of 'Allsweet' and 'Tendersweet Orange Flesh'; g^Mg^M for medium stripe of 'Crimson Sweet'; g^Ng^N for narrow stripe of 'Red-N-Sweet'; and *gg* for gray or solid light green of 'Charleston Gray' and 'King&Queen'. The g^S allele from 'Golden Honey' may be the same as g^M from 'Crimson Sweet', but additional crosses are needed to verify that. The difference between the solid light green of 'King&Queen' and the gray of 'Charleston Gray' needs further investigation. An allelism test between wide stripe and medium stripe is also needed. The solid dark green rind in 'Black Diamond' was evaluated. The intermediate rind pattern in the F_1 and the continuous green shades in the F_2 indicate that the background color shade and stripe are controlled by different genes and solid color shade is controlled by multiple genes. This result seems to be consistent with the research of Yang et al. (2015).

The watermelon gene *p* for *pencilled* rind pattern has been reported in the gene lists since 1976 (Robinson et al. 1976). The name "penciled" first appeared in 1944 to describe inconspicuous lines on self-colored rind of 'Japan 6' (Poole, 1944), but the spelling was changed later to "*pencilled*" in the gene lists. The cross 'Japan 6' x 'China 23' was used by Weetman to study the inheritance of solid light green vs. striped rind and lined (later renamed *pencilled*) vs. netted rind (Weetman, 1937). 'Japan 6' had solid light green rind with inconspicuous stripes, usually associated with the furrow. 'China 23' had dark green stripes on a light green background and a network running through the dark stripes (netted type). Weetman confirmed his hypothesis of two independent genes regulating the presence of stripes and the pencilled vs. netted pattern, recovering four phenotypic classes in a 9:3:3:1 ratio (striped, netted : striped, pencilled : non-striped, netted : non-striped, pencilled) in the F_2 generation and in a 1:1:1:1 ratio in the backcross to the double recessive non-striped, pencilled 'Japan 6'. However, Weetman did not name the two genes.

Seeds of the two type lines used by Weetman ('Japan 6' and 'China 23') are not available, nor are Porter's data and germplasm, thus making it difficult to confirm the inheritance of the *p* gene or to identify current inbreds allelic to pencilled and netted rind patterns. In 1944, Poole used the experiment of Weetman to name the single recessive gene *p* for the lined (pencilled, or very narrow stripe) type. The inheritance of the

p gene was measured by Weetman against the netted type in 'China 23' and not a "self-colored" (or solid green) type as reported by Poole. Previously, Porter reported that studies of rind striping were underway and specifically cited a pencilled pattern in the F_1 of the cross 'California Klondike' x 'Golden Honey' (Porter, 1937). Probably, the *P* allele produces the netted type, as originally described by Weetman.

The *m* gene for mottled rind was first described by Weetman in 'Long Iowa Belle' and 'Round Iowa Belle' (Weetman, 1937). Weetman described the rind as "medium-dark green with a distinctive greenish-white mottling", the 'Iowa Belle' (IB) type. In the cross 'Iowa Belle' x 'China 23', Weetman observed that the IB type was inherited as a single recessive gene.

However, in the cross 'Iowa Belle' x 'Japan 6', he recovered the two parental types (IB and non-IB, respectively) along with an intermediate type (sub-IB), described as inconspicuous mottling. In the backcross to 'Iowa Belle' (the recessive parent for the mottled rind), though, the traits segregated with a perfect fit to the expected 1:1 ratio. He explained the presence of the intermediate type as determined by interfering genes from 'Japan 6'. There was no other mention of the IB-type until Poole (1944) attributed its inheritance to the *m* gene from 'Iowa Belle', based on the article by Weetman. 'Iowa Belle' is not currently available and the IB mottling has not been identified in other mutants since the 1937 study by Weetman.

The homozygous genotypes produced by the genes known to regulate rind color and pattern in watermelon should have the following phenotypes (type-line shown in parentheses): *GGMMPP* or *GGMMpp* = solid dark green ('Angeleno'), *GGmm* = mottled dark green ('Iowa Belle', not available), *ggMM* = solid light green ('?'), *ggMMpp* = pencilled ('Japan 6', not available), *ggPP* = yellowish green or gray ('Thurmond Gray'), and *gsgsPP* = medium-stripe netted ('Crimson Sweet'). It would be useful to study *g*, *m*, *p*, and other genes controlling rind pattern, to determine the interactions and develop inbred lines having interesting patterns for the gene stock collection.

The background rind color, foreground stripe pattern and depth of rind color were mapped on chromosome 4, 6 and 8, respectively (Park et al., 2016). Dou et al. (2018a) mapped a dominant locus for yellow skin in a 59.8 Kb region on chromosome 4, developing a tightly linked functional SNP marker for the yellow skin phenotype. A major QTL for depth of rind color was initially mapped in a 2.07 Mb region on chromosome 8 (Li et al., 2018a*). ClCGMenG* (*ClCG08G017810*), as a candidate gene, encodes a 2-phytyl-1,4-β-naphthoquinone methyltransferase protein involved in the biosynthesis of phylloquinone, which is more highly expressed in dark green rind than in light green rind. A nonsynonymous SNP of the coding region in light green rind materials converted an arginine to glycine. The SNP might be associated with rind color of 103 watermelon germplasm lines (Li et al., 2019). A major QTL for the foreground stripe has mapped on chromosome 6; *Cla97C06G126770* belonging to a MORC family was identified as the most likely candidate gene. The unstriped allele corresponds to the 3 bp insertion in eighth exon of *Cla97C06G126770*, which may regulate the stripe model by DNA methylation (Wang et al., 2022).

Resistance genes

Watermelon anthracnose resistance is generally controlled by dominant single genes. Resistance to race 1 and 3 of anthracnose (*Colletotrichum lagenarium*, formerly *Glomerella cingulata* var. *orbiculare*) is controlled by a single dominant gene *Ar-1* (Layton, 1937). Resistance to race 2 of anthracnose is also controlled by a single dominant gene *Ar-2-1* (Winstead et al., 1959). The resistant allele *Ar-2-1* is from W695 citron as well as PI 189225, PI 271775, PI 271779, and PI 299379; the susceptible allele *ar-2-1* is from 'Allsweet', 'Charleston Gray', and 'Florida Giant'; resistance in *Citrullus colocynthis* is due to other dominant factors, with resistance from R309 and susceptibility from 'New Hampshire Midget' (Love and Rhodes, 1988, 1991; Sowell et al., 1980; Suvanprakorn and Norton, 1980; Winstead et al., 1959). Interestingly, the germplasm PI 189225 which is resistant to race 2 anthracnose, had a susceptible genotype (*ar-1ar-1*) for race 1 anthracnose (Bhatta et al., 2022). Jang et al. (2019) and Bhatta et al. (2022) both reported a major QTL for resistance to race 1 on chromosome 8, developing co-segregating SNP markers. *Cla97C08G146430* encoding CC-NBS-LRR resistance protein was firstly identified, and a non-synonymous SNP may confer resistance to anthracnose race 1 by affecting the expression of the corresponding gene transcripts. In addition, the newly proposed LRR domain harboring the SNP is evolutionary conserved in the *Cucurbitaceae* and *Fabaceae*.

Resistance to race 1 of *Fusarium oxysporum* f. sp. *niveum* (Fon) is controlled by a single dominant gene *Fo-1* (Henderson et al., 1970; Netzer and Weintall, 1980). A major QTL for resistance to Fon race 1 in 'Calhoun Gray' and 'HMw017' was mapped to a 6.1 cM interval of chromosome 1, which can effectively distinguish the resistance/susceptibility to Fon race 1 in cultivated watermelon by developing three linked CAPS/dCAPS markers. Additional independent, but minor QTLs were identified on chromosome 1 (LOD 4.16), chromosome 3 (LOD 4.36), chromosome 4 (LOD 4.52), chromosome 9 (LOD 6.8), and chromosome 10 (LOD 5.03 and 4.26) (Zhang et al., 2013; Lambel et al., 2014). Ren et al. (2015) further narrowed the major QTL (Qfon1.1) for Fon race 1 to between 1bin2 and 1bin3 (5~7.1cM) on chromosome 1, explaining 48.1 % of the phenotypic variation. One receptor kinase (*Cla97C01G000710*), one glucan endo-1,3-bglucosidase

precursors (*Cla97C01G001440*) and three acidic chitinase (*Cla97C01G000690*, *Cla97C01G000780* and *Cla97C01G000790*) located in the Qfon1.1 and flanking 1 M genomic region. These enzymes synthesis and accumulation are a common plant defense mechanism against pathogen infection. Future research work is required to identify whether these genes are associated with resistance to Fon race 1 in watermelon. Resistance gene to Fon race 2 is thought to be controlled by two major effect QTLs. Ren et al. (2015) mapped Fon race 2 QTL from a cross between the resistant parent, PI 296341-FR, and susceptible cultivar 97103, while PI 296341-FR provided the resistance allele for the QTL on chromosome 9, resistance in chromosome 10 was contributed by the susceptible parent 97103. Branham et al (2017b) further narrowed the major QTL for resistance to Fon race 2 in 1.2 Mb region on Chromosome 9, and 4 minor QTL were also found. Although a single major QTL was associated with Fon race 2 resistance, it explained less than half of the phenotypic variation (43%).

Gummy stem blight (GSB), caused by *Didymella bryoniae* (Auersw.) Rehm is inherited by a recessive gene *db* (Norton, 1979). Stewart et al. (2015) found that GSB is caused by three distinct species of *Stagonosporopsis*, *S. cucurbitacearum* (syn. *Didymella bryoniae*), *S. caricae* and *S. citrulli*. Gusmini et al. (2017) demonstrated that GSB resistance in four crosses between elite watermelon cultivars and resistant PIs, including PI 198225, is quantitatively inherited. In recent studies, Ren et al. (2020) used a population derived from K3 (*C. lanatus*) and PI 189225 and an isolate of *S. cucurbitacearum* to map a GSB resistance QTL on chromosome 8. Lee et al. (2021) used a population derived from '920533' (C. lanatus) and PI 189225 and unknown species of Stagonosporopsis to map GSB resistance QTL, two on chromosome 8 and one on chromosome 6. The QTL mapped by the two studies on chromosome 8 are distinct from one another. Gimode et al. (2021) used a population derived from 'Crimson Sweet' (*C. lanatus*) and PI 482276 (*C. amarus*) and *S. citrulli* isolate 12178A to map GSB resistance QTL on chromosomes 5 and 7. Differences in the locations of these QTL, especially those derived from the same resistant parent (PI 189225), are likely due to either differences in resistance to the various species or isolates of *Stagonosporopsis* used for phenotyping or differences in phenotyping methodologies. Lee et al. (2021) evaluated lesion severity on the stems separately from leaf lesions, while Ren et al. (2020) scored only leaf lesions and Gimode et al. (2021) scored the entire seedling. Adams and McGregor. (2022) identify QTL on chromosomes 5 associated with resistance to *S. citrulli* in a population derived from a cross between 'Sugar Baby' (susceptible) and PI 189225 (resistant). These studies suggest that different loci might control resistance to different species of *Stagonosporopsis* causing GSB.

Watermelons were resistant to older races of *Sphaerotheca fuliginea* (named also *Podosphaera xanthii*) present in the U.S. in the 1970s, but a single recessive gene *pm* (Robinson et al., 1975) for high susceptibility to powdery mildew (PM) was found in the plant introduction, PI 269677. Races 1W and 2W of PM are now present in the U.S. and induce a susceptible reaction in most cultivars. PI 269677 is highly susceptible to the new races. A major QTL located on chromosome 2 for resistance to race 1W of *Podosphaera xanthii* explained phenotypic variation (R^2 = 80.0%), and the genetic distance of the linkage marker was 4.0 cM (Kim et al., 2013; 2015). The HRM marker for race 1W resistance was tighty linked to the phenotype (R^2 = 95.7%) (Han et al., 2016). Mandal et al. (2020) reported a dominant resistance gene, *ClPMR2* (*Cla97C02G042200*) encoding an NBS-LRR protein, that is homologous with AtRPW8 in Arabidopsis and has widespread resistance to PM races.

Bacterial fruit blotch (BFB), caused by *Acidovorax citrulli* (formerly, *Acidovorax avenae* subsp. *citrulli*), was first reported in 1965. PI 482246 was among the most resistant PIs in the USDA *Citrullus* germplasm collection, and PI 482273, PI 482277, and PI 4822246 from Zimbabwe and PI 500328 and PI 500331 from Zambia were also resistant to BFB (Ma and wehner, 2015). Branham et al. (2019) described the foliar resistance to *A. citrulli* in *Citrullus amarus* to be complicated by low heritability, strong environmental influence, and significant genotype-by-environment interactions. The six QTLs for BFB were identified on chromosomes 1, 2, 3 and 8 explaining 5% to 15% of the phenotypic variations for the *A. citrulli*-induced percentage of affected leaf area in *C. amarus* line 'USVL246-FR2'. Wu et al. (2019) identified two QTLs on chromosomes 6 and 10 in a diverse *C. amarus*, *C. lanatus*, and *C. mucosospermus* populations. Yeo et al. (2022) identified two QTLs associated with BFB resistance in PI 189225 both on chromosome 10 explaining 18.84% and 15.41% of the phenotypic variation, respectively. High-throughput HRM markers were developed and validated to facilitate the selection of BFB resistance on chromosome 10.

Resistance to *Papaya ringspot virus-watermelon strain* (PRSV-W) was reported in accessions PI 244017, PI 244019 and PI 485583. It was controlled by a single recessive gene, *prv* (Guner et al., 2018). Branham et al. (2020) identified a single QTL significantly associated on chromosome 3 with PRSV-W resistance in the F_2 population from susceptible 'USVL252-FR2' (derived from PI 482252) and resistant PI 244019 with a LOD score of 9.1 and that explained 24.2% phenotypic variation, which adhered to expectations of a prior study indicating a single-gene recessive inheritance. Chanda et al. (2022) reported the orthologous *RIP-I* and *RIP-II* in *C. amarus*

(PI 244019), which has been shown to have resistance to potyviruses, including PRSV-W. The expression of *RIP-I* was higher than *RIP-II* in all tissue types. *RIP-II* had very weak levels of expression in all tissues, except in the mature leaves. In the virus resistant *C. amarus*, a significant 4-fold increase in the expression of the *RIP-I* gene was observed at 3 dpi and then a 6-fold increase in the expression of the *RIP-II* gene at 8 dpi in the resistant inoculated plants, in comparison with the mock inoculated plants.

A moderate level of resistance to Zucchini yellow mosaic virus was found in four landraces of *Citrullus lanatus* but was specific to the Florida strain of the virus. Resistance was conferred by a single recessive gene *zym-FL* (Provvidenti 1991). A high level of resistance to *Zucchini yellow mosaic virus*-Florida strain was found in PI 595203 that was controlled by a single recessive gene, *zym-FL-2* by (Guner et al. 2018). It was not the same as *zym-FL* because the virus caused a different reaction on PI 482322, PI 482299, PI 482261, and PI 482308. The four accessions were resistant in the study by Provvidenti, but susceptible in the study by Guner and Wehner. Resistance to the China strain of *Zucchini yellow mosaic virus* (ZYMV) was reported in PI 595203, controlled by a single recessive gene *zym-CH* (Xu et al. 2004). The gene may be allelic to *zym-FL-2,* but it is difficult to test a segregating F_2 progeny for resistance to two different viruses found in different parts of the world. Analysis of the nucleotide sequences between the ZYMV-resistant PI 595203 and the ZYMV-susceptible 'New Hampshire Midget' showed the polymorphic sites (A241C) at key identification and association domain of *eIF4E* (*Cla97C03G058500*) encoding eukaryotic translation initiation factor 4E on chromosome 3, were co-segregated with resistant trait. The amino acid replacements of polymorphic sites were similar with the resistance to *Potato Y virus* strain in other plants. In addition, another SNP (A171G) results in another amino acid substitution from four ZYMV-resistant *C. lanatus* var. *citroides* (PI 244018, PI 482261, PI 482299, and PI 482322) (Ling et al., 2009).

Guner et al. (2019) further screened the watermelon germplasm collection for ZYMV resistance and to verify the disease rating for the most resistant and most susceptible accessions. The PI accessions with high resistance to ZYMV-FL that also exhibited resistance to other watermelon viruses were PI 595203, PI 386015, PI 386016, PI 386024, PI 386025, PI 386026, PI 244018, PI 244019, PI 485583, PI 494528, and PI 494529. The ZYMV-FL retest of the most resistant 46 PI accessions showed that there were some escapes. Sixteen resistant PI accessions had a rating of 3.0 or less for the average and maximum ratings: PI 595203, PI 537277, PI 560016, PI 386016, PI 386019, PI 485580, PI 494529, PI 595200, PI 494528, PI 595201, PI 386025, PI 494530, PI 386015, PI 386021, PI 386026, and PI 596662. PI 595203 had the highest resistance according to both the germplasm screening and the retest studies.

Xu et al. (2004) reported that PI 595203, which is resistant to ZYMV, was moderately resistant to *Watermelon mosaic virus* (WMV, formerly *Watermelon mosaic virus 2*). Strange et al. (2002) reported that PI 595203 also was resistant to Papaya ringspot virus-watermelon strain. The high tolerance to WMV was controlled by at least three recessive genes. Broad-sense heritability was high (0.84 to 0.85, depending on the cross), and narrow-sense heritability was low to high (0. 14 to 0.58, depending on the cross).

Resistance to *Cucumber green mottle mosaic virus-watermelon strain* (CGMMV) was reported in accessions PI 595203, but a few plants had mild symptoms. It was controlled by the recessive gene, *cgmm*, and might be more than one genetic locus. Cai et al. (2023) firstly identified the WPR (WEB1/PMI2-related) protein family gene *ClWPRb* (*Cla97C04G073090*) for *cgmm* in resistant material PI 595203, which encodes a blue light weak chloroplast motility 1 and plastid motility impaired 2 protein, indicating negative association with watermelon CGMMV resistance.

Genes for insect resistance have been reported in watermelon. Fruit fly (*Dacus cucurbitae*) resistance was controlled by a single dominant gene *Fwr* (Khandelwal and Nath, 1978), and red pumpkin beetle (*Aulacophora faveicollis*) resistance was controlled by a single dominant gene *Af* (Vashishta and Choudhury, 1972). Stress resistance has been found in watermelon. Seedlings grown at temperatures below 20°C often develop a foliar mottle and stunting. A persistent low temperature is conducive to more prominent foliar symptoms, malformation, and growth retardation. The single dominant gene *Ctr* was provided cool temperature resistance (Provvidenti, 1992, 2003).

Watermelon bud necrosis disease caused by watermelon bud necrosis orthotospovirus (WBNV, *Tospoviridae, Bunyavirales*) has emerged as a devastating disease of watermelon in India. The resistance to WBNV is governed by a major dominant gene *Wbn* along with other background minor genes (Nagesh et al., 2018). The segregation pattern of WBNV resistance in Nagesh et al. (2020) also suggests dominant inheritance. Maragal et al. (2021) reported three QTLs on Chromosome 2, 3 and 7 as potential candidate regions for WBNV resistance. These QTLs may be investigated as putative candidates for WBNV resistance in watermelon.

Only a few studies have reported resistances to other viruses in watermelon. Kousik et al. (2012) reported the resistance to *Squash vein yellowing virus* (SqVYV) in PI 386015 (accession of *C. colocynthis*), PI 386024 (from Iran) and the African accession of *C. lanatus* PI 482266 and PI 392291. Root-knot nematode (*Meloidogyne enterolobii*) resistance involved

in multiple genes, which was identified in chromosome 3, 4 and 8 by genome wide association analysis (GWAS) based on 108 inbred *C. amarus* lines derived from diverse plant introductions (PIs) originally obtained from the USDA-GRIN collection (Waldo et al., 2022).

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Table 1. The morphological and resistance genes of watermelon, including gene symbol (Symb.), synonym (Synon.), gene description and type lines, references, and availability (C= mutant available from Cucurbit Genetics Cooperative watermelon gene curator; P = mutants are available as standard cultivars or accessions from the plant introduction collection; ? = availability not known; L = mutant has been lost). Asterisks on cultigens and associated references indicate the source of information for each.

Symb.	Synon.	Gene description and type lines	References	Supplemental references	Availability
a		*andromonoecious*; recessive to monoecious; *a* from 'Angeleno' (black seeded); *A* from cultivars 'Conqueror' and 'Klondike'.	Rosa, 1928; Porter, 1937; Poole, 1944		C
Af		*Aulacophora faveicollis* resistance; resistance to the red pumpkin beetle; dominant to susceptibility; A*f* from Sl.72 and Sl.98 inbreds; *af* from 'Sugar Baby'.	Vashishta and Choudhury, 1972	-	?
Ar-1	*B, Gc*	*Anthracnose resistance to races 1* and *3* of *Glomerella cingulata* var. *orbiculare (Colletotrichum lagenarium)*; *Ar-1* from 'Africa 8'*, 'Africa 9'*, and 'Africa 13'* and 'Charleston Gray'**; *ar-1* from 'Iowa Belle 476', 'Iowa Belle 487'* and N.C.9-2, N.C. 11, and 'New Hampshire Midget'**.	Layton, 1937*; Hall et al., 1960; Robinson et al., 1967; Winstead et al., 1959**		C
Ar-2-1		*Anthracnose resistance to race 2* of *Colletotrichum lagenarium*; *Ar-2-1* from W695 citron* and PI 189225, PI 271775, PI 271779, and PI 299379**; *ar-2-1* from 'Allsweet', 'Charleston Gray', and 'Florida Giant'; resistance in *Citrullus colocynthis* is due to other dominant factors; resistance from R309***; susceptibility from 'New Hampshire Midget'.	Winstead et al., 1959*	Love and Rhodes, 1988***, 1991; Sowell et al., 1980**; Suvanprakorn and Norton, 1980	P
B	*Y*	*Yellow flesh; Wf* is epistatic to *B* (*Y* renamed *B* by Henderson*); flesh color segregated into 12 white, 3 yellow and 1 red in the F2; *WfWf BB* or *WfWf bb* white fleshed; *wfwf BB* yellow fleshed; *wfwf bb* red fleshed; *B* from breeding line V.No.3 and *b* from V.No.1.	Shimotsuma, 1963	Henderson, 1992	?
Rbf		*Rind bloom formation*; dominant to *bloomless* (*rbf*); the main component of bloom is Ca, not Si; *rbf* from 'FD061129'; *Rbf* from 'SIT55616RN'.	Lee et al., 2022		?
C		*Canary yellow flesh*; dominant to coral red (or other colors controlled by the *y* locus); *i-C* inhibitory to *C*, resulting in red flesh; in the absence of *i-C, C* is epistatic to *Y; CC* from 'Honey Cream'* and NC-517, *cc* from 'Dove'*; *CC YY I-C I-C* from 'Yellow Baby' F1** and 'Yellow Doll' F1**; *cc y-oy-o I-C I-C* from 'Tendersweet Orange Flesh'**; *cc yy I-C I-C* from Golden Honey'**; *cc YY i-C i-C* from Sweet Princess'**.	Poole, 1944*; Henderson et al., 1998**		C

cgmm		Resistance to *cucumber green mottle mosaic virus*; recessive to susceptibility; *cgmm* from PI 595203 (a few plants have mild symptoms); *Cgmm* from 'M1511-3'.	Cai et al., 2023		?
cr		*cracked seed coat;* recessive to *Cr* (non-cracked) seed coat; *cr* from 'Leeby' and *Cr* from 'Kaho' and 'Congo'.	El-Hafez et al., 1981	-	?
csm		*clear stripe margin*; a single recessive to blurred stripe margin (*Csm*); *csm* from 'RedN-Sweet'; *Csm* from 'Crimson Sweet'.	Lou and Todd, 2016		?
Ctr		*Cool temperature resistance; Ctr* from line PP261-1 (a single plant selection of PI 482261 from Zimbabwe); *ctr* from 'New Hampshire Midget'; resistant to leaf mosaic injury when grown at air temperature below 20°C.	Provvidenti, 1992	Provvidenti, 2003	P
d		*dotted seed coat*; black dotted seeds when dominant for color genes *r, t*, and *w; d* is a specific modifier of black seed coat color wherein *RR TT WW DD* is solid black and *RR TT WW dd* is dotted black seed coat; *d* from 'Klondike' and 'Hope Giant'; *D* from 'Winter Queen'.	Poole et al., 1941; Poole, 1944; Kanda, 1951		C
db		resistance to *gummy stem blight* caused by *Didymella bryoniae*; *db* from PI 189225; *Db* from 'Charleston Gray'.	Norton, 1979		P
dg		*delayed green*; cotyledons and young leaves are initially pale green but later develop chlorophyll; first reported to be hypostatic to *I-dg*; more recent evidence indicates a simple recessive; *dg* from breeding line 'Pale 90'; *Dg* from 'Allsweet'.	Rhodes, 1986		?
dw-1		*dwarf-1*; short internodes, due to fewer and shorter cells than normal forms; allelic to *dw-1s; dw-1* from 'Bush Desert King' (also, 'Bush Charleston Gray', 'Bush Jubilee', 'Sugar Bush'); *Dw-1* from 'Sugar Baby' and 'Vine Desert King'.	Mohr, 1956; Liu et al., 1972		C
dw-1-s		*short vine*; allelic to *dw-1*; vine length intermediate between normal and dwarf; hypocotyl somewhat longer than normal vine and considerably longer than dwarf; *dw-1-s* recessive to normal; *dw-1-s* from 'Somali Local' (All-Union Research Institute of Plant Growing No.4641).	Dyutin and Afanas'eva, 1987	-	?
dw-2		*dwarf-2*; short internodes, due to fewer cells; *dw-2* from inbred line *WB-2*; *Dw-2* from 'Sugar Baby' and 'Vine Desert King'.	Liu and Loy, 1972	Mohr and Sandhu, 1975	?
dw-3		*dwarf-3*; dwarf with fewer leaf lobes (intermediate between normal leaf and non- lobed leaf); *dw-3* from 'Dwarf Male-Sterile Watermelon *(DMSW)*'; *Dw-3* from 'Changhui', 'Fuyandagua', and 'America B'.	Hexun et al., 1998	-	?
dw-4		*dwarf-4*; dwarf with less branching; recessive to *Dw-4* normal plants; *dw-4* from 'd5-6y'; *Dw-4* from 'Sugarlee', 'All sweet' and 'PL3'.	Yang and Li, 2009		?

e	*t*	*explosive rind*; thin, tender rind, bursting when cut; *e* from 'California Klondike'; *E* from 'Thurmond Gray'.	Porter, 1937	Poole, 1944	?
eg		*egusi seed*; recessive to normal seed phenotype; four main quantitative trait loci were identified for seed oil percentage with the *eg* locus contributing 84% of the explained phenotypic variation (R^2); immature seeds with fleshy pericarp, becoming normal at maturity; *eg* from PI 560023 PI 490383 selection 'NCG- 529' and 'PI 560006'; *Eg* from PI 279461, 'Calhoun Gray' and 'Charleston Gray'.	Gusmini et al., 2003	Prothro et al., 2012	C
f		*furrowed fruit surface*; recessive to smooth; type inbreds not given; *f* like 'Stone Mountainc or 'Black Diamond'; *F* like 'Mickylee'.	Poole, 1944	-	?
Fo-1		*Fusarium wilt resistance for race 1*; dominant gene for resistance to race 1 of *Fusarium oxysporum* f. sp. *niveum*; *Fo-1* from 'Calhoun Gray' and 'Summit'; *fo-1* from 'New Hampshire Midget'.	Henderson et al., 1970	Netzer and Weintall, 1980	C
Fwr		*Fruit fly resistance caused by Dacus cucurbitae*; dominant to susceptibility; *Fwr* from breeding lines J 18-1 and J 56-1; *fwr* from 'New Hampshire Midget', 'Bykovski', 'Red Nectar' and breeding line 'J 20-1'.	Khandelwal and Nath, 1978	-	?
g^W		*wide stripe fruit rind pattern;* has five alleles; *G* (solid medium or dark green), g^W (wide stripe), g^M (medium stripe), g^N (narrow stripe); *g* (solid light green or gray); Their dominance is $G > g^W > g^M > g^N > g$. *GG* from 'Peacock Shipper', 'Black Diamond', and 'California Klondike'; g^Wg^W from 'Allsweet' and 'Tendersweet Orange Flesh'; g^Mg^M from 'Crimson Sweet'; g^Ng^N from 'Red-N-Sweet'; *gg* from 'Charleston Gray' and 'King&Queen'.	Lou and Wehner, 2016		?
g^M	g^S, *ds*	*medium stripe fruit rind pattern;* has five alleles; *G* (solid medium or dark green), g^W (wide stripe), g^M (medium stripe), g^N (narrow stripe); *g* (solid light green or gray); Their dominance is $G > g^W > g^M > g^N > g$. *GG* from 'Peacock Shipper', 'Black Diamond', and 'California Klondike'; g^Wg^W from 'Allsweet' and 'Tendersweet Orange Flesh'; g^Mg^M from 'Crimson Sweet'; g^Ng^N from 'Red-N-Sweet'; *gg* from 'Charleston Gray' and 'King&Queen'.	Weetman, 1937; Poole et al, 1944; Lou and Wehner, 2016		?
g^N		*narrow stripe fruit rind pattern*; has five alleles; *G* (solid medium or dark green), g^W (wide stripe), g^M (medium stripe), g^N (narrow stripe); Their dominance is $G > g^W > g^M > g^N > g$. *GG* from 'Peacock Shipper', 'Black Diamond', and 'California Klondike'; g^Wg^W from 'Allsweet' and 'Tendersweet Orange Flesh'; g^Mg^M from 'Crimson Sweet'; g^Ng^N from 'Red-N-Sweet'; *gg* from 'Charleston Gray' and 'King&Queen'.	Lou and Wehner, 2016		?

g-1	*d*	*solid light green or grey fruit rind pattern*; *solid light green or grey* fruit recessive to *solid medium or dark green (G)* and striped green *(g^W, g^M, g^N)*; *g* from 'Thurmond Gray' 'King&Queen' and 'Charleston Gray'; *G* from 'California Klondike', 'Peacock Shipper' and 'Black Diamond'; g^W from 'Allsweet' and 'Tendersweet Orange Flesh'; g^M from 'Crimson Sweet'; g^N from 'Red-NSweet'; Interacts in a two-gene system, with *G-1G-1 G-2G-2* producing solid dark green of 'Mountain Hoosier' and 'Early Arizona', and *g-1g-1 g-2g-2* producing light green of 'Minilee'; the double recessive is required for light green; otherwise it is solid dark green.	Weetman, 1937; Kumar and Wehner, 2011	Poole, 1944; Porter, 1937; Lou and Wehner, 2016	?
g-2		*solid light green or grey fruit rind pattern*; solid light green or grey fruit recessive to solid medium or dark green *(G)* and striped green *(g^W, g^M, g^N)*; *g* from 'Thurmond Gray' 'King&Queen' and 'Charleston Gray'; *G* from 'California Klondike', 'Peacock Shipper' and 'Black Diamond'; g^W from 'Allsweet' and 'Tendersweet Orange Flesh'; g^M from 'Crimson Sweet'; g^N from 'Red-NSweet'; Interacts in a two- gene system, with *G-1G-1 G-2G-2* producing solid dark green of 'Mountain Hoosier' and 'Early Arizona', and *g-1g-1 g-2g-2* producing light green of 'Minilee'; the double recessive is required for light green; otherwise it is solid dark green.	Kumar and Wehner, 2011	Poole, 1944; Porter, 1937; Lou and Wehner, 2016	?
gf		*light green flower color; gf* from 'KW- 695' and 'Dalgona'; *Gf* from Korean watermelon accession 'SS-4'.	Kwon and Dane, 1999		?
gms	*msg*	*glabrous male sterile*; foliage lacking trichomes; male sterile caused by chromosome desynapsis (named glabrous male sterile by Robinson*); *gms* from 'Sugar Baby' irradiated with gamma rays.	Watts, 1962,1967	Robinson et al., 1976*; Ray and Sherman, 1988	?
go	*c*	*golden yellow color of older leaves and mature fruit;* (named golden by Robinson*); *go* from 'Royal Golden'; *Go* from 'NC 34-9-1' and 'NC 34-2-1'.	Barham, 1956	Robinson et al., 1976*	C
gy		*Gynoecious flowering habit;* a recessive mutant line has *gy* with all pistillate flowers on the vine; *Gy* from elite cultivars.	Jiang and Lin, 2007	-	-
i-C	*i*	*inhibitor of canary yellow*, resulting in red flesh (renamed by Rhodes and Dane*); *CC YY I- C I-C* from 'Yellow Baby' F1 and 'Yellow Doll' F1; *cc yoyo I-C I-C* from 'Tendersweet Orange Flesh'; *cc yy I-C I-C* from 'Golden Honey'; *cc YY i-C i-C* from 'Sweet Princess'.	Henderson et al., 1998	Rhodes and Dane, 1999*	C
i-dg		*inhibitor of delayed green*; epistatic to *dg; I-dgI-dg dgdg* plants are pale green; and *i-dgi-dg dgdg* plants are normal; *dg* from breeding line Pale 90; *Dg* from 'Allsweet'; *i-dg* gene was lost when advanced inbreds were made.	Rhodes, 1986	Jiang, X.T. and D.P. Lin, 2007	L

ins		*Intermittent stripes*; narrow dark stripes at the peduncle end of the fruit becoming irregular in the middle and nearly absent at the blossom end of the fruit; *ins* from 'Navajo Sweet'; *Ins* from 'Crimson Sweet'.	Gusmini and Wehner, 2006	-	C
ja		*juvenile albino*; chlorophyll in seedlings, leaf margins, and fruit rind reduced when grown under short days; *ja* from 'Dixielee mutant' and 'G17AB' F2; *Ja* from 'Sweet Princess' and '20J57'.	Zhang et al., 1996b	-	?
l		*long (or large) seeds*; interacts with *s*; long recessive to medium or short; *LLSS* for medium, *llSS* for long, and *LLss* or *llss* for short seed; *llSS* from 'Peerless'; *LLSS* from 'Klondike'; *LLss* from 'Baby Delight'.	Poole et al., 1941		?
la		*lethal albino*; recessive to normal plants (*La*); plants that can turn green and growth normally are heterozygous (*Lala*) for *la* gene; *la* from '5508' mutant.	Ma and Zhang, 1999		?
m		*mottled skin*; greenish white mottling of fruit skin; randomly-distributed, irregularly-shaped light green spots on a mostly solid dark-green rind pattern; *m* from 'Long Iowa Belle' (seeds not available) and 'Round Iowa Belle' (seeds not available); *M* from 'Japan 4' (seeds not available) and 'China 23' (seeds not available).	Weetman, 1937	Poole, 1944	?
ms-1	*ms*	*male sterile*; plants with small, shrunken anthers and aborted pollen; *ms-1* from 'Nongmei 100'; *Ms* from most cultivars, e.g. 'Allsweet'.	Zhang and Wang, 1990; Zhang et al., 1994b		?
ms-2		*male sterile* with high seed productivity; *ms-2* from 'Kamyzyakskii'; *Ms-2* from cultivars like 'Allsweet'.	Dyutin, and Sokolov, 1990	-	?
ms-3		*male sterile* with unique foliar characteristics; *ms-3* from ????; *Ms-3* from cultivars like 'Allsweet'.	Bang et al., 2006	-	?
Ms-4		*male sterile*; conferred by a single dominant gene; *Ms-4* from 'G42' mutant (by pollen-EMS mutagenesis).	Deng et al., 2022		?
ms-dw		*male sterile*, *dwarf; ms-dw* from 'Dwarf Male-Sterile Watermelon (DMSW)'; *Ms-dw* from 'Changhui', 'Fuyandagua', and 'America B'.	Huang et al., 1998	-	?
nl	*sn*	*nonlobed leaves*; leaves lack the typical lobing; sinuate leaves (named nonlobed by Robinson*); leaves lack the typical lobing of most cultivars, slightly lobed with the sinus obscure; Incomplete dominance; *Nl* is not sinuate, but pinnatifid (deeply pinnately lobed, with prominent sinuses) like most cultivars; *nl* from spontaneous mutant of 'Black Diamond', and probably 'Sunshade; *Nl* from 'Black Diamond', and most cultivars such as 'Allsweet' and 'Calhoun Gray'.	Mohr, 1953	Robinson et al., 1976*	C

O		*Elongate fruit*; incompletely dominant to spherical, so that *Oo* is oval; *O* from 'Long Iowa Belle'; *o* from 'Round Iowa Belle', 'China 23', 'Japan 4', and 'Japan 6'.	Weetman, 1937	Poole and Grimball, 1945	P
ob		*oblong fruit*; most recessive to elongate (Ob^E with most dominant) and round (Ob^R); intermediate to oval and elongate; *ob* from 'Tendersweet Orange Flesh' and 'Peacock Shipper'; Ob^E from 'Charleston Gray'; Ob^R from 'Red-N-Sweet' and 'Crimson Sweet'.	Lou and Wehner. 2016		?
p		*pencilled lines on skin;* inconspicuous stripes; greenish- white mottling* (called pencilled by Robinson**); inconspicuous, very narrow, pencil-width stripes running the length of the fruit (originally spelled penciled by Poole); recessive to netted fruit; *p* from 'Japan 6' (seeds not available) and *P* from 'China 23' (seeds not available).	Weetman, 1937*	Robinson et al., 1976**	?
pa		*partial andromonoecy*; single recessive to monoecy; *pa* plants produce male, female, bisexual, and hermaphrodite flowers within the same plant; *pa* from 'P84'.	Aguado et al., 2020		?
Tr		*Trimerous*; dominant to pentamerous (*tr*); *Tr* from 'W1-17'; *tr* from 'ZXG01553'.	Qiu et al., 2022		?
pl		*pale leaf*; seedlings are pale green in color; *pl* from breeding line HY477; *Pl* from 'Allsweet'.	Yang, 2006	-	?
pm		*powdery mildew susceptibility;* susceptibility to *Sphaerotheca fuliginea* is recessive; *pm* from PI 269677; *Pm* from 'Sugar Baby' and most cultivars.	Robinson et al., 1975		P
prv		*Papaya ringspot virus-watermelon strain resistance*; resistance to PRV-W is recessive; *prv* from PI 244017, PI 244019, and PI 485583; *Prv* from 'Allsweet', 'Calhoun Gray', and 'New Hampshire Midget'.	Guner et al., 2018	-	P
psf		*photosensitive flesh*; conferred by a single recessive gene; a yellow fleshed mutant with ζ-carotene accumulation; the initial yellow color can be photobleached under intense sunlight; *psf* is a mutant from red-fleshed line '302'.	Zhang et al., 2022		?
r		*red seed coat*; genes *r, t* and *w* interact to produce seeds of different colors; dotted black from 'Klondike' *(RR TT WW*); clump from 'Sun Moon and Stars' (*RR TT ww*); tan from 'Baby Delight' (*RR tt WW*); white with tan tip from 'Pride of Muscatine' (*RR tt ww*); green from unknown line (*rr TT WW*); red from 'Red Seeded Citron' (*rr tt WW*); white with pink tip from 'Peerless' (*rr tt ww*).	Poole et al., 1941		?
s		*short (or small) seeds*; epistatic to *l*; long recessive to medium or short; *LL SS* for medium, *ll SS* for long, and *LL ss* or *ll ss* for short seed; *ll SS* from 'Peerless'; *LL SS* from 'Klondike'; *LL ss* from 'Baby Delight'.	Poole et al., 1941		?

sf		*soft flesh*; higher contents of abscisic acid than hard flesh; applying exogenous ethylene can reduce flesh firmness; the flesh firmness in F_2 population was between the firmness values of two parental lines, showing the continuous distribution; *sf* from '203Z'; *Sf* from 'HWF'.	Anees et al., 2023		?
slv		*seedling leaf variegation*; conferred by a single recessive gene in PI 482261; linked or pleiotropic with a dominant allele for resistance to cool temperature injury (20°C for greenhouse-grown plants); *slv* from PI 482261 (resistant to ZYMV-FL); *Slv* from 'New Hampshire Midget'.	Provvidenti, 1994		P
So		*Sour*; caused by the accumulation of organic acid; *So* from PI 271769 (Ph=4.52); *so* from '203Z' (pH=5.76).	Gao, 2018		?
Sp		*Spotted cotyledons, leaves and fruit*; dominant to uniform foliage and fruit color; *Sp* from 'Sun, Moon and Stars'* and 'Moon and Stars'**; *sp* from 'Allsweet'.	Poole, 1944*	Rhodes, 1986**	C
su	*Bi,* *suBi*	*suppressor of bitterness*; (*su* named by Robinson*); non-bitter fruit; *su* from 'Hawkesbury'; *Su* from bitter-fruited mutant of 'Hawkesbury'; bitterness in *C. colocynthis* is due to *SuSu* genotype.	Chambliss et al., 1968	Robinson et al., 1976*	?
t	*bt*	*tan seed coat*; genes *r, t* and *w* interact to produce seeds of different colors; dotted black from 'Klondike' *(RR TT WW)*; clump from 'Sun Moon and Stars' (*RR TT ww*); tan from 'Baby Delight' (*RR tt WW*); white with tan tip from 'Pride of Muscatine' *(RR tt ww)*; green from unknown line (*rr TT WW*); red from 'Red Seeded Citron' (*rr tt WW*); white with pink tip from 'Peerless' (*rr tt ww*).	McKay, 1936	Poole et al., 1941	?
T^1		*Tannish seed coat*; a novel locus or a different allele of the *T;* the tannish seed coat color was different from the range of brown color used to describe tan seed coat color by Poole (1941); *T^1* is defined in the crossing population of PI 189225 (red seed) and 'Sugar Baby'/ 'Charleston Gray' (dotted black seed).	Paudel et al., 2019a		?
Ti		*Tiny seed*; dominant over medium seed (*ti*); *Ti* from 'Sweet Princess'; *ti* from 'Fujihikari'.	Tanaka et al., 1995	-	?
tl	*bl*	*tendrilless* (formerly *called branchless**), after 4th or 5th node, vegetative axillary buds are transformed into flower buds and leaf shape is altered; *tl* from 'Early Branchless'; *Tl* from breeding lines 'G17AB', 'ASS-1', 'YF91-1-2', and S173 breeding line.	Rhodes, Zhang, Baird and Knapp, 1999; Zhang, Rhodes, Baird and Skorupska, 1996a	Lin, Tong, Wang, Zhang and Rhodes, 1992*	?
tm		*trimonoecious;* a possible modifying gene; *a* is epistatic to *tm*; *tm* plants have staminate, pistillate and perfect flowers; *tm* from 'SL3H' and 'AKKZW'.	Ji et al., 2015		?

ts	*tss*	*tomato seed*; seeds smaller than short (*LL ss* or *ll ss*), almost the size of a tomato seed; *ts* from tomato seed Sugar Baby mutant; *Ts* from 'Gn-1'.	Zhang et al., 1994a	Zhang, 1996	C
w		*white seed coat*; genes *r, t* and *w* interact to produce seeds of different colors; dotted black from 'Klondike' (*RR TT WW*); clump from 'Sun Moon and Stars' (*RR TT ww*); tan from 'Baby Delight' (*RR tt WW*); white with tan tip from 'Pride of Muscatine' (*RR tt ww*); green from unknown line (*rr TT WW*); red from 'Red Seeded Citron' (*rr tt WW*); white with pink tip from 'Peerless' (*rr tt ww*).	Poole et al., 1941		?
Wbn		Resistance to watermelon bud necrosis orthotospovirus (WBNV); Wbf from 'BIL-53' and 'IIHR-19'; wbf from 'IIHR-140'.	Nagesh et al., 2018, 2020		?
Wf	W	*White flesh*; (named white flesh by Robinson*); *Wf* is epistatic to *B* (*Y* renamed *B* by Henderson**); *WfWf BB* or *WfWf bb* white fleshed; *wfwf BB* yellow fleshed; *wfwf bb* red fleshed; *B* from breeding line V.No.3 and *b* from V.No. 1; flesh color segregated into 12 white, 3 yellow and 1 red in the F_2.	Shimotsuma, 1963	Robinson et al., 1976*; Henderson, 1992**	?
w-yl		*whole growth period leaf yellowing watermelon*; recessive to green leaves (*W-yl*); the leaves in the whole growth period were yellow, including cotyledon and fruit; a significant reduction in chlorophyll and chlorophyll precursors content; *w-yl* from 'yellow leaf (*w-yl*) mutant'; *W-yl* from 'ZK'.	Zhu et al., 2022		?
Y^{Scr}	*Scr*	*Scarlet red flesh*; dominant to coral red flesh (Y^{Crl}); orange flesh (y^{O}) and salmon yellow flesh (y); Y^{Scr} from 'Dixielee' and 'Red-N-Sweet'; Y^{Crl} from 'Angeleno' (black seeded); y^{O} from 'Tendersweet Orange Flesh'; *y* from 'Golden Honey'.	Gusmini and Wehner, 2006	Gusmini and Wehner, 2006	C
Y^{Crl}	*Y, Rd*	*Coral red flesh*; recessive to scarlet red flesh (Y^{Scr}); dominant to orange flesh (y^{O}) and salmon yellow flesh (y); Y^{Scr} from 'Dixielee' and 'Red-N-Sweet'; Y^{Crl} from 'Angeleno' (black seeded); y^{O} from 'Tendersweet Orange Flesh'; *y* from 'Golden Honey'.	Porter, 1937	Poole, 1944; Henderson, 1989; Henderson et al., 1998	C?
y^{O}		*orange flesh*; recessive to scarlet red flesh (Y^{Scr}) and coral red flesh (Y^{Crl}); dominant to salmon yellow flesh (y); Y^{Scr} from 'Dixielee' and 'Red-N-Sweet'; Y^{Crl} from 'Angeleno' (black seeded); y^{O} from 'Tendersweet Orange Flesh'; *y* from 'Golden Honey'.	Henderson, 1989; Henderson et al., 1998	Poole, 1944; Porter, 1937	C
y	*rd*	*salmon yellow flesh*; recessive to scarlet red flesh (Y^{Scr}), coral red flesh (Y^{Crl}) and orange flesh (y^{O}); Y^{Scr} from 'Dixielee' and 'Red-N-Sweet'; Y^{Crl} from 'Angeleno' (black seeded); *yO* from 'Tendersweet Orange Flesh'; *y* from 'Golden Honey'.	Porter, 1937	Poole, 1944; Henderson, 1989; Henderson et al., 1998	C

Y^{Car}		*Unique orange flesh of accumulates β-carotene*; no lycopene; co-dominant to canary yellow (*C*), scarlet red (*Y^{Scr}*), coral red (*Y^{Crl}*) and orange flesh with pro-lycopene accumulation (*y^{O}*); *Y^{Car}* from 'NY0016', *C* from 'Early Moon Beam'; *Y^{Scr}* from 'Dixilee'; *Y^{Crl}* from 'Charleston Gray'; *y^{O}* from 'Orange Flesh Tender Sweet'.	Tadmor et al., 2005; Branham et al., 2017a		?
Y^{pg}		*pale green flesh*; incompletely recessive to pale yellow flesh; three phenotypes (pale yellow, yellow flesh and green mixed with yellow flesh) were isolated in F_2; accumulating chlorophyll; *Y^{pg}* from 'ZXG1555',	Pei et al., 2021		?
Yb	-	*yellow belly*; yellow colored ground spot on the fruit; *Yb* from 'Black Diamond Yellow Belly'; *yb* from 'Black Diamond'.	Gusmini and Wehner, 2006	-	C
Yl	*Y*	*Yellow leaf*; incompletely dominant to green leaf (*yl*); (*Y* renamed *Yl* by Henderson*). *Yl* from 'Yellow Skin'.	Warid and Abd-El-Hafez, 1976	Henderson, 1991*	?
zym-CH	-	*Resistance to zucchini yellow mosaic virus* (*ZYMV-CH*); resistance is specific to the China strain; *zym-CH* from PI 595203, *Zym-FL* from elite cultivars.	Xu et al., 2004	-	P
zym-FL	*zym*	*Resistance to zucchini yellow mosaic virus* (*ZYMV-FL*); resistance is specific to the Florida strain; *zym-FL* from PI 482322, PI 482299, PI 482261, and PI 482308 (Provvidenti, 1991); higher resistance in PI 595203 (Egun), PI 386026, PI 386025 (Boyhan et al.), and in PI 386019, PI 490377, PI 596662, PI 485580, PI 560016, PI 494528, PI 386016, PI 482276, PI 595201; *Zym-FL* from elite cultivars.	Provvidenti, 1991	Boyhan et al., 1992; Guner et al., 2018	P

Table 2. Isozyme and molecular markers for watermelon, including gene symbol (Sym.), synonym (Synon.), description, and references.

Sym.	Synon.	Gene description and type lines	References
Aco-1		*Aconitase-1*.	Navot et al., 1990
Aco-2		*Aconitase-2*.	Navot et al., 1990
Adh-1		*Alcohol dehydrogenase-1*; one of five codominant alleles, each regulating one band.	Navot and Zamir 1986, 1987; Zamir et al., 1984
Adh-1-1		*Alcohol dehydrogenase-1-1*; one of five codominant alleles, each regulating one band; found in *C; lanatus* var. *citroides* and *C. colocynthis*.	Navot and Zamir 1986, 1987; Zamir et al., 1984
Adh-1-2		*Alcohol dehydrogenase-1-2*; one of five codominant alleles, each regulating one band; found in *C. lanatus* var. *citroides* and *C. colocynthis.*	Navot and Zamir 1986, 1987; Zamir et al., 1984
Adh-1-3		*Alcohol dehydrogenase-1-3*; one of five codominant alleles, each regulating one band; found in *Praecitrullus fistulosus*.	Navot and Zamir 1986, 1987; Zamir et al., 1984

Adh-1-4		*Alcohol dehydrogenase-1-4*; one of five codominant alleles, each regulating one band; found in *Acanthosicyos naudinianus*.	Navot and Zamir 1986, 1987; Zamir et al., 1984
Aps-1		*Acid phosphase-1*.	Navot et al., 1990; Navot and Zamir 1986, 1987; Zamir et al., 1984
Aps-2-1		*Acid phosphatase-2-1*; one of two codominant alleles, each regulating one band; found in *C. lanatus* and *C. colocynthis.*	Navot et al., 1990; Navot and Zamir 1986, 1987
Aps-2-2		*Acid phosphatase-2-2*; one of two codominant alleles, each regulating one band; found in *Acanthosicyos naudinianus.*	Navot et al., 1990; Navot and Zamir 1986, 1987
Dia-1		*Diaphorase-1*.	Navot et al., 1990
Est-1	-	*Esterase-1*; one of six codominant alleles, each regulating one band; found in *C. lanatus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987
Est-1-1	-	*Esterase-1-1*; one of six codominant alleles, each regulating one band; found in *C. lanatus* var. *citroides* and *C. colocynthis.*	Navot et al., 1990; Navot and Zamir, 1986, 1987
Est-1-2	-	*Esterase-1-2*; one of six codominant alleles, each regulating one band; found in *C. colocynthis*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Est-1-3	-	*Esterase-1-3*; one of six codominant alleles, each regulating one band; found in *Praecitrullus fistulosus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Est-1-4		*Esterase-1-4*; one of six codominant alleles, each regulating one band; found in *C. ecirrhosus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Est-1-5		*Esterase-1-5*; one of six codominant alleles, each regulating one band; found in *Acanthosicyos naudinianus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987
Est-2		*Esterase-2*; one of five codominant alleles, each regulating one band; found in *C. lanatus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Est-2-1		*Esterase-2-1*; one of five codominant alleles, each regulating one band; found in *C. colocynthis*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Est- 2- 2		*Esterase-2-2*; one of five codominant alleles, each regulating one band; found in *C. colocynthis*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Est-2-3		*Esterase-2-3*; one of five codominant alleles, each regulating one band; found in *Praecitrullus fistulosus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987
Est-2-4		*Esterase-2-4*; one of five codominant alleles, each regulating one band; found in *Acanthosicyos naudinianus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987
Fdp-1		*Fructose 1,6 diphosphatase-1*.	Navot et al., 1990; Navot and Zamir, 1986
For-1		*Fructose 1,6 diphosphatase-1*.	Navot et al., 1990
Gdh-1		*Glutamate dehydrogenase-1*; isozyme located in cytosol.	Navot and Zamir, 1986
Gdh-2		*Glutamate dehydrogenase-2*; isozyme located in plastids.	Navot et al., 1990; Navot and Zamir, 1986

Got-1		*Glutamate oxaloacetate transaminase-1*; one of four codominant alleles, each regulating one band; found in *C. lanatus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Got-1-1		*Glutamate oxaloacetate transaminase-1*; one of four codominant alleles, each regulating one band; found in *C. colocynthis* and *Praecitrullus fistulosus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Got-1-2		*Glutamate oxaloacetate transaminase-1-2*; one of four codominant alleles, each regulating one band; found in *C. lanatus* var. *citroides*.	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Got1-3		*Glutamate oxaloacetate transaminase-13*; one of four codominant alleles, each regulating one band; found in *Acanthosicyos naudinianus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Got-2		*Glutamate oxaloacetate transaminase-2*; one of five codominant alleles, each regulating one band; found in *C. lanatus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Got-2-1		*Glutamate oxaloacetate transaminase-21*; one of five codominant alleles, each regulating one band; found in C. colocynthis.	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Got-2-2		*Glutamate oxaloacetate transaminase-22*; one of five codominant alleles, each regulating one band; found in *C. ecirrhosus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Got-2-3		*Glutamate oxaloacetate transaminase-2-3*; one of five codominant alleles, each regulating one band; found in *Praecitrullus fistulosus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Got-2-4		*Glutamate oxaloacetate transaminase-24*; One of five codominant alleles, each regulating one band; found in *Acanthosicyos naudinianus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Got-3		*Glutamate oxaloacetate transaminase-3*.	Zamir et al., 1984
Got-4		*Glutamate oxaloacetate transaminase-4*.	Navot et al., 1990; Zamir et al., 1984
hsp-70		*heat shock protein 70*; one gene presequence 72-kDa hsp70 is modulated differently in glyoxomes and plastids.	Wimmer et al., 1997
Idh-1		*Isocitrate dehydrogenase-1*.	Zamir et al., 1984
Lap-1		*Leucine aminopeptidase-1*.	Navot et al., 1990; Navot and Zamir, 1986
Mdh-1		*Malic dehydrogenase-1*; one of two codominant alleles, each regulating one band; found in *C. lanatus.*	Navot and Zamir, 1987; Zamir et al., 1984
Mdh-1-1		*Malic dehydrogenase-1-1*; one of two codominant alleles, each regulating one band; found in *Praecitrullus fistulosus.*	Navot and Zamir, 1987; Zamir et al., 1984

Mdh-2		*Malic dehydrogenase-2*; one of three codominant alleles, each regulating one band; found in *C. lanatus.*	Navot and Zamir, 1987
Mdh-2-1		*Malic dehydrogenase-2-1*; one of three codominant alleles, each regulating one band; found in *C. colocynthis.*	Navot and Zamir, 1987
Mdh-2-2		*Malic dehydrogenase-2-2*; one of three codominant alleles, each regulating one band; found in *Praecitrullus fistulosus.*	Navot and Zamir, 1987
Me-1		*Malic enzyme-1*; one of three codominant alleles, each regulating one band; found in *C. lanatus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Me-1-1		*Malic enzyme-1-1*; one of three codominant alleles, each regulating one band; found in *Praecitrullus fistulosus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Me-12		*Malic enzyme-12*; one of three codominant alleles, each regulating one band; found in *C. colocynthis.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Me-2		*Malic enzyme-2*.	Zamir et al., 1984
Pgd-1	*6 Pgdh-1*	*6-Phosphogluconate dehydrogenase-1*; one of three codominant alleles, each regulating one plastid band; found in *C. lanatus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgd-1-1	*6 Pgdh-1-1*	*6-Phosphogluconate dehydrogenase-1-1*; one of three codominant alleles, each regulating one plastid band; found in *Praecitrullus fistulosus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgd-1-2	*6 Pgdh-1-2*	*Phosphogluconate dehydrogenase-1-2*; one of three codominant alleles, each regulating one plastid band; found in *Acanthosicyos naudinianus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgd-2	*6 Pgdh-2*	*6-Phosphogluconate dehydrogenase-2*; one of five codominant alleles, each regulating one cytosolic band; found in *C. lanatus.*	Navot and Zamir, 1986; Zamir et al., 1984
Pgd-2-1	*6 Pgdh-2-1*	*6-Phosphogluconate dehydrogenase-21*; one of five codominant alleles, each regulating one cytosolic band; found in *C. ecirrhosus.*	Navot and Zamir, 1987; Zamir et al., 1984
Pgd-2-2	*6 Pgdh-2-2*	*6-Phosphogluconate dehydrogenase-2-2*; one of five codominant alleles, each regulating one cytosolic band; found in *Praecitrullus fistulosus.*	Navot and Zamir, 1987; Zamir et al., 1984
Pgd-2-3	*6 Pgdh-2-3*	*6-Phosphogluconate dehydrogenase-2-3*; one of five codominant alleles, each regulating one cytosolic band; found in *C. colocynthis*.	Navot and Zamir, 1987; Zamir et al., 1984
Pgd-2-4	*6 Pgdh-2-4*	*6-Phosphogluconate dehydrogenase-2-4*; one of five codominant alleles, each regulating one cytosolic band; found in *Acanthosicyos naudinianus.*	Navot and Zamir, 1987; Zamir et al., 1984
Pgi-1		*Phosphoglucoisomerase-1*; one of three codominant alleles, each regulating one plastid band; found in *C. lanatus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987
Pgi-1-1		*Phosphoglucoisomerase-11*; one of three codominant alleles, each regulating one plastid band; found in *C. colocynthis.*	Navot et al., 1990; Navot and Zamir, 1986, 1987

Pgi-1-2		*Phosphoglucoisomerase-1-2*; one of three codominant alleles, each regulating one plastid band; found in *Acanthosicyos naudinianus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Pgi-2		*Phosphoglucoisomerase-2*; one of six codominant alleles, each regulating one cytosolic band; found in *C. lanatus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgi-2-1		*Phosphoglucoisomerase-2-1*; one of six codominant alleles, each regulating one cytosolic band; found in *C. lanatus* and *C. colocynthis.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgi-2-2		*Phosphoglucoisomerase-2-2*; one of six codominant alleles, each regulating one cytosolic band; found in *C. ecirrhosus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgi-2-3		*Phosphoglucoisomerase-2-3*; one of six codominant alleles, each regulating one cytosolic band; found in *Praecitrullus fistulosus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgi-2-4		*Phosphoglucoisomerase-2-4*; one of six codominant alleles, each regulating one cytosolic band; found in *C. lanatus* var. *citroides*.	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgi-2-5		*Phosphoglucoisomerase-2-5*; one of six codominant alleles, each regulating one cytosolic band; found in *Acanthosicyos naudinianus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgm-1		*Phosphoglucomutase-1*; one of four codominant alleles, each regulating one plastid band; found in *C. lanatus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgm-1-1		*Phosphoglucomutase-1-1*; one of four codominant alleles, each regulating one plastid band; found in *C. colocynthis.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgm-1-2		*Phosphoglucomutase-1-2*; one of four codominant alleles, each regulating one plastid band; found in *Acanthosicyos naudinianus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgm-1-3		*Phosphoglucomutase-1-3*; one of four codominant alleles, each regulating one plastid band; found in *Praecitrullus fistulosus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Pgm-2		*Phosphoglucomutase-2;* one of four codominant alleles, each regulating one cytosolic band; found in *C. lanatus*.	Navot and Zamir, 1987; Zamir et al., 1984
Pgm-2-1		*Phosphoglucomutase-2-1*; one of four codominant alleles, each regulating one cytosolic band; found in *Acanthosicyos naudinianus.*	Navot and Zamir, 1987; Zamir et al., 1984
Pgm-2-2		*Phosphoglucomutase-2-2*; one of four codominant alleles, each regulating one cytosolic band; found in *C. lanatus*.	Navot and Zamir, 1987; Zamir et al., 1984
Pgm-2-3		*Phosphoglucomutase-2-3*; one of four codominant alleles, each regulating one cytosolic band; found in *Praecitrullus fistulosus.*	Navot and Zamir, 1987; Zamir et al., 1984

Prx-1	-	*Peroxidase-1*; one of seven codominant alleles, each regulating one band; found in *C. lanatus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Prx-11		*Peroxidase-11*; one of seven codominant alleles, each regulating one band; found in *C. colocynthis*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Prx-12		*Peroxidase-12*; one of seven codominant alleles, each regulating one band; found in *Praecitrullus fistulosus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987
Prx-13		*Peroxidase-13*; one of seven codominant alleles, each regulating one band; found in *C. lanatus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Prx-14		*Peroxidase-14*; one of seven codominant alleles, each regulating one band; found in *C. ecirrhosus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987
Prx-15		*Peroxidase-15*; one of seven codominant alleles, each regulating one band; found in *C. lanatus* and *C. colocynthis*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Prx-16		*Peroxidase-16*; one of seven codominant alleles, each regulating one band; found in Acanthosicyos naudinianus.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Prx-2		*Peroxidase-2*.	Navot and Zamir,1987
Prx-3		*Peroxidase-3*.	Navot and Zamir,1987
Sat		*Serine acetyltransferase*; catalyzes the formation of O-acetylserine from serine and acetyl-CoA.	Saito et al., 1997
Skdh-1		*Shikimic acid dehydrogenase- 1.*	Zamir et al., 1984
Skdh-2		*Shikimic acid dehydrogenase-2*; one of six codominant alleles, each regulating one band.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Skdh-21		*Shikimic acid dehydrogenase-21*; one of six codominant alleles, each regulating one band; found in *C. colocynthis*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Skdh-22		*Shikimic acid dehydrogenase-22*; one of six codominant alleles, each regulating one band; found in *C. colocynthis.*	Navot et al., 1990; Navot and Zamir, 1986, 1987
Skdh-23		*Shikimic acid dehydrogenase-23*; one of six codominant alleles, each regulating one band; found in *Acanthosicyos naudinianus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987
Skdh-24		*Shikimic acid dehydrogenase-24*; one of six codominant alleles, each regulating one band; found in *C. ecirrhosus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Skdh-25		*Shikimic acid dehydrogenase-25*; one of six codominant alleles, each regulating one band; found in *Praecitrullus fistulosus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987
Sod-1		*Superoxide dismutase-1*; one of three codominant alleles, each regulating one band; found in *C. lanatus.*	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Sod-11		*Superoxide dismutase-11*; one of three codominant alleles, each regulating one band; found in *C. colocynthis*.	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984

Sod-12		*Superoxide dismutase-12*; one of three codominant alleles, each regulating one band; found in *Acanthosicyos naudinianus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984
Sod-2		*Superoxide dismutase-2*; one of two codominant alleles, each regulating one band; found in *C. lanatus.*	Navot and Zamir, 1987
Sod-21		*Superoxide dismutase-21*; one of two codominant alleles, each regulating one band; found in *Acanthosicyos naudinianus*.	Navot and Zamir, 1987
Sod-3		*Superoxide dismutase-3*; one of two codominant alleles, each regulating one band; found in *C. lanatus.*	Navot and Zamir, 1987
Sod-31		*Superoxide dismutase-31*; one of two codominant alleles, each regulating one band; found in *Praecitrullus fistulosus.*	Navot and Zamir, 1987
Spr-1		*Seed protein-1*.	Navot and Zamir, 1986
Spr-2		*Seed protein-2*.	Navot and Zamir, 1986
Spr-3		*Seed protein-3*.	Navot and Zamir, 1986
Spr-4		*Seed protein-4*.	Navot et al., 1990; Navot and Zamir, 1986
Spr-5		*Seed protein-5*.	Navot et al., 1990; Navot and Zamir, 1986
Tpi-1		*Triosephosphatase isomerase-1*. one of four codominant alleles, each regulating one band; found in *C. lanatus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Tpi-11		*Triosephosphatase isomerase-11*; one of four codominant alleles, each regulating one band; found in *C. colocynthis*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Tpi-12		*Triosephosphatase isomerase-12*; one of four codominant alleles, each regulating one band; found in Praecitrullus fistulosus.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Tpi-13		*Triosephosphatase isomerase-13*; one of four codominant alleles, each regulating one band; found in *Acanthosicyos naudinianus*.	Navot et al., 1990; Navot and Zamir, 1986, 1987
Tpi-2		*Triosephosphatase isomerase-2*; one of three codominant alleles, each regulating one band; found in *C. lanatus*.	Navot and Zamir, 1987
Tpi-21		*Triosephosphatase isomerase-21*; one of three codominant alleles, each regulating one band; found in *Acanthosicyos naudinianus.*	Navot and Zamir, 1987
Ure-1		*Ureaase-1*.	Navot and Zamir, 1987

Table 3. Functional genes for watermelon, including gene ID, symbol (Sym.), description and type lines, availability (? = undefined; D = defined), references, and notes.

Gene ID	Sym.	Gene description and type lines	Availability	References	Notes
CitACS4 (Cla97C03G066110)	*a*	*1-aminocyclopropane-1-carboxylate synthase 4*; a mutation of *CitACS4* that reduces the enzyme activity and the production of ethylene in pistillate floral buds, promoting the conversion of female into hermaphrodite flowers; found in 'AKKZW' (*aa*) and 'Halep Karasi' (*aa*).	?	Boualem et al., 2016; Ji et al., 2016; Manzano et al., 2016.	
Cla001017 (Cla97C08G146430)		Cc-nbs-lrr resistance protien; a non-synonymous SNP that may be involved in resistance to anthracnose race 1; the gene expression was upregulated in the resistant line after inoculation; found in 'DrHs7250' and 'Charleston Gray'.	?	Jang et al., 2019; Bhatta et al., 2022	Unknown allele with *Ar-1*
Cla97C01G020050	*Rbf*	*CSC1-like*; the CSC1-like protein is an osmosensitive Ca-permeable cation channel; may be involved in Ca accumulation as a white powder on the watermelon surface; found in the cross 'SIT55616RN' and 'FD061129'.	?	Lee et al., 2022	
ClLCYB (Cla97C04G070940)		*lycopene* β-*cyclase*; to catalyze the conversion of lycopene to β-carotene; domestication selection of two amino acids lead to reduction of protein stability, the accumulation of the substrate lycopene, and formation of the red flesh; canary yellow from PI 165002 and '97103'; red flesh from PI 593380 and 'Cream of Saskatchewan'.	D	Bang et al., 2007; Zhang et al., 2020b.	
ClWPRb (Cla97C04G073090)	*cgmm*	*a weak chloroplast movement under blue light 1 and plastid movement impaired 2-related*; may be negatively associated with CGMMV resistance; the mutation on *ClWPRb* may affect the movement of the pathogen, resulting in disease resistance; found in the cross PI 595203 and 'M1511-3'.	?	Cai et al., 2023	
ClCG03G010030		*FtsH extracellular protease family*; involved in early chloroplast development; a single SNP causing missense mutation may be closely related to delayed green leaf; found in the cross 'Houlv' (delayed green Leaf) and 'Charleston gray' (green leaf).	?	Kidanemariam, 2020.	Unknown allele with *dg*
ClGA20ox (Cla97C07G143880)		*gibberellin 20-oxidase-like*; one of the dwarfing genes; involved in gibberellin biosynthesis; two promoter sites are involved in the regulation of gene expression; found in *dsh* mutant (GA-deficient mutant) from 'I911' inbred line.	D	Dong et al., 2018; Dong et al., 2021b	unknown allele with *dw-1*, *dw-2*, *dw-3* and *dw-4*

Cla010337 (Cla97C09G179710)	*dw-1*	*ATP-binding cassette transporter* (*ABC transporter*); a dwarf candidate gene; there are two SNPs and one InDel on the exon, short cell as well as low expression level in dwarf line WM102 (from 'Bush Sugar Baby').	?	Zhu et al., 2019.	
ClGA3ox (Cla97C09G164590)		*gibberellin 3 β-hydroxylase*; a dwarf candidate gene; a 13 bp deletion in the coding sequence in dwarf line and results in a truncated protein lacking the conserved domain for binding 2-oxoglutarate; found in the cross 'N21' (GA-deficient mutant) and 'M08'.	?	Wei et al., 2019	unknown allele with *dw-1*, *dw-2*, *dw-3* and *dw-4*
Cla010254 (Cla97C09G178830)		*GID1L2 gibberellin receptors*; a dwarf candidate gene; gene frameshift mutation and low expression level in the dwarf line; found in the cross 'ZXG01061' (GA insensitive mutant) and 'W1-1'.	?	Liu et al., 2022a	unknown allele with *dw-1*, *dw-2*, *dw-3* and *dw-4*
ClERF4 (Cla97C10G187120)		*ethylene-responsive factor 4*; involved in the xylem biosynthesis and cell wall modification; an 11-bp deletion as well as a neighboring SNP, which resulted in a frame-shift deletion and earlier termination that is associated with low rind hardness in F_2 segregating populations and 104 germplasm accessions; found in the cross 'P-b' (low hardness) and 'P-a' (high hardness).	?	Liao et al., 2020	rind hardness was positively correlated with explosive rind characteristics; unknown allele with *e (explosive rind)*.
ClEPFL4 (Cla97C06G116000)	*eg*	*epidermal patterning factor-like 4*; a group of cysteine-rich secreted peptides that regulate a range of developmental processes; which is only gene of the narrowed candidate region on Chr 6 for the *eg* locus, found in the cross egusi seeds 'B3' (*C. mucosospermus*; thin seed coat) and 'X1625' (*C. lanatus*; thick black seed coat).	?	Paudel et al., 2019b; Li et al., 2023	
ClCGMenG (ClCG08G017810)		*2-phytyl-1,4-beta-naphthoquinone methyltransferase*; associated with formation of solid dark green rind and stripe rind pattern; higher expression in solid dark green rind than in light green rind with dark stripe; a nonsynonymous SNP mutation of the coding region in light green rind converted an arginine to glycine; found in the cross '9904' (dark green rind) and 'Handel' (light green rind with dark stripe).	?	Li et al., 2019	light green and stripe rind with unknown allele to g^W (wide stripe), g^M (medium stripe), or g^N (narrow).
Cla019205 (Cla97C06G126770)		*MORC family CW-type zinc finger protein 3*; may influence the efficiency of DNA methylation at certain target loci; associated with formation of stripe and netted fruit rind pattern; a 3 bp InDel in the coding region may alter protein function; found	?	Wang et al., 2022	netted fruit rind from 'WM204' with unknown allele to *P* from

		in the cross 'WT-2' (stripe rind) and 'WM204' (netted fruit rind).			'China 23' (seeds not available); stripe rind from 'WT-2' with unknown allele to g^W (wide stripe), g^M (medium stripe), or g^N (narrow).
ClWIP1 (Cla97C02G049440)	*gy*	a putative C2H2 zinc finger transcription factor; loss-of-function producing gynoecious lines; expressed specifically in carpel primordia and is related to the abortion of carpel primordia in early floral development; found in a spontaneous gynoecious mutant 'XHBGM' from the monoecious wild type 'XHB'.	?	Zhang et al., 2020a	
ClPEX1 (Cla97C06G112900)	*ms-1*	*leucine-rich repeat protein*; a male sterility candidate gene; specifically expressed in pollen grains; RNAi fruits exhibited a markedly inhibited seed set; found in 'G17AB'.	?	Dong et al., 2021.	
ClATM1 (Cla97C06G117840)		*Abnormal Tapetum 1*; a basic helix-loop-helix (bHLH) transcription factor; a male sterility genes; a 10 bp deletion and produces a truncated protein without the bHLH interaction and functional (BIF) domain in 'Se18' male sterility line; could activate its own transcriptional expression through promoter binding; found in 'Se18' (a spontaneous mutant of 'Sugarlee').	?	Zhang et al., 2005; Zhang et al., 2021	unknown allele with *ms-2* and *ms-3*
ClMS1 (Cla97C09G181360)	*Ms-4*	*Heat shock 70 kDa protein 4*; a dominant candidate gene for male sterility; an SNP (G1509A) may have a high impact on protein function and fertility; found in a mutant of 'G42'.	?	Deng et al., 2022	
ClLL1 (Cla97C04G076510)		homeobox-leucine zipper-like protein; two InDel that may be related to leaf form polymorphisms (lobed and sinuate leaves) by disturbing the characteristic spacing of the leucine zipper and interfering with gene function; found in a mutant from 'Lingxiu' (sinuate leaves) inbred line.	?	Wei et al., 2017	unknown alleles with *sn*
ClSUN (Cla97C03G066390)		IQD protein (SUN gene) family; to have association with cytoskeleton arrays and Ca2+-CaM signaling modules; a 159 bp deletion or non-synonymous point mutation in exon 3 is associated with elongated fruit; *O* from 'Klondike Black Seeded', 'Charleston Gray' and 'Duan125'.	?	Dou et al., 2018b; Legendre et al., 2020	unknown alleles with *O* or *ob*

ClCG01G020800	*pa*	*Chitinase-like protein*; involved in floral organ development in *Arabidopsis* and rice; a frameshift deletion of 38 bp could be responsible of the partial andromonoecy phenotype; found in 'P84'.	?	Aguado et al., 2020	
ClRPK2 (Cla97C07G143260)	*Tr*	Receptor-like protein kinase 2; eight non-synonymous SNPs may affect carpel number (trimerous or pentamerous); *Tr* found in 'W1-17'; *tr* found in 'ZXG01553'.	?	Qiu et al., 2022	
ClPMR2 (Cla9702G042200)		*NBS-LRR resistance protein*; with homology to the *Arabidopsis thaliana* powdery mildew resistance protein, RPW8. A non-synonymous SNP leads to translation termination, which may be related to susceptible to race 1 of *P. xanthii* and *P. capsici*; found in the cross 'USVL677-PMS' and 'TS34' (susceptible) and 'USVL531-MDR' and 'Arka Manik' (resistant).	?	Kim et al., 2015; Mandal et al., 2020	unknown alleles with pm (powdery mildew susceptibility).
ClZISO (Cla97C07G142750)	*psf*	*15-cis-ζ-carotene isomerase*; catalyzes the conversion of 9,15,9'-tri-cis-ζ-carotene to 9,9'-di-cis-ζ-carotene; the truncated protein produced by G-A transversion lost this catalytic function, and light treatment can partially compensate ClZISO isomerase activity; found in a photosensitive flesh mutant from red-fleshed line '302'.	?	Zhang et al., 2022	
ClPPO (Cla97C03G057100)	*RR TT WW DD*	*polyphenol oxidase*; melanin as the main compound in black seed coat; there is a single-nucleotide insertion in the coding region of ClPPO, which is co-separated from the light yellow seeds of '9904'; black seed coat from 'Handel'.	?	Li et al., 2020a	
Cla004102 (Cla97C06G118630)	*sf*	auxin responsive protein (Aux/IAA); involved in some fruit development and ripening; the relative expression decreases and remains lower than that of the hard flesh with fruit development; *sf* found in '203Z'.	?	Anees et al., 2023	
Cla011508 (Cla97C01G003400)	*su*	BHLH transcription factor; homologous to the *Bt* genes in cucumber; truncated protein produced by a non-synonymous mutation may affect the cucurbitacin biosynthetic pathway; found in '9904' from original *C. mucosospermus* and in other eight bitterness accessions.	?	Li et al., 2018a; Gong et al., 2022a	
ClTFL1 (Cla97C04G076830)		*TERMINAL FLOWER 1*; a key gene regulating indeterminate/determinate growth; the ratio of FT /TFL1 affects the plant architecture and flower development; the SNP mutation of C to A in the coding region may result in few lateral branches; found in the cross 'WCZ' (branchless inbred line).	?	Dou et al., 2022	Unknown allele with *tl*

ClPSY1 (Cla97C01G008760)	*Y^{Car}*	phytoene synthase; catalyzes the conversion of two molecules of GGPP to phytoene (colorless) to produce the first carotenoid; several base mutations in the promoter and a nonsynonymous SNP mutations in the coding region are likely to the change in flesh color of orange and pale yellow; orange flesh (*Y^{Car}*) from PI 192938 and 'NY0016'; pale-yellow or canary yellow flesh from 'Cream of Saskatchewan' or 'Early Moon Beam'.	?	Branham et al., 2017a; Liu et al., 2022b	
Cla97C10G185970	*Y^{pg}*	*plastid lipid-associated protein 3* (*chloroplastic-like*); may be involved in the synthesis and metabolism of chlorophyll and may potentially regulate green flesh coloration; two SNPs in the coding region could be used to distinguish green flesh colour from non-green flesh color; found in the cross 'ZXG1555' (pale green flesh) and 'COS' (pale yellow flesh).	?	Pei et al.,2021	
eIF4E (Cla97C03G058500)	*zym-FL*	*eukaryotic translation initiation factor 4E*; closely associated with ZYMV resistance; SNP241 which resulted in an amino acid substitution (proline to threonine) is located in the critical cap recognition and binding area, found in the cross ZYMV-resistant PI 595203 and ZYMV-susceptible 'New Hampshire Midget'.	?	Ling et al., 2009	
Cla009226 (Cla97C06G113810)	*So*	Beta-glucosidase A; a candidate gene for *So*; having polygalactosidase activity, catalytic and hydrolytic activities; may determine the accumulation of fruit organic acids; found in the cross PI 271769 (Ph=4.52) and '203Z' (pH=5.76).	?	Gao, 2018	
Cla009218 (Cla97C06G113740)	*So*	Polygalacturonase; a candidate gene for *So*; having polygalactosidase activity, catalytic and hydrolytic activities; may determine the accumulation of fruit organic acids; found in the cross PI 271769 (Ph=4.52) and '203Z' (pH=5.76).	?	Gao, 2018	
ClFT (Cla97C03G060990)		Flowering locus T-like 2; a candidate gene for flowering time; a flowering hormone that can be transported over long distance; found in the cross 'Klondike Black Seeded' (later) and 'New Hampshire Midget' (earlier).	?	Gimode et al., 2019	
ClPP2C (Cla97C03G061230)		Phosphatase 2C family protein; a candidate gene for flowering time; a distinct family of Ser/Thr protein phosphatase; found in the cross 'Klondike Black Seeded' (later) and 'New Hampshire Midget' (earlier).	?	Gimode et al., 2019	

Cla97C02G045390		Acyl-CoA Nacyltransferases (NAT) superfamily protein; a candidate gene for tomato seed trait; gene deletion may produce tomato seed; found in the cross 'B38' (medium seed) and 'B166' (tomato seed).	?	Li et al., 2021	Unknown allele with *ts* (*tomato seed*)
Cla97C02G045400		BAG family molecular chaperone regulator 1-like; a candidate gene for tomato seed trait; gene deletion may produce tomato seed; found in the cross 'B38' (medium seed) and 'B166' (tomato seed).	?	Li et al., 2021	Unknown allele with *ts* (*tomato seed*)
Cla97C05G104360		Phosphatase 2C family protein; a candidate gene for seed size; relatively higher gene expression in the three smaller-seeded materials; may negatively regulate ABA content and affect watermelon seed size; found in 197 accessions.	?	Gong et al., 2022b	
Cla97C05G104380		Chaperone protein dnaJ 15; a candidate gene for seed size; relatively higher gene expression in the three smaller-seeded materials; may negatively regulate ABA content and affect watermelon seed size; found in 197 accessions.	?	Gong et al., 2022b	
ClBG1 (Cla97C08G153160)		*beta-glucosidase 40*; to catalyze the hydrolysis of ABA-glucose ester to release free ABA; Seed size and weight were significantly reduced in functional deficiency mutant, which was attributed to decreased cell number resulting from decreased ABA levels; found in 'ZXJM' knockout mutant.	D	Wang et al., 2021	
ClAGA2 (Cla97C04G070460)		*Alkaline alpha-galactosidase*; a functional gene for Raffinose content; to control fruit Raffinose hydrolysis and sugar content in fruits; two SNPs in the promoter affect the recruitment of the transcription factor ClNF-YC2 to regulate self-expression; found in the cross '97103' (high sugar) and PI 296341-FR (nonsweet).	D	Ren et al., 2021	
ClVST1 (Cla97C02G031010)		*Vacuolar sugar transporter*; a functional gene for sucrose content; expression in fruit phloem is positively associated with accumulation of sucrose; a SNP at the coding region results in the truncation of 45 amino acids and shifts the localization to plasma membranes in sweet watermelons; found in the cross '97103' (high sugar) and PI 296341-FR (nonsweet).	D	Ren et al., 2020	
ClTST2 (Cla97C00G000440)		*Tonoplast sugar transporter*; a functional gene for sucrose content; gene expression is positively associated with tonoplast uptake and accumulation of sugars in fruit cells; found in the cross '97103' (high sugar) and PI 296341-FR (nonsweet).	D	Ren et al., 2018	

ClSWEET3 (Cla97C01G000640)		*Sugars will eventually be exported transporter 3*; a functional gene for sugar content; involved in plasma membrane sugar transport; positively correlated with sugar content; knockout line affected fruit sugar accumulation; found in the cross '97103' (high sugar) and PI 296341-FR (nonsweet).	D	Ren et al., 2021	