

# Cucurbit Genetics Cooperative

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## Report 45

Special Edition: Melon Gene List



# Cucurbit Genetics Cooperative Report

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**On the front cover:**

Watercolor of a melon with a slice taken out of it, attributed to Jacques Le Moyne de Morgues, French school, ca. 1575. Used with permission from the Victoria and Albert Museum, London.

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# 2022 Gene List for Melon

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## Introduction

Melon (*Cucumis melo* L.) is an economically important, cross-pollinated species. Melon has  $2n=2x=24$  chromosomes and a relatively small genome (454 Mb), a high intraspecific genetic variation and morphologic diversity (Pitrat, 2016a). A great variety of genetic and molecular studies have been conducted on important agronomic traits, such as resistance to pathogens and insects, and floral and fruit traits. Comprehensive genomic resources have emerged in recent years.

This is the latest version of the gene list for melon. Previous gene lists were organized by Dogimont (2011), Pitrat (Pitrat, 2006), (Pitrat, 2002), (Pitrat, 1998), (Pitrat, 1994), (Pitrat, 1990), (Pitrat, 1986), (Committee, 1982). This current list has been modified from previous lists in that (1) it provides an update of the known genes and QTL, (2) it updates the description for reported genes including sources of resistance and resistance genes, phenotypes of mutants and traits related to seeds, seedlings, plant morphology and architecture, flowers, fruits and some abiotic stress tolerance genes and (3) it reports transgenic melon plants (Table 1, 2 and 3). Locations of the reported genes on the melon genetic map and linked markers useful for marker-assisted selection were reported where available. Genetic and genomic basis of melon agronomic traits has been well-studied over the past few years. There is so much research done on melon genetics, we hope we didn't miss to add some important genes to this list. Please inform us of omissions or errors in the gene list.

The first molecular marker-based melon map was published in 1996 (Baudracco-Arnas and Pitrat, 1996). In 2011, an integrated map was constructed in the framework of the International Cucurbit Genomic Initiative, by merging data from eight independent mapping populations using genetically diverse parental lines (Díaz et al., 2011). It spanned 1150 cM distributed across the 12 melon linkage groups and comprised more than 1500 markers. The linkage groups were named according to Perin et al. (2002a) and the same nomenclature will be adopted hereafter.

In 2012, the first complete melon genome sequence was published (Garcia-Mas et al., 2012). The sequenced genotype was the doubled haploid line DHL92, which derives from a cross between an *inodorus* type of melon (Piel de Sapo) and an accession corresponding to *C. melo* ssp. *agrestis* var. *chinensis*

(PI 161375). Updated versions have been published (Ruggieri et al., 2018) and a high-quality genome was recently assembled using new sequencing technologies (v3.6.1) (Castanera et al., 2020). Data are available in the International Cucurbit Genomics Initiative website ([www.icugi.org](http://www.icugi.org)). Other melon genotypes belonging to various horticultural groups have been sequenced using long-read technologies of sequencing, Harukei-3, a Japanese variety of the *C. melo* Horticultural Group Reticulatus, Payzawat in Group Inodorus, and a *C. melo* ssp. *agrestis* accession (Zhang et al., 2019; Yano et al., 2020; Yang et al., 2020a). Recently, a chromosome scale *C. melo* Group Cantalupensis sub-group Charentais mono genome was assembled using a combination of latest technologies [single-molecule sequencing, 10x Genomics link-reads, high-density optical and genetic maps, and chromosome conformation capture (Hi-C)]. By integrating RNA-seq, Hi-C, and histone and DNA methylation marks, the chromatin architecture was analysed to better understand the regulation of gene expression (Pichot et al., 2022). Annotation of melon genomes identified between 23,000 and 33,000 coding genes.

The availability of these genome-wide data has revolutionised melon genetic maps, allowing the mapping of single nucleotide polymorphism (SNP) and deletion/insertion (Indels) markers on the chromosomes of the melon genome (Diaz et al., 2015). The resequencing of 1,175 accessions, representing the global diversity of the species, has provided new data on the evolutionary history of melon and identified three independent domestication events, two in India and one in Africa, likely leading to all melon botanical groups (Zhao et al., 2019a). A large-scale metabolomic profiling was also performed on melon accessions belonging to different botanical groups (Moing et al., 2020).

## Host Plant Resistance Genes

Considerable attention has been given to resistance genes in melons. Genes for resistance to viruses, bacteria, insects, fungi and oomycetes have been reported. Several publications have reviewed resistance genes in melon (Dogimont and Boissot, 2016; Pitrat, 2016b; Thakur et al., 2019; Martin-Hernandez and Pico, 2021).

## Resistance to Viral Diseases

Melon resistance has been reported to viruses transmitted by aphids, whiteflies and by other mode of transmission.

Sources of resistance to cucumber mosaic virus (CMV, Cucumovirus) were reported in several melon genotypes. Several cultivars originating from Asia and belonging to Oriental pickling melon (var. *conomon*) and to Oriental melon (var. *makuwa*) were reported to be highly resistant to this virus (Enzie, 1943; Webb and Bohn, 1962; Risser et al., 1977; Hirai and Amemiya, 1989; Daryono et al., 2003; Diaz et al., 2003). Interestingly, some accessions from Iran (Arzani and Ahoonmanesh, 2000) as well as the Indian IC274014 (Dhillon et al., 2007) and the Turkish Kav 281 (Solmaz et al., 2016) were also found resistant to CMV. CMV resistance was first reported to be controlled by three recessive genes in the cross Freeman Cucumber x Noy Amid (Karchi et al., 1975). Resistance to the CMV-B2 strain in the accession Yamatouri was reported to be controlled in a single dominant manner. SCAR markers linked to the gene, named *Creb-2*, were identified (Daryono et al., 2010). Seven QTL were shown to be involved in resistance to three different strains of CMV in the cross Védrantais x PI 161375 (Dogimont et al., 2000); one of them, located in linkage group XII (cmvqw12.1) explains a large part of the resistance to the strain P9 and two minor QTL in LG III (cmvqw3.1) and LG X (cmvqw10.1) for resistance to strains M6 and TL (Dogimont et al., 2000; Essafi et al., 2009; Guiu-Aragones et al., 2014). A mutation in the melon Vacuolar Protein Sorting 41 was shown to encode the gene *cmv1* and prevent systemic infection of CMV in PI 161375 (Giner et al., 2017; Pascual et al., 2019).

Among about 500 accessions tested, resistance to cucurbit aphid borne yellows virus (CABYV, Polerovirus, transmitted by aphids on a persistent manner) was identified in the Indian accessions 90625 (= PI 313970), Faizabadi Phoont, PI 124112, PI 282448, and PI 414723, in the Korean accession PI 255478 and in PI 124440 from South Africa (Dogimont et al., 1996). The Indian PI 164323 was also found to exhibit a complete resistance, whereas the Sudanese genotype HSD 2458 was found to be tolerant with very mild mottle (Pitrat et al., 2012). Complete resistance to CABYV in PI 124112 was shown to be conferred by two independent complementary recessive genes, named *cab-1* and *cab-2* (Dogimont et al., 1997). The genetic control of partial resistance to CABYV in TGR-1551 was studied in a population obtained from the cross between TGR-1551 and the susceptible Spanish 'Bola de Oro'. Segregation was consistent with one dominant gene and at least two modifier genes that confer the resistance (Kassem et al., 2015).

Papaya ringspot virus-watermelon type (PRSV, formerly called WMV-1, Potyvirus) resistance was reported in the

Indian accessions PI 180280 (Webb and Bohn, 1962; Webb, 1979), PI 180283 (Quiot et al., 1971), PI 414723 (Anagnostou and Kyle, 1996), and PI 124112 (McCreight and Fashing-Burdette, 1996) and in TGR-1551 (C-105) from Zimbabwe (Gómez-Guillamón et al., 1998). Resistance to PRSV-W is conferred by a single dominant gene, *Prv*, in PI 180280 (Webb, 1979) as well as in the lines B66-5 and WMR 29, derived from PI 180280. An allele at the same locus was shown to incite a lethal necrotic response against French strains of PRSV-W in PI 180283 and in 72025, derived from PI 180283 (Pitrat and Lecoq, 1983). These alleles were called *Prv<sup>1</sup>* and *Prv<sup>2</sup>*, *Prv<sup>1</sup>* being dominant over *Prv<sup>2</sup>* (Pitrat, 1986). *Prv* has been mapped to the linkage group IX (former 5) (Pitrat, 1991; Perin et al., 2002a), closely linked to the gene *Fom-1* conferring resistance to *Fusarium oxysporum* races 0 and 2 (Pitrat, 1991; Perin et al., 2002a; Brotman et al., 2005). Both genes were isolated using a positioning cloning strategy. They encode a pair of head-to-head-oriented TIR-NLR proteins. The *Prv*-encoded protein has an unusual structure with an additional NB domain (Brotman et al., 2013). A single dominant gene, *Prv-2*, was also reported to control an incompatible reaction of PI 124112 after inoculation with PRSV (McCreight and Fashing-Burdette, 1996).

Partial resistance to watermelon mosaic virus (WMV, formerly WMV-2, Potyvirus) has been reported in melon line 91213, which was selected from PI 371795 and related to PI 414723 (Moyer et al., 1985; Gray et al., 1988; Moyer, 1989), in the Korean accession PI 161375 (Pitrat, 1978), in the accessions from Iran (Latifah-1, Tashkandi and Khorasgani) and in an exotic line (Galicum) (Arzani and Ahoonmanesh, 2000). Partial resistance was reported in breeding lines obtained by successive backcrossing with selection from PI 414723; inoculated plants develop mosaic symptoms on inoculated leaves but recover from symptoms and virus infection in the youngest leaves. This partial resistance was reported to be controlled by a single dominant gene, *Wmr*, linked to the ZYMV resistance gene, *Zym* (Gilbert et al., 1994; Anagnostou et al., 2000). PI 414723 was observed to be highly susceptible to WMV after inoculation with European strains of WMV (Gómez-Guillamón et al., 1998). The accession TGR-1551 (PI 482420) was reported to exhibit very mild symptoms and a very reduced titer of virus; this partial resistance was essentially determined by a recessive gene (Diaz-Pendon et al., 2005). The recessive gene, named *wmv (1551)* was fine-mapped to a region in chromosome 11 using a population of recombinant inbred lines, derived from a cross between TGR-1551 and 'Bola de Oro'. Moreover, three minor QTL in chromosomes 4, 5, and 6 were identified (Perez-de-Castro et al., 2019). The *CmVPS4* gene was recently demonstrated to be responsible for the recessive resistance

QTL in chromosome 11 in TGR-1551. It encodes a protein involved in the formation of membrane vesicles, which is part of the ESCRT complex (Endosomal sorting complexes required for transport) (Agaoua et al., 2021; Agaoua et al., 2022).

The first source for resistance to zucchini yellow mosaic virus (ZYMV, Potyvirus), and for a long time the only known source, was the Indian accession PI 414723 (Pitrat et al., 1996). Resistance in PI 414723 has been described as isolate-dependent (Lecoq et al., 2002). The resistance proved to be strain-specific and was not effective against a second pathotype of the virus. The screening of about 60 cultivars from Iran allowed the identification of three immune cultivars: Magolalena Vertbrod, Soski and Bahramabadi (Arzani and Ahoonmanesh, 2000). Among 200 melons collected in Sudan, resistance sources to ZYMV were found, mainly in wild forms (Mohamed, 1999). Other resistance sources to ZYMV, such as IC 274014 and IC 274007 (Dhillon et al., 2007) or IC 274006 (Sanchis, 2018), have been reported within germplasm from India.

Resistance to ZYMV in PI 414723 was reported to be controlled by a single dominant gene, *Zym* (Pitrat and Lecoq, 1984), which mapped to the linkage group II (former LG 4), linked to the gene *a* (*andromonoecious*) (Pitrat, 1991; Perin et al., 2002a). Using the ZYMV-Nat strain (pathotype 1), Danin-Poleg et al. (1997) found that three genes were needed to confer the resistance in PI 414723 (*Zym-1*, *Zym-2* and *Zym3*). Molecular markers linked to the resistance were identified by bulk segregant analysis (Danin-Poleg et al., 2000; Danin-Poleg et al., 2002). Recently, the *Zym* gene was fine-mapped in chromosome 2 in a region comprising R-gene homologs encoding CC-NLR proteins (Adler-Berke et al., 2021).

A semi-dominant gene named *Fn*, independent of *Zym*, was reported to control in 'Doublon' plant wilting and necrosis after inoculation with strains of the F pathotype of ZYMV (Risser et al., 1981). The *Fn* gene was located in the linkage group V (formerly 2), at 12 cM of the *Vat* gene, conferring *A. gossypii* resistance (Pitrat, 1991). Necrosis after inoculation with watermelon mosaic virus-Morocco (Potyvirus) was reported to be controlled by a single dominant gene *Nm* in 'Védrantais' (*nm* in Ouzbèque) (Quiot-Douine et al., 1988).

Partial resistance to the beet pseudo yellows virus (BPYV, Crinivirus), transmitted by the whitefly *Trialeurodes vaporariorum*, was reported in a few accessions of Asian origin: Nagata Kim Makuwa, PI 161375, Cma, a wild melon collected in Northern Korea and a Spanish landrace Tendral type (Esteva et al., 1989; Nuez et al., 1991). The resistance of Cma, expressed as a delayed and milder infection, resulted from the cumulative effect of an antixenosis against the vector and resistance to the virus (Soria et al., 1996; Nuez et al., 1999). Study of segregating families under natural infection

suggested that the partial resistance to BPYV in Nagata Kim Makuwa, PI 161375 and Cma was controlled by single genes, partially dominant in Nagata Kim Makuwa (gene *My*) and Cma, and partially recessive in PI 161375 (Esteva and Nuez, 1992; Nuez et al., 1999).

Resistance to cucurbit chlorotic yellows virus (CCYV, Crinivirus) was reported in the accession JP 138332, a snap melon (*Momordica* group) originating from India (Okuda et al., 2013). A single recessive QTL was located on chromosome 1 (near the SSR marker ECM230) using F2 populations obtained from the cross of two susceptible cultivars ('Harukei No. 3' and 'AnMP-5') with JP 138332, evaluated for symptoms after inoculation in a greenhouse with the use of CCYV-infected *Bemisia tabaci* (Kawazu et al., 2018).

Melon breeding line MR-1 and PI 124112, PI 179901, PI 234607, PI 313970 and PI 414723 were reported to exhibit a partial resistance to cucurbit leaf crumple virus (CuLCrV), a geminivirus transmitted by *B. tabaci* biotype B, while PI 236355 was found to be completely resistant. A single recessive gene, named *culcrv*, was reported to control resistance in PI 313970, and likely in the other resistant accessions (McCreight et al., 2008).

Resistance to cucurbit yellow stunting disorder virus (CYSDV, Crinivirus) was first reported in the accessions TGR-1551 (C-105, PI 482420) and TGR-1937 (PI 482431) (Lopez-Sese and Gomez-Guillamon, 2000). Delayed and only slight symptoms were reported in a few accessions under natural infection conditions in the United Arab Emirates (Jupiter, Muskotaly, PI 403994) and in Spain (Hassan et al., 1991; Lopez-Sese and Gomez-Guillamon, 2000). Resistance to the California and Arizona CYSDV strain was identified in several accessions of Indian origin, most notably PI 313970 (McCreight and Wintermantel, 2008). The resistance in TGR-1551 was initially reported to be controlled by a single dominant gene, called *Cys* (Lopez-Sese and Gomez-Guillamon, 2000), but re-evaluations have shown that the F1 obtained from the cross of TGR-1551 with several susceptible cultivars showed delayed symptoms and intermediate or similar virus accumulation to the susceptible parent, which is consistent with a recessive inheritance (McCreight et al., 2017). Resistance in PI 313970 was also reported as monogenic recessive (McCreight and Wintermantel, 2011) and likely allelic to the resistance in TGR-1551 (McCreight et al., 2019). Using recombinant inbred lines obtained from the cross between TGR-1551 and 'Bola de Oro' and derived advanced backcrosses, two QTL based on disease reaction phenotype and virus titer were identified in a 700 kb interval in chromosome 5, which overlaps the cluster of NLR genes comprising the *Vat* gene (Perez-de-Castro et al., 2020). Two QTL were identified in field conditions in a cross of the

susceptible 'Top Mark' with PI 313970, a major one on chromosome 5 and a second one on chromosome 3 (Tamang et al., 2021).

A large number of melon accessions were tested for lettuce infectious yellows virus (LIYV, Crinivirus) resistance in natural infection by *B. tabaci* biotype A in California. A snake melon originating from Saudi Arabia was shown to exhibit very mild LIYV symptoms (McCreight, 1991; McCreight, 1992). After successive field tests and confirmation in controlled-inoculation greenhouse tests, the Indian accession PI 313970 was shown to be the most interesting source of resistance to LIYV, although an occasional plant of this accession may appear symptomatic, or have a positive ELISA for LIYV (McCreight, 1998, 2000). Resistance to LIYV in PI 313970 was shown controlled by a single dominant allele at the locus designated *Liy* (McCreight, 2000).

A complete resistance to tomato leaf curl New Delhi virus (ToLCNDV, Begomovirus) was identified in at least five melon accessions in Indian *momordica* and in wild *agrestis* accessions (Lopez et al., 2015). Three genomic regions were found to control ToLCNDV in the highly resistant wild Indian accession WM 7, one major locus in chromosome 11 and two additional regions in chromosomes 12 and 2 (Saez et al., 2017). Candidate genes for ToLCNDV resistance have been recently proposed by comparing transcriptomes of the resistant WM 7 and the susceptible 'Pinonet Piel de Sapo' in ToLCNDV and mock inoculated plants (Saez et al., 2022). Segregation data from a cross between the susceptible 'Védrantais' and the resistant Indian accession IC-274014 were compatible with one recessive gene and two independent dominant genes, simultaneously required to control ToLCNDV resistance. Genes were named *begomovirus resistance 1 (bgm-1)*, *Bgm-2*, and *Tomato leaf curl New Delhi virus resistance (Tolcndv)*, the first two being involved in resistance to another begomovirus, melon chlorotic mosaic virus (MeCMV). Resistance to MeCMV in IC-274014 was found to be controlled by three genes, *bgm-1* and *Bgm-2* and the recessive *melon chlorotic mosaic virus resistance (mecmv)* (Romay et al., 2019).

Gonzalez-Garza et al. (1979) reported three phenotypes when they inoculated various melon cultivars with melon necrotic spot virus (MNSV, Carmovirus): - cultivars susceptible to systemic infection showing local lesions on the inoculated leaves followed by systemic necrotic spotting, necrotic streaks on stems, conducting finally infected plants to collapse; - cultivars showing local lesions but no systemic symptoms: 53% of the accessions tested; - immune lines remaining free of symptoms ('Improved Gulfstream', 'Perlita', 'Planters Jumbo', 'PMR 5', WMR 29 and PMR Honeydew). Among a broad germplasm collection of melons inoculated

with MNSV (532 accessions), Pitrat et al. (1996) found 7% immune accessions. The resistance was confirmed to be quite common in American cantaloupe cultivars and was also found in accessions originating from Far East and India. One recessive gene, *nsv*, controls the resistance to MNSV (Coudriet et al., 1981). First described in the American cultivar Gulfstream, the same gene was shown to be present in other American germplasm ('PMR 5', 'Planters Jumbo', VA 435) and the Asian accession PI 161375 (Coudriet et al., 1981; Pitrat, 1991). *nsv* was mapped on the linkage group XII (formerly 7) (Pitrat, 1991; Baudracco-Arnas and Pitrat, 1996; Perin et al., 2002a). The fine mapping and the cloning of the gene revealed that the resistance corresponds to a single nucleotide substitution in the translation initiation factor eIF4E (Morales et al., 2002; Morales et al., 2005; Nieto et al., 2006). The same substitution was found in all the MNSV-resistant accessions, suggesting that the resistance has a unique origin (Nieto et al., 2007). Two independent dominant genes, named *Mnr-1* and *Mnr-2*, were reported to control resistance to systemic infection of MNSV in 'Doublon'; *Mnr-1* is linked to *nsv* at 19 cM (Mallor et al., 2003).

No complete sources of resistance to squash mosaic virus (SqMV, Comovirus) have been reported in melons. Tolerance was, however, observed in accessions originating from India, Afghanistan, China and Pakistan (Webb and Bohn, 1962; Provvidenti, 1989, 1993). The Korean and Chinese accessions PI 161375 and China 51 (Group Makuwa) were described to develop delayed mosaic symptoms, reduced virus multiplication, and, interestingly, complete resistance to seed transmission of SqMV (Maestro-Tejada, 1992; Provvidenti, 1998). Resistance to seed transmission was shown to be effective against four different strains of SqMV (Provvidenti, 1998). Tolerance to foliar symptoms incited by a melon strain of SqMV was shown to be controlled by a single recessive gene in China 51, but appeared to be partially dominant against a squash pathotype of SqMV (Provvidenti, 1998). Unnamed so far, we propose to name the gene *sqmv*.

Partial resistance (restriction to the virus movement) to the SH isolate of cucumber green mottle mosaic virus (CGMMV, Tobamovirus) was reported in the *makuwa* type Chang Bougi accession (Sugiyama et al., 2006). The segregation ratios in F2 and backcross progeny indicated that the resistance to CGMMV is dependent on two independent complementary, recessive genes, called *cgmmv-1* and *cgmmv-2* (Sugiyama et al., 2007). Recently, the *conomon* melon type from Japan, Freeman's Cucumber, was identified as a potential source for resistance, showing few or no symptoms following inoculation with either a European or an Asian isolate of CGMMV. Two Spanish cultivars, Rochet and Alficos, showed a

milder response to the European and Asian isolates of CGMMV, respectively (Ruiz et al., 2021).

Resistance to a complex of viruses from Egypt in PI 378062 was reported to be controlled by a single dominant gene, named *Imy*, *Interveinal mottling and yellowing resistance* (Hassan et al., 1998).

### ***Insect Resistance***

Insect resistance in melon was reviewed in Dogimont and Boissot (2016). Resistance to the melon-cotton aphid, *Aphis gossypii* (Homoptera: Aphididae), was first reported by Kishaba et al. (1971). A dominant gene, *Ag*, was reported to control antixenosis, antibiosis under controlled no-choice tests and free-curling tolerance in LJ 90634, later called PI 414723 (Kishaba et al., 1971, 1976). Pitrat and Lecoq (1980) reported resistance in PI 161375 and in PI 414723 to several viruses when they are transmitted by *A. gossypii*. The resistance is vector-specific (only *A. gossypii*), and non-specific to viruses (CMV, ZYMV, WMV...). It co-segregates with antixenosis described previously. Resistance to viruses when they are transmitted by *A. gossypii*, is controlled by a single gene, named *Vat* (*Virus aphid transmission*). The *Vat* locus was mapped to a subtelomeric position on the linkage group V (formerly 2) (Pitrat, 1991; Baudracco-Arnas and Pitrat, 1996; Brotman et al., 2002; Perin et al., 2002a). Four additive and two couples of epistatic QTL affecting behaviour and biotic potential of *A. gossypii* were mapped in recombinant inbred lines derived from the cross Védraçais x PI 161375; among them, a major QTL, which affects both behavior and biotic potential of *A. gossypii*, corresponds to the *Vat* gene (Boissot et al., 2010). Using a map-based cloning strategy and functional validation by stable transformation in melon, a single gene, which confers both aphid resistance and virus resistance when they are transmitted by *A. gossypii*, was shown to encode a CC-NLR protein (Dogimont et al., 2014). More than 25 accessions, mostly from Asia, exhibit the double phenotype (Boissot et al., 2016).

A single dominant gene, named *Lt*, was reported to control resistance to the leafminer *Liriomyza trifolii* (Diptera: Agromyzidae) in the old French cultivar Nantais Oblong (Dogimont et al., 1999). Resistant plants exhibit fewer mines and a very high larval mortality. The resistance is inefficient towards *L. huidobrensis*. Four new sources of resistance to *L. sativae* were collected and selected in the Northeast region of Brazil, CNPH 11-1072 and CNPH 11-1077, because they exhibited lower levels of infestation by the insect (antixenosis) and CNPH 00-915(R) and BAGMEL 56-R, characterized by the death of larvae soon after leafminers begin feeding on leaves. A single dominant gene named *Ls* was found to control

resistance to *L. sativae* in BAGMEL 56-R (Celin et al., 2017 a and b).

Two complementary recessive genes (*dc-1* and *dc-2*) for resistance to the melon fruit fly, *Bactrocera cucurbitae* (formerly *Dacus cucurbitae*, Diptera: Tephritidae) have been reported by Sambandam and Chelliah (1972). New sources of resistance have been identified under field conditions in India; the Indian varieties 'AHMM/BR-1', 'RM-50' and 'AHMM/BR-8' and the accessions IC-430190, DKS-AHS 2011/4 and DKS-AHS 2011/3 were the most resistant (Haldhar et al., 2013; Haldhar et al., 2018).

A monogenic recessive resistance to cucumber beetles was reported in C922-174-B in crosses among non-bitter genotypes. The gene named *cb<sub>1</sub>* (=cb) was shown to be efficient towards three species of Coleoptera: the banded beetle *Diabrotica balteata*, the spotted beetle *D. undecimpunctata howardi* and the striped beetle *Acalymna vittatum* (Nugent et al., 1984). In 'AR Top Mark', resistance to *D. undecimpunctata howardi* was also reported to be recessive and linked to the bitterness trait, controlled by the dominant gene *Bi* (Lee and Janick, 1978) that makes the melon attractive to the spotted beetle (Nugent et al., 1984).

A dominant gene, named *Af*, was reported to control resistance to the red pumpkin beetle (*Aulacophora foveicollis*, Coleoptera: Chrysomelidae) in Casaba (Vashistha and Choudhury, 1974).

Resistance to *Meloidogyne incognita* was identified in the melon cultivar Gaucho Redondo (Ito et al., 2014). Resistance is controlled by more than one locus, as confirmed by the quantitative analysis that revealed the presence of six genes (Candido et al., 2017).

### ***Resistance to Fungal Diseases***

**Fusarium wilt resistance.** Three genes were reported to control resistance to *Fusarium oxysporum* f.sp. *melonis*. A single dominant gene, *Fom-1*, controls resistance to *F. oxysporum* races 0 and 2; it was reported in the old French cultivar Doublon (Risser, 1973; Risser et al., 1976). *Fom-1* was mapped at a distal end of the linkage group IX (formerly 5), closely linked to the PRSV resistance gene, *Prv<sup>2</sup>* (Perin et al., 2002a). Molecular markers for *Fom-1*, useful for marker assisted selection, were developed (Brotman et al., 2005; Oumouloud et al., 2008; Tezuka et al., 2009 and 2011). The *Fom-1* gene was isolated by positioning cloning. As previously mentioned, it encodes a TIR-NLR protein, which may share the promoter region with the *Prv* gene (Brotman et al., 2013). A single dominant gene, *Fom-2*, controls resistance to *F. oxysporum* races 0 and 1; it was reported in CM17187 (Risser, 1973; Risser et al., 1976). *Fom-2* was mapped to the linkage group XI (Perin et al., 2002a). The gene *Fom-2* was cloned and

reported to encode a NLR protein of the CC-NLR subfamily (Joobeur et al., 2004). Molecular markers linked to *Fom-2* were developed (Zheng et al., 1999; Zheng and Wolff, 2000), but their use was not completely satisfying because of recombination (Sensoy et al., 2007). Molecular markers were designed within the gene (Wang et al., 2011a). Resistance to *F. oxysporum* races 0, 1 and 2 is quite frequent (Alvarez et al., 2005). The *Fom-3* gene was reported in Perlita FR; it confers the same phenotype as *Fom-1* but segregates independently from *Fom-1* (Zink and Gubler, 1985). Resistance to *F. oxysporum* races 0 and 2 in the Spanish Group Cantalupensis accession Tortuga was reported to be controlled by two independent genes, one dominant and the other one recessive. The dominant likely is *Fom-1*; the recessive one was named *fom-4* (Oumouloud et al., 2010). A single dominant gene was reported to govern fusarium wilt resistance in a cross between Punjab Sunheri and the resistant KP4HM-15 introgressed from snapmelon. The gene was named *Fom-5<sup>(v)</sup>* (Deol et al., 2022). A major recessive gene, named *fom1.2a*, was reported to confer resistance to *F. oxysporum* race 1.2 in the Israeli breeding line BIZ. The gene was located at a distal end of the LG II (opposite to the gene *a*, *andromonoecious*) (Herman et al., 2008). A second recessive gene was previously reported to segregate in the same population (Herman and Perl-Treves, 2007). In contrast, nine QTL were reported to control the recessive resistance to race 1.2 in the French cultivar Isabelle, derived from the Far East resistant accession Ogon 9 (Perchepped and Pitrat, 2004; Perchepped et al., 2005a). The resistance of the Group Cantalupensis accession BG-5384 from Portugal to *F. oxysporum* race 1.2 (Y pathotype) was also reported to be polygenic and recessive (Chikh-Rouhou et al., 2008; Chikh-Rouhou et al., 2010). Two accessions with a high level of resistance to *F. oxysporum* race 1.2 were recently identified in Tunisian germplasm (Chikh-Rouhou et al., 2021).

Resistance to a relatively new melon pathogen, *Fusarium oxysporum* f.sp. *radicis-cucumerinum* (Forc), which kills the plants prematurely and leads to crown rot, was identified as the cultivar Hemed. Resistance was shown to be controlled by two genes, one dominant (*Forc-1*) and the other recessive (*forc-2*) by crossing the highly resistant Hemed and by the susceptible U.S. cultivar 'Dulce' genotypes (Elkabetz et al., 2016).

**Powdery mildew resistance.** Several dominant resistance genes to powdery mildew were reported in melon. Genetic relationship between these genes is still confused, as is the definition of powdery mildew races (McCreight, 2006; Lebeda et al., 2011). Mapping of powdery mildew resistance genes and QTL in several crosses has thus far located them in seven distinct melon linkage groups or chromosomes. Jagger et al. (1938) reported a dominant resistance gene, *Pm-1*, to

powdery mildew in 'PMR 45'. In the original paper, *Pm-1* was reported to confer resistance to *Erysiphe cichoracearum* but the pathogen was misidentified and was later determined to have been *Podosphaera xanthii*. *Pm-1* likely corresponds to the gene *Pm-A*, which confers resistance to *P. xanthii* race 1 in 'PMR 45', described in Epinat et al. (1993). The powdery mildew resistance gene from 'PMR 45', introgressed into a yellow-fleshed breeding line, was reported to be located in the linkage group IX, loosely linked to the PRSV resistance gene, *Prv* (Teixeira et al., 2008).

A single dominant gene, *Pm-x*, confers resistance to *P. xanthii* race 1 and 2 (at least) in PI 414723; it was located in the linkage group II, linked to the ZYMV resistance gene *Zym* and to the andromonoecious gene *a* (Pitrat, 1991; Perin et al., 2002a).

A single dominant gene was reported in WMR 29, *Pm-w*, which confers resistance to *P. xanthii* races 1, 2 and 3 (Pitrat, 1991). It likely corresponds to *Pm-B* in Epinat et al. (1993). It was located in the linkage group V (formerly 2), closely linked to the *Vat* locus (Pitrat, 1991; Perin et al., 2002a).

Harwood and Markarian (1968a) reported two dominant genes in PI 124112, *Pm-4* and *Pm-5*. These genes may correspond to the two genes of PI 124112 reported in Perchepped et al. (2005b), *PmV.1* and *PmXII.1*. *PmV.1* confers resistance to *P. xanthii* races 1, 2, and 3 and was located in the linkage group V, closely linked to the *Vat* locus. *Pm-XII.1* confers resistance to *P. xanthii* races 1, 2 and 5 and to *Golovinomyces cichoracearum* race 1 and was mapped to the linkage group XII. It may correspond to one of the two genes, *Pm-F* and *Pm-G*, which were reported to interact for controlling resistance to *G. cichoracearum* in PI 124112 (Epinat et al., 1993).

Two genes were reported in 'PMR 5', *Pm-1* and *Pm-2* (Bohn and Whitaker, 1964). Allelism tests clearly showed that 'PMR 5' has the same gene as 'PMR 45' to control *P. xanthii* race 1. *Pm-2* likely corresponds to *Pm-C*, which confers resistance to *P. xanthii* race 2 in interaction with *Pm-1*. Two genes, *Pm-C* (*Pm-2*) and *Pm-E*, were suggested to interact in 'PMR 5' to control resistance to *G. cichoracearum* (Epinat et al., 1993). Later, two QTL of resistance to *P. xanthii* race 1 and N1 were located in the linkage groups II and XII in recombinant inbred lines derived from the cross PMAR No.5 x Harukei No.3 (Fukino et al., 2006; Fukino et al., 2008). These two QTL may correspond to the same genomic regions as reported in PI 124112, with different alleles. PMAR No.5 (= AR 5) was obtained from an aphid resistant line and successive backcrosses to 'PMR 5' (McCreight et al., 1984). The results obtained by (Fukino et al., 2006; Fukino et al., 2008) suggest that powdery mildew resistance genes in PMAR No.5 may be

different from those in 'PMR 5', as *Pm-1* is expected to be located in the linkage group IX (Teixeira et al., 2008).

Harwood and Markarian (1968a) reported a single dominant resistance gene in PI 124111, *Pm-3*. Kenigsbuch and Cohen (1989) reported a second gene in PI 124111, *Pm-6*, independent from *Pm-3*, which confers resistance to *P. xanthii* race 2. Their relationship with the other powdery mildew resistance genes is unknown.

Resistance to the Chinese race of *P. xanthii* (with a unique reaction pattern of the commonly used melon race differentials) in the Indian accession PI 134198 (= Ames 31282) was reported to be controlled by a single dominant gene, designated *Pm-8*, which was suggested to be located in the linkage group VII (Liu et al., 2010).

Resistance to powdery mildew in Ano2 was reported to be conferred by a dominant gene, which was named *Pm-AN* (Wang et al., 2011b).

Resistance to *P. xanthii* races 1, 2 and 5 in TGR-1551 was reported to be controlled by two independent genes, one dominant and one recessive, each one conferring resistance to all three races (Gómez-Guillamón et al., 2006; Yuste-Lisbona et al., 2008). The dominant gene, *Pm-R* was located in the linkage group V, closely linked to the *Vat* and *Pm-w* loci; the recessive gene was putatively located in the linkage group VIII, with a LOD score lower than the threshold score (Yuste-Lisbona et al., 2011a).

In the same manner, resistance to *P. xanthii* in PI 313970 and 90625 was reported to be controlled by dominant, co-dominant, and recessive genes (McCreight, 2003; McCreight and Coffey, 2007; Pitrat and Besombes, 2008). PI 313970 resistance to the race S, a new strain of *P. xanthii* from Southwestern U.S.A., virulent on all the commonly used resistance differentials, was reported to be controlled by a single recessive gene, named *pm-S*. The relationship of *pm-S* with the previously reported resistance genes in PI 313970 is unknown (McCreight and Coffey, 2011).

Resistance to *P. xanthii* race 1 in MR-1 was located in a single dominant QTL in chromosome 12 using a bulk segregant analysis sequencing (BSASeq) strategy in an F2 population derived from the cross of MR-1 x Top Mark (Li et al., 2017). A dominant gene in chromosome 12 was shown to control resistance in MR-1 leaves (named *CmPMRI*, that we propose to rename *PMRI*), whereas stem resistance was shown to be under the control of a recessive gene (named *CmPMrs* that we propose to rename *pmrs*), located in chromosome 10, with the dominant gene having an epistatic effect on the recessive gene (Cui et al., 2022a). Quantitative resistance to *P. xanthii* race 1 was mapped in a densely genotyped recombinant inbred line melon population obtained from MR-1 crossed to the susceptible Israeli melon

cultivar Ananas Yokne'am. Two major (qPx1-5 and qPx1-12) and two minor (qPx1-4 and qPx1-10) QTL were identified that encode putative R genes with missense mutations between the parents (Branham et al., 2021).

Resistance to *P. xanthii* race 1A in 'Edisto 47' was controlled by two dominant genes mapped on LG II and LG V and resistance to *P. xanthii* 1B was controlled by one dominant gene in a cross Edisto 47 x Queen (Ning et al., 2014).

Using BSASeq, a single QTL for resistance to *P. xanthii* in the resistant breeding line wm-6 was also identified in chromosome 12. A gene encoding an ankyrin repeat-containing (ANK) protein was reported to be the most likely candidate gene to confer PM resistance (Cao et al., 2021).

**Resistance to other fungi.** Several genes have been described to control resistance to gummy stem blight, caused by *Stagonosporopsis cucurbitacearum* (syn. *Didymella bryoniae*; (asexual form *Mycosphaerella citrullina*). Four independent dominant genes, *Gsb-1* through *Gsb-4*, were reported to confer a high level of resistance in PI 140471, PI 157082, PI 511890, and PI 482398 (Prasad and Norton, 1967; Frantz and Jahn, 2004). In the latter accession, a recessive gene, *gsb-5*, independent from *Gsb-1*, *Gsb-2*, *Gsb-3* and *Gsb-4* was also reported (Frantz and Jahn, 2004). A single dominant gene (previously named *Mc-2*) was reported to confer a moderate level of resistance in C-1 and C-8 (Prasad and Norton, 1967); we propose to rename it *Gsb-6*. A single recessive gene was reported to control gummy stem blight resistance in the accession PI 482399, which may be the same as *gsb-5* reported in PI 482398. The gene was mapped on chromosome 9 and markers in a candidate gene encoding a TIR-NLR protein have been proposed (Hassan et al., 2018).

A single dominant gene, *Ac*, was reported to control resistance to *Alternaria cucumerina* in the line MR-1 (Thomas et al., 1990). Two QTL were identified in a F2 population obtained from the cross of the *Alternaria*-resistant parent MR-1 and the susceptible parent 'Ananas Yokneum' (Daley et al., 2017).

A semi-dominant gene, *Mvd*, was reported to control partial resistance to melon vine decline caused by *Acremonium cucurbitacearum* and *Monosporascus cannonballus* in the wild type accession Pat 81 (Iglesias et al., 2000).

### Oomycete Resistance

Sources of resistance to downy mildew caused by the oomycete *Pseudoperonospora cubensis* were reported in several Indian accessions (Dhillon et al., 2007; Fergany et al., 2011). In recent years some Turkish accessions (Kav 28, Kav 71, Kav 237 and Kav 255) were also found resistant to downy mildew (Solmaz et al., 2016). Downy mildew resistance was

reported to be controlled by two partially dominant, complementary genes, *Pc-1* and *Pc-2*, in the Indian accession PI 124111 (Cohen et al., 1985; Thomas et al., 1988; Kenigsbuch and Cohen, 1992). This accession was reported to be resistant to the six known pathotypes of downy mildew (Cohen et al., 2003). Two complementary, dominant genes (*Pc-4* and *Pc-1* or *Pc-2*) were also reported to control resistance to downy mildew in another Indian accession PI 124112 (Kenigsbuch and Cohen, 1992). Nine QTL for resistance to *P. cubensis* were located on a melon map developed from the cross Védrantais x PI 124112. Among them, a major QTL, *Pc-XII.1*, was located in the linkage group XII, closely linked to the powdery mildew resistance QTL *Pm-XII.1*, which confers resistance to *P. xanthii* races 1, 2 and 5 and *G. cichoracearum* race 1 (Perchepey et al., 2005b). A single dominant gene of partial resistance, *Pc-3*, was reported in the Indian accession PI 414723 (Epinat and Pitrat, 1989). The gene *Pc-5* was reported to interact with the modifier gene, *M-Pc-*, to control downy mildew resistance in the line 5-4-2-1; in presence of *M-Pc-5*, the resistance conferred by the gene *Pc-5* is dominant, while in absence of *M-Pc-5*, the resistance is recessive (Angelov and Krasteva, 2000). Nine QTL for resistance to a genetically characterized clone of *P. cubensis* (clade 1, mating type A2) were mapped using a population of recombinant inbred line obtained from a cross between the resistant inbred line MR-1 and susceptible cultivar Ananas Yok'neam. Two major QTL were located on chromosome 10 and 8 (Toporek et al., 2021).

### Bacterial Disease Resistance

Sources of resistance to bacterial fruit blotch (BFB) caused by *Acidovorax citrulli* were identified in the accessions I-136 and A-43 (de Assuncao et al., 2021). High level of resistance was found in the accessions PI 353814 and PI 140471 and moderate level of resistance in PI 420145 and SCNU1154 and cultivars ME6 and ME5 (Islam et al., 2020a). BFB resistance was controlled by a single dominant gene located on chromosome 9 in a F2 population obtained from the cross of the resistant PI 353814 and the susceptible PI 614596 parental accessions (Islam et al., 2020b).

### Abiotic Stress Tolerance Genes

Global climate change brings with it some negative environmental conditions (low and high temperatures, salinity, floods, etc.) that can encourage a significant decrease in crop productivity. Some studies have begun to be conducted at the gene level on impacts of abiotic stresses in melon plants but the inheritance of response to stress is still largely unknown in melon.

Genes that are upregulated in melon roots subjected to high salt stress were identified using salt-sensitive and salt-tolerant melon cultivars (Wei et al., 2013; Wei et al., 2014). Among them, several genes encoding for NAC transcription factor proteins were shown to be deregulated in melon seedling roots by salt stress. The expression of *CmNAC14* continually increased in 12 h under salt stress and its overexpression increased the sensitivity of *Arabidopsis* transgenic lines to salt stress (Wei et al., 2016). In the same manner, the overexpression of *CmRAV1* (related to ABI3/VP1) in transgenic *Arabidopsis* plants resulted in enhanced salt tolerance at the seed germination and seedling growth stages (Zhao et al., 2019b). The *CmUBC* gene that encodes the melon Ubiquitin-Conjugating Enzyme was upregulated during drought and salinity stresses (Baloglu and Patir, 2014). Genes of the lignin pathway (*CmCAD* encoding Cinnamyl alcohol dehydrogenase) were shown to be deregulated in stems and roots under salt and wound treatment (Liu et al., 2018). Expression of genes of the Glutathione S-Transferase pathway (*CmGST*) was studied under cold stress in Hami melon (Song et al., 2021) and miRNA expression level was investigated in Piel de Sapo melon exposed to six biotic and abiotic stress treatments (cold, salinity, short day, and infection with a fungus). Twenty-two miRNA families responding to double and/or triple stresses were identified, which could not be easily predicted from the study of individual stresses (Villalba-Bermell et al., 2021).

### Seed and Seedling Genes

Three genes were reported to control seed coat color: the *r* gene (*red stem*) controls brown seed color and a red stem in PI 157083 (30569) (Bohn, 1968; McCreight and Bohn, 1979). The gene *Wt* (*White testa*) controls white seed testa color and is dominant to yellow or tan seed coat color (Hagiwara and Kamimura, 1936). A *White testa* gene (*Wt-2*) was also reported in PI 414723, dominant to yellow seed testa color and mapped to the linkage group IV (Périn et al., 1999). Recently, yellow seed color was finely mapped on chromosome 6 in a cross of IC2508 with a yellow seed coat and IC2518 with a brown seed coat. A candidate gene (*MEL03C019554*) was identified, which encodes a homeobox protein (PHD transcription factor) related to the flavonoid pathway (Hu et al., 2022).

The pine-seed shape of the seeds of PI 161375 is controlled by a single recessive gene, *pin*, *pine-seed shape*, which was mapped to the linkage group III (Perin et al., 2002a). This trait is common in melons in the Pinonet Spanish type. The presence of a gelatinous sheath around the seeds (versus absence) was reported to be controlled by a single dominant gene *Gs*, *Gelatinous sheath* (Ganesan, 1988).

Many QTL for seed size were identified and reviewed in Guo et al. (2020). A candidate gene for a major effect of QTL for seed length and width on chromosome 3 was identified using a cross between the small seeded PI 161375 and the large seed Kalakesai (Zhang et al., 2022).

Several chlorophyll deficient mutants were reported in melon. A single recessive gene, *alb*, (*albino*) controls the white cotyledon, lethal mutant in Trystorp (Besombes et al., 1999). The dominant pale cotyledons mutant *Pa*, *Pale*, is a lethal mutation as *PaPa* are albinos and die early, while *PaPa+* have yellow cotyledons and leaves (McCreight and Bohn, 1979); *Pa* was shown to be linked to the *gl* (*glabrous*) and *r* (*red stem*) mutant genes (Pitrat, 1991). A single recessive gene, *yg* (*yellow green*), controls light green cotyledons and leaves in the line 26231 (Whitaker, 1952); it was located in the linkage group XI (former 6) (Pitrat, 1991). An allele of *yg*, first described as *lg* (*light green*) in the cross Dulce x TAM-Uvalde, was renamed *yg<sup>w</sup>* (*yellow green Weslaco*) (Cox, 1985; Cox and Harding, 1986). A single recessive gene, *f* (*flava*), controls bronze yellow cotyledons and leaves and a reduced plant growth in the Chinese accession K2005 (Pitrat et al., 1986); it was reported to be closely linked to the *lmi* (*long main stem internode*) gene (Pitrat, 1991). A recessive mutant with a yellow ring on the cotyledons that later disappears, leaving the plants a normal green, was named *h* (*halo*) (Nugent and Hoffman, 1974); it was shown to be linked to the genes *a* (*andromonoecious*), *Pm-x* (*Powdery mildew resistance x*) and *Zym* (*Zucchini yellow mosaic virus resistance*) and was then located in the linkage group II (former 4) (Pitrat, 1991; Perin et al., 2002a). Three recessive *virescent* genes *v*, *v-2* and *v-3* control pale cream cotyledons and hypocotyls, which turn green later; the younger leaves are light green while the older ones are normal green (Hoffman and Nugent, 1973; Dyutin, 1979; Pitrat et al., 1995); the *v-3* gene was shown to be independent to *v* (Pitrat et al., 1995). Two yellow *virescent* recessive mutant genes, *yv* (*yellow virescent*) and *yv-2*, were reported (allelism unknown); they control pale cotyledons, yellow green young leaves and tendrils and green older leaves, associated with a severely reduced plant growth (Zink, 1977; Pitrat et al., 1991).

The incapacity of a mutant to efficiently absorb Fe (iron) and Mn (manganese) was reported to be controlled by a recessive gene, *fe*; the mutant chlorotic leaves with green veins turn to green when iron is added to the nutrient solution (Nugent and Bhella, 1988; Jolley et al., 1991). Recently, the *fe* gene of the C940-*fe* mutant was mapped on chromosome 8. The fine mapping led to the identification of the candidate gene *bHLH38*, a homolog of subgroup *lb* *bHLH* genes from *Arabidopsis thaliana* that are involved in transcriptional regulation of Fe. Hairy root transformation of mutant *fefe* plants using wild-type *bHLH38* resulted in functional

complementation of the chlorotic *fefe* phenotype. The insertion of a retrotransposon of 5 kb within *bHLH38* is responsible for the defect in *bHLH38* in *fefe* (Ramamurthy and Waters, 2017).

A single recessive gene, *ech* (*exaggerated curvature of the hook*), was shown to control the triple response of seedling germination in the dark in the presence of ethylene. Seedlings exhibit a very strong, 360° hook curvature of hypocotyls in PI 161375 (*ech*), while they exhibit a moderate, 180° curvature in 'Védrantais' and PI 414723 (*Ech*). The *ech* gene was mapped to the linkage group I (Perin et al., 2002a).

Seedling bitterness due to the presence of cucurbitacins, common in honeydew or Charentais type, was shown to be dominant over non-bitter, found in most American cantaloupes, and controlled by a single gene *Bi* (*Bitter*) (Lee and Janick, 1978). Genetic analysis of F2 and BC1 populations derived from non-bitter (C68) and bitter (C69) parental lines identified 3 QTL for bitterness in 2 linkage groups (2 and 5) (Shang et al., 2020).

A single recessive *delayed lethal* mutant, *dlet* (formerly *dl*) was described by Zink (1990); it exhibits a reduced growth, necrotic lesions on leaves leading to premature death.

## Leaf and Foliage Genes

Several genes control leaf and foliage traits in melon. Two linked dominant genes, *Ala* (*Acute leaf apex*) and *L* (*Lobed leaves*) were reported to control leaf shape in 'Main Rock' (*Ala* and *L*) crossed with 'PV Green' (*ala* and *l*) (Ganesan and Sambandam, 1985). Highly indented leaves, instead of round, are controlled by a single recessive gene, *dl* (*dissected leaf*), in URRS 4 (Dyutin, 1967). An allele of *dl* in 'Cantaloup de Bellegarde', previously described as *cut leaf*, was named *dl<sup>v</sup>*, *dissected leaf Velich* (Velich and Fulop, 1970). A second gene *dl-2* (*dissected leaf-2*), allelism unknown, was reported as "hojas hendidas" (Esquinas Alcazar, 1975). A single dominant gene, *Sfl*, was reported to control the *subtended floral leaf* trait; the leaves bearing hermaphrodite/pistillate flowers in their axis, are sessile, small and enclosing the flowers in 'Makuwa', *Sfl*, while normal in 'Annamalai', *sfl* (Ganesan and Sambandam, 1979). Cox (1985) reported two recessive leaf mutant genes, *brittle leaf dwarf* (*bd*) and *curled leaf* (*cl*), which both affect female fertility. Spoon-shaped leaves with upward curling of the leaf margins were reported to be controlled by a single recessive gene, named *cf* (*cochleare folium*) in a spontaneous mutant in 'Galia' (Lecouviour et al., 1995). A single recessive gene, *gl* (*glabrous*), was reported to control completely hairless plants in Arizona glA (Foster, 1963). A single recessive gene, *r* (*red stem*), controls in PI 157083 (30569) a red striped hypocotyl and red stem, especially at internodes, that is photosensitive, and reddish or tan seed coat color (Bohn,

1968; McCreight and Bohn, 1979). The genes *gl* and *r* were shown to be linked in a same linkage group (LG III) comprising also *Pa* (*Pale*) and *ms-1* (*male sterile-1*) (McCreight, 1983a; Pitrat, 1991).

Recently, map-based cloning localized a recessive gene (*Cmgl* rename *gl-2*) in melon chromosome VIII in a completely glabrous muskmelon line NSL73046 and identified a single candidate gene that encodes a class IV homeodomain-associated leucine zipper transcription factor that controls multicellular trichome initiation. A single base substitution resulting in a premature termination codon and a truncated protein likely results in the glabrous phenotype (Zhu et al., 2018).

## Plant Architecture Genes

A single gene, recessive or incompletely dominant, called *slb*, *short lateral branching* (formerly *sb*) was suggested to control the short lateral branching trait in LB-1, a wild melon from Russia (Ohara et al., 2001). In 2008, Fukino et al. reported two QTL for short lateral branching in a cross between a breeding line Nou 4 derived from LB-1 and the normal branching 'Earl's Favourite' (Harukei 3). The QTL mapped to LG VII and LG XI, explained, respectively, 14.8 % (The allele of Harukei 3 contributed to shorter length branches) and 42.2% (The allele of 'Nou 4' contributed to shorter length branches).

A mutant lacking lateral branches, named *ab*, *abranchiate*, was reported; it produces only male flowers (Foster and Bond, 1967).

Five recessive genes that control short-internodes, *si-1*, *si-2*, *si-3*, *si-4* (*short internode-1, -2, -3, -4*) and *mdw1* (*mutant dwarf 1*) have been reported in five melon lines, UC Topmark Bush, Persia 202, 'Maindwarf', PNU-D1 and M406 (Denna, 1962; Paris et al., 1984; Knavel, 1990; Hwang et al., 2014; Yang et al., 2020b). *si-1* plants display a bush phenotype, with an extremely compact growing habit and very short ( $\approx 1$  cm) internode length (Denna, 1962; Zink, 1977); *si-1* is linked to the gene *yv*, *yellow virescent* (Pitrat, 1991). Internodes of *si-2* and *si-3* plants are short but less compact than *si-1* plants. In *si-2* plants, the first internodes are short, leading to a 'bird's nest' phenotype; later internodes are not modified. In *si-3* plants, internode length is reduced at all plant development stages. *mdw1* in the breeding dwarf-type mutant line PNU-D1 with shortened internodes and shorter lateral branches was mapped in chromosome 7 (Hwang et al., 2014). The semidwarf phenotype of M406 is also due to a reduced internode length and a reduced length of lateral branches at each node (Yang et al., 2020b). Yang et al. (2020b) reported the map-based cloning and functional characterization of the first recessive semidwarf gene *short internode* (*Cmsi* that we

propose to rename *si-4*) in the mutant M406. *si-4* was fine-mapped on chromosome 7 and encodes an ERECTA-like receptor kinase regulating internode elongation. Overexpression of *CmSI* in Arabidopsis and cucumber increased their plant height.

A single recessive gene, *lmi* (*long main-stem internode*), controls a long hypocotyl and a long internode length ( $\approx 20$  cm) in the main stem but does not affect internode length of lateral branches in 48764 (McCreight, 1983b). Fasciation of the main stem (reaching up to 15 cm) in the Charentais type line Vilmorin 104 was controlled by a single recessive gene, named *fas*, *fascinated* (Gabillard and Pitrat, 1988).

## Flower Genes

Sex determination in melon is controlled by two major genes, *a* and *g*. The *andromonoecious* gene *a* (Rosa, 1928; Poole and Grimball, 1939; Wall, 1967) controls the monoecious versus andromonoecious sex type in melon. The gene mapped to the linkage group II (Perin et al., 2002a; Silberstein et al., 2003). The gene was fine-mapped and cloned. It was shown to encode an ACC synthase gene, *CmACS7* and has been named gene *M* (*Monoecious*) to be consistent with the denomination in cucumber. The transition between monoecy and andromonoecy is conferred by a single substitution, which leads to an inactive form of this key enzyme in the ethylene biosynthesis (Boualem et al., 2008). Molecular markers linked to the gene (Noguera et al., 2005; Sinclair et al., 2006; Kim et al., 2010) and within the gene are available (Boualem et al., 2008).

The *gynoecious*, *g*, gene controls the transition of monoecious plants to gynoecious plants carrying only female flowers (Poole and Grimball, 1939). The gene was mapped to a distal end of the linkage group V, opposite to the *Vat* gene. Positional cloning of the gene showed that the gene *G* encodes for a transcription factor of the WIP family, *CmWIP1*. The gynoecious allele *g* corresponds to the insertion of a transposable element, which epigenetically represses the expression of *CmWIP1* (Martin et al., 2009). In addition, a gene, named *gy* (*gynomonoecious*, previously also called *n* or *M*), interacts with *a* and *g* to produce stable gynoecious plants in the gynoecious line WI 998 (Kenigsbuch and Cohen, 1987, 1990).

A third gene, *androecious*, located in the linkage group III was shown to encode another ethylene biosynthesis gene, *CmACS11* that represses the expression of the male promoting gene *CmWIP1* by recruiting histone modifiers. ACS11 loss-of-function mutants lead to androecious plants that bear only male flowers (Boualem et al., 2015).

Five single recessive genes of male-sterility including *ms-1* to *ms-5* were reported in melon (Bohn and Whitaker, 1949;

Bohn and Principe, 1964; Lozanov, 1983; McCreight and Elmstrom, 1984; Lecouviour et al., 1990) in Pitrat (1991, 2002). Each of these genes displays a unique phenotype. The five sterility genes were located in five different linkage groups (Pitrat, 1991; Park et al., 2009a). McCreight (1983a) and Pitrat (1991) reported loose linkages between red stem (*r*) and the *ms-1* gene, and between yellow green leaves (*yg*) and the *ms-2* gene, respectively. Park et al. (2009a) mapped the *ms-3* gene to the linkage group 9 of the linkage map Deltex x TGR-1551, which corresponds to the linkage group VII. The gene *ms-5* has been localized in a 30-kb candidate region on chromosome 9 comprising 6 genes and the ABORTED MICROSPORES (AMS) gene was identified as the most likely candidate (Sheng et al., 2017; Wang et al., 2021).

A *Macrocalyx* dominant gene, *Mca*, was reported to control the presence of large, leafy sepals in staminate and hermaphrodite flowers in the Japanese cultivar Makuwa (Ganesan and Sambandam, 1979). Two recessive genes were reported to modify the color of petals; *gp* (*green petals*) and *gyc* (*greenish yellow corolla*) control the presence of a green corolla with venation or the presence of a greenish yellow corolla, instead of the normal yellow corolla (Mockaitis and Kivilaan, 1965; Zink, 1986).

Rosa (1928) reported that tricarpellary ovary was monogenically inherited over pentacarpellary ovary found in Cassaba melons; the gene, named *p* (*pentamerous*) was mapped to the linkage group XII, closely linked to the major QTL for CMV resistance (Dogimont et al., 2000; Perin et al., 2002a; Essafi et al., 2009). Using a genome-wide-association analysis, the gene *CmCLAVATA3* was shown to determine the carpel number in melon, as in tomato and cucumber (Liu et al., 2020).

A single recessive gene, *n* (*nectarless*), was reported to control the absence of nectar in all flowers in the mutant 40099 (Bohn, 1961).

## Fruit Genes

### Fruit Shape

Fruit shape was reported to be controlled by a single gene *O* (*Oval shape*), dominant to round, and associated with *andromonoecious* gene *a* (Wall, 1967). As early as 1928, Rosa (1928) noted the association of elongate fruit with pistillate flowers (monoecious plants) and globular fruit with perfect flowers (*andromonoecious* plants) in segregating populations. Mapping has identified hundreds of QTL for shape that are distributed across all 12 chromosomes (Perin et al., 2002b; Monforte et al., 2004; Eduardo et al., 2007; Fernandez-Silva et al., 2010; Díaz et al., 2011; Monforte et al., 2014; Wu et al., 2018; Oren et al., 2020; Pan et al., 2020). Spherical fruit shape was also reported to be controlled by a single gene, *sp*

(*spherical fruit shape*), recessive to an obtuse fruit shape (Lumsden, 1914; Bains and Kang, 1963); this gene may be the same as the gene *O*. A major fruit shape QTL co-localized with the *andromonoecious a(M)* locus on chromosome 2; it was recently demonstrated that the same gene *CmACS7*, involved in ethylene biosynthesis pathway, controls both the monoecious sexual type and the elongated fruit shape QTL in chromosome 2 (Boualem et al., 2022).

A QTL co-localized with the *pentamerous (p)* gene on chromosome 12, with 5-carpel fruits tending to be rounder than 3-carpel fruits. The gene *CmCLV3* that determines carpel number has also been suggested to affect fruit shape in the *andromonoecious* genetic background (Boualem et al., 2008; Liu et al., 2020). A fruit shape QTL was finely mapped on chromosome 8 in two crosses. A gene encoding an OVATE family protein (OFP) was identified as the most likely candidate. A retrotransposon insertion in the promoter was shown to be responsible for elevating the gene expression and was associated with development of fruits in the flat-round shape HP22 (Martinez-Martinez et al., 2021; Ma et al., 2022).

A single dominant gene, *Ec* (*Empty cavity*), was reported to control the presence of separated carpels at fruit maturity, leaving a cavity in PI 414723 fruit (*ec* in 'Védraçais') (Périn et al., 1999). The *Ec* gene was mapped to the linkage group III (Perin et al., 2002a).

### External Fruit Appearance

Rind color of melon fruit varieties includes white, yellow, orange, or green, and can be variegated. The white color of immature fruits was reported to be dominant to green immature fruits and controlled by a single gene, *Wi*, *White color of immature fruit* (Kubicki, 1962). The white color of mature fruits was, in contrast, reported to be controlled by the gene *w*, *white*, recessive to dark green fruit skin in a cross between Honeydew (*w*) and Smiths' Perfect cantaloupe (*W*, dark green) (Hughes, 1948). Melon rind color was shown to be based on different combinations of three major pigments, chlorophyll, carotenoids and naringerin-chalcone, a flavonoid pigment responsible for the yellow color of mature fruits in Yellow Canari melon type (Tadmor et al., 2010). Accumulation of naringerin-chalcone was reported to be inherited as a monogenic dominant trait in the cross Noy Amid (yellow rind) x Tendral Verde Tardio (dark green rind); accumulation of chlorophyll and carotenoids segregates jointly as a single dominant gene, independent to naringerin-chalcone accumulation (Tadmor et al., 2010). The gene *CmKFB*, that controls the biosynthesis of flavonoids in ripe melon rind, was shown to confer the yellow external color typical of Yellow Canary melon type. It is located on chromosome 10. The gene two-component Response Regulator-like Protein *CmAPRR2*

was identified as a major regulatory gene of chlorophyll accumulation in the immature fruit rind of melon (Oren et al., 2019).

Vein tracts, formerly and incorrectly referred to as sutures, on the fruit rind were reported to be controlled by a single recessive gene *s*, *sutures* (Bains and Kang, 1963; Davis, 1970). The same inheritance was found in two crosses: Védraçais (*s-2*, presence of sutures) x PI 161375 (*S-2*, without sutures) and Védraçais x PI 414723 (*S-2*). The *s-2* gene was mapped to the linkage group XI (Perin et al., 2002a). Stripes on the rind were reported to have a monogenic recessive inheritance (gene *st* for *striped epicarp*) by (Hagiwara and Kamimura, 1936). The presence of stripes on young fruits of 'Dulce' (before netting development) was also reported to be controlled by a single recessive gene, *st-2* (*striped epicarp-2*), in the cross Dulce (*st-2*) x PI 414723 (*St-2*, non-striped) (Danin-Poleg et al., 2002); the gene *st-2* was mapped to the linkage group XI. Further studies would be required to clarify the relationship between *st-2* and *s-2*, also located in the linkage group XI. A single dominant gene (*St-3*) controlled the striped rind trait within a F2 derived from a cross between X010 (green rind with stripes) and M1-113 (white rind without stripes). The *St-3* gene was mapped on chromosome 4 (Liu et al., 2019).

The ridge fruit surface was reported to be controlled by a single gene, *ri* (*ridge* in C68), recessive to ridgeless (*Ri* in 'Pearl') (Takada et al., 1975). The speckled epidermis of the fruit is controlled by a single recessive gene, *spk* (*speckled fruit epidermis*) in PI 414723 (*Spk* in 'Védraçais') and was mapped to the linkage group VII (Perin et al., 2002a).

The mottled rind of melon is a relatively complex trait. A single gene, *Mt* (*Mottled rind pattern*), was reported to control a mottled rind in 'Annamalai', dominant to uniform color *mt* in 'Makuwa' (Ganesan, 1988). The presence of dark spots ( $\approx 1$  cm in diam.) on the rind (versus no spots) has a monogenic recessive inheritance in crosses Védraçais (*Mt-2*) x PI 161375 (*mt-2*) and Védraçais (*Mt-2*) x PI 414723 (*mt-2*), as the F<sub>1</sub> fruits have a uniform color rind (Périn et al., 1999). *mt-2* was mapped to the linkage group II (Perin et al., 2002a). The mottled rind was controlled also reported to be controlled by a dominant gene, which was mapped on chromosome 2 (Pereira et al., 2018; Lv et al., 2018) and on chromosome 4 (Liu et al., 2019). In a recent study, two dominant genes (*CmMt1* and *CmMt2*) with epistatic effects were reported for the mottled rind within an F<sub>2</sub> population derived from SC (Songwhan Charmi or PI 161375, mottled rind) and MG (Mi Gua non-mottled rind) lines. The genes mapped to chromosome 2. *CmAPRR2*, regulating young fruit rind color, was the candidate epistatic gene for *CmMt1*, and MELO3C026282 encoding an AtCPSFL1 homolog, was the most likely candidate for *CmMt2* (Shen et al., 2021). It seems

that the recessive/dominance inheritance of this trait depends on the non-mottle rind parent or on the parental line used as female.

A single dominant gene governing the development of net tissue, regardless of the degree of netting, was reported in BIZ in a cross with smooth-skinned PI 414723 (Herman et al., 2008). We propose to name the gene *Rn* (*Rind netting*) instead of *N*. The gene was mapped to the linkage group II, closely linked to *fom1.2a* for Fusarium wilt resistance; additional minor loci likely affect the density of the net (Herman et al., 2008). Several QTL for the height and the width of the net in 'Deltex' were detected in a cross between netted 'Deltex' and net-free TGR-1551 (Park et al., 2009b). A major netting QTL was mapped on chromosome 2 in RIL populations derived from crosses between a smooth rind, large-fruited honeydew line ('Tam Dew', 'Noy Amid' or PI 414723) and a densely netted, medium-sized reticulatus line ('Dulce'), together with additional interacting QTL on chromosome 2 and 9 (Oren et al., 2020).

Melon fruit flesh color was proposed to be controlled by two genes, *gf* for *green flesh* in Honeydew, recessive to orange flesh (*Gf* in Smiths' Perfect cantaloupe) (Hughes, 1948) and *wf* for *white flesh* (Iman et al., 1972). Genetic control of melon mesocarp color likely differs among market types. Clayberg (1992) confirmed that green and white mesocarps are recessive to orange and indicated that *gf* and *wf* interact epistatically. Mesocarp color (orange vs. green) segregated as a single recessive gene in recombinant inbred lines derived from orange flesh Védraçais x green flesh PI 161375 (Perin et al., 2002a) and orange flesh AR 5 x green flesh Harukai N°3 (Fukino et al., 2008). The segregating gene, named *gf*, mapped to the linkage group IX. Several QTL for fruit flesh color were described in near isogenic lines derived from the cross between green mesocarp PI 161375 and white mesocarp Piel de Sapó T111 (Eduardo et al., 2007; Obando et al., 2008). Three QTL associated with color variation (white, green, orange) with putative epistatic interaction were identified in the cross between the white-fleshed Chinese line Q3-2-2 and orange-fleshed 'Top Mark' (Cuevas et al., 2009; Cuevas et al., 2010). Five QTL associated with beta-carotene content, which is related to color intensity of the mesocarp, were identified in the cross between two orange-fleshed genotypes, USDA 846-1 and 'Top Mark' (Cuevas et al., 2008). More recently, the gene *CmOr* was shown to determine the orange flesh color in ripe melon when the dominant allele is present, by inducing the accumulation of  $\beta$ -carotene (Tzuri et al., 2015). Mapped in chromosome 9, it likely corresponds to *gf*.

Sweet melon cultivars are characterized by high sucrose and low acid levels in mature fruit flesh. A single, incompletely recessive gene, *suc*, controlled accumulation of sucrose in the

cross between the low sucrose Faqqous (Group Flexuosus) and the high sucrose 'Noy Yizre'el' (Burger et al., 2002). Several QTL associated with total soluble solid content and sugar content have been described in several populations (Monforte et al., 2004; Sinclair et al., 2006; Park et al., 2009a; Harel-Beja, 2010). In a study with a large collection of germplasm it was found an important variability at both the phenotypic and candidate gene levels for ripening behaviour and sugar accumulation in melon fruit (Leida et al., 2015). In recent years, three important clusters of QTL related to sugar content were detected on chromosome 4, 5 and 7 in the cross between a "Piel de Sapo" type and Songwhan Charmi (PI 161375) (Argyris et al., 2017).

A dominant gene, *So* (*Sour*) was reported to control high acidity in melon fruit (Kubicki, 1962). A single dominant gene, *So-2* (*Sour-2*) for *sour taste* of the mature fruit, was also reported in PI 414723 (Périn et al., 1999; Burger et al., 2003). A single recessive gene, *pH*, was reported to control fruit flesh acidity in PI 414723 (Low pH value in PI 414723 was dominant to high pH value in 'Dulce') and mapped to the linkage group VIII (Danin-Poleg et al., 2002; Harel-Beja et al., 2010). The *pH* gene was isolated by a map-based cloning strategy using a RIL population 'Dulce' x PI 414723 and a near-isogenic pair of melon lines derived from the cross of 'Noy Yizre'el' and the low-pH snake melon 'Faqqous' (Cohen et al., 2014).

While ripe melon fruits usually do not have a bitter taste, young fruits are divided into two types: bitter and non-bitter. A single dominant gene, *Bif-1* (*Bitter fruit-1*, formerly *Bif*), was reported to control the strong bitter taste of tender fruits in Indian wild melon (Parthasarathy and Sambandam, 1981). A monogenic dominant inheritance for the bitterness of young fruits was confirmed in wild melons from Africa and China. The cross of non-bitter melon lines (Groups Conomon and Makuwa with Groups Inodorus and Cantalupensis) yielded, however, bitter young melons, which suggests complementary gene action of two independent genes, *Bif-2* and *Bif-3* (*Bif-2\_ Bif-3\_* are bitter; *bif-2bif-2 Bif-3\_* and *Bif-2\_ bif-3bif-3* are non-bitter) (Ma et al., 1997). One of them may be the same as *Bif-1*. The relationship with the gene *Bi* controlling seedling bitterness (Lee and Janick, 1978) is unknown. The bitterness was found dominant to non-bitterness in a cross of C68 with non-bitter taste and C69 with bitter taste; three QTL were located in two linkage groups II and V (Shang et al., 2020).

While the single dominant gene *Mealy*, *Me*, was reported to control mealy flesh texture by Ganesan (1988) in an accession named *C. callosus* crossed with a crisp-fleshed Makuwa, a monogenic recessive inheritance was found for the mealy flesh texture in the Group Momordica accession PI 414723

(*me-2*) crossed with 'Védrantais' (*Me-2*) (Périn et al., 1999). A monogenic recessive inheritance was reported for the juicy character of melon fruit flesh; the gene was named *juicy flesh*, symbolized *jf* (Chadha et al., 1972). A single gene was reported to control the musky flavor of *C. melo callosus* (*Mu*, *Musky*), dominant to the mild flavor in 'Makuwa' or 'Annamalai' (*mu*) (Ganesan, 1988).

Fruit abscission at maturity was reported to be controlled by two independent loci in two independent studies. In absence of allelism tests, the genes were named abscission layer *Al-1* and *Al-2* in C68, *al-1* and *al-2* in 'Pearl' (Takada et al., 1975), and *Al-3* and *Al-4* in the climacteric Charentais type 'Védrantais'. *Al-3* and *Al-4* were mapped to the linkage groups VIII and IX in a recombinant inbred population derived from a cross between 'Védrantais' and the non-climacteric PI 161375 (Perin et al., 2002c). A single dominant gene, *Al-5*, was reported to control fruit abscission layer formation in the climacteric western shipper type 'TAM Uvalde' in the cross with the non-climacteric Casaba type 'TAM Yellow Canary' (Zheng et al., 2002). A major QTL for ripening in chromosome 8 and other minor QTL that may modulate the climacteric response were identified in a cross of the climacteric variety 'Védrantais' (Groups Cantalupensis) by the non-climacteric Piel de Sapo T111 (Groups Inodorus) (Pereira et al., 2020 and 2021).

## Organogenesis

Organogenic competence varies among melon genotypes. *In vitro* shoot regeneration capacity was reported to be controlled by two independent genes, partially dominant, *Org-1* and *Org-2* (*Organogenic* response) (Molina and Nuez, 1996). A single dominant gene, *Org-3*, was reported to control the high regeneration competence in the line BU-21/3, in crosses with the low regeneration competent lines 'PMR 45' and 'Ananas Yokneam' (Galperin et al., 2003).

## Transgenic Melons

In addition to conventional and molecular breeding, plants that are resistant to various diseases and pests, tolerant to abiotic stresses or some plant or fruit characters have been developed with transgenic plant technology, which has also been developed in melon since the 1990s (Baranski et al., 2019). Thus, the potential of transgenic technology has been proven in melons, for functional analysis as well as for breeding new traits. In table 3, some of the transgenic melon studies modified from Kesh and Kaushik (2021) are presented as examples.

**Table 1. Reported host plant resistance and morphological genes of melon, including genes symbol, synonyms, descriptions, and linkage groups.<sup>z</sup>**

Gene symbol		Character	LG <sup>y</sup>	References
Preferred	Synonym			
<i>a</i>	<i>M</i>	<b><i>andromonoecious</i>. Mostly staminate, fewer perfect flowers; on <i>A_</i> plants, pistillate flowers have no stamens; epistatic to <i>g</i>.</b>	<b>(4) II</b>	(Rosa, 1928; Poole and Grimball, 1939; Wall, 1967)
<i>ab</i>	-	<i>abrachiate</i> . Lacking lateral branches. Interacts with <i>a</i> and <i>g</i> , e.g., <i>abab aa G_</i> plants produce only staminate flowers.		(Foster and Bond, 1967)
<i>Ac</i>	-	<b><i>Alternaria cucumerina</i> resistance, in MR-1.</b>		(Thomas et al., 1990)
<i>Af</i>	-	<i>Aulacophora foveicollis</i> resistance. Resistance to the red pumpkin beetle.		(Vashistha and Choudhury, 1974)
<i>Ag</i>	-	<b><i>Aphis gossypii</i> tolerance. Freedom of leaf curling following aphid infestation; in PI 414723.</b>		(Bohn et al., 1973)
<i>Ala</i>	-	<i>Acute leaf apex</i> . Dominant over obtuse apex, linked with <i>Lobed</i> leaf, <i>Ala</i> in Maine Rock, <i>ala</i> in PV Green.		(Ganesan and Sambandam, 1985)
<i>alb</i>	-	<b><i>albino</i>. White cotyledons, lethal mutant; in Trystorp.</b>		(Besombes et al., 1999)
<i>Al-1</i>	<i>Al<sub>1</sub></i>	<i>Abscission layer-1</i> . One of two dominant genes for abscission layer formation, <i>Al-1Al-2</i> in C68, <i>al-1al-2</i> in Pearl. See <i>Al-2</i> .		(Takada et al., 1975)
<i>Al-2</i>	<i>Al<sub>2</sub></i>	<i>Abscission layer-2</i> . One of two dominant genes for abscission layer formation. See <i>Al-1</i> .		(Takada et al., 1975)
<i>Al-3</i>		<b><i>Abscission layer-3</i>. One dominant gene for abscission layer formation in PI 161375. Relationship with <i>Al-1</i> or <i>Al-2</i> is unknown.</b>	<b>VIII</b>	(Perin et al., 2002c)
<i>Al-4</i>		<b><i>Abscission layer-4</i>. One dominant gene for abscission layer formation in PI 161375. Relationship with <i>Al-1</i> or <i>Al-2</i> is unknown.</b>	<b>IX</b>	(Perin et al., 2002c)
<i>Al-5</i>	-	<b><i>Abscission layer-5</i>. One dominant gene for abscission layer formation; full-slip in TAM Uvalde.</b>		(Zheng et al., 2002)
<i>Bfb</i>		<b><i>Bacterial fruit blotch</i>. One dominant gene in PI 353814.</b>		<b>(Islam et al., 2020b)</b>
<i>bd</i>	-	<i>brittle dwarf</i> . Rosette growth with thick leaf. Male fertile, female sterile; in TAM-Perlita 45.		(Cox, 1985)
<i>Bi</i>	-	<b><i>Bitter</i>. Bitter seedling. Common in honeydew or in Charentais type while most American cantaloupes are <i>bi</i>.</b>		(Lee and Janick, 1978)
<i>Bif-1</i>	<i>Bif</i>	<i>Bitter fruit-1</i> . Bitterness of tender fruit in wild melon. Relation with <i>Bi</i> is unknown.		(Parthasarathy and Sambandam, 1981)

<b>Bif-2</b>	-	<i>Bitter fruit-2</i> . One of two complementary independent genes for bitter taste in young fruit: <i>Bif-2_ Bif-3_</i> are bitter. Relationships with <i>Bi</i> and <i>Bif-1</i> are unknown.	(Ma et al., 1997)
<i>Bif-3</i>	-	<i>Bitter fruit-3</i> . One of two complementary independent genes for bitter taste in young fruit: <i>Bif-2_ Bif-3_</i> are bitter. Relationships with <i>Bi</i> and <i>Bif-1</i> are unknown.	(Ma et al., 1997)
<b>cab-1</b>	-	<b><i>cucurbit aphid borne yellows virus resistance-1</i>. One of two complementary independent genes for resistance to this polerovirus: <i>cab-1cab-1 cab-2cab-2</i> plants are resistant; in PI 124112.</b>	(Dogimont et al., 1997)
<b>cab-2</b>	-	<b><i>cucurbit aphid borne yellows virus resistance-2</i>. One of two complementary independent genes for resistance to this polerovirus: <i>cab-1cab-1 cab-2cab-2</i> plants are resistant; in PI 124112.</b>	(Dogimont et al., 1997)
<i>cb</i>	<i>cb1</i>	<i>cucumber beetle</i> resistance. Interacts with <i>Bi</i> , the nonbitter <i>bibi cbcb</i> being the more resistant; in C922-174-B.	(Nugent et al., 1984)
<b>cf</b>	-	<b><i>cochleare folium</i>. Spoon-shaped leaf with upward curling of the leaf margins; spontaneous mutant in Galia.</b>	(Lecouviour et al., 1995)
<i>cgmmv-1</i>		<i>cucumber green mottle mosaic virus resistance-1</i> . One of two complementary genes for resistance to this tobamovirus in Chang Bougi.	(Sugiyama et al., 2007)
<i>cgmmv-2</i>		<i>cucumber green mottle mosaic virus resistance-2</i> . One of two complementary genes for resistance to this tobamovirus in Chang Bougi.	(Sugiyama et al., 2007)
<i>cl</i>	-	<i>curled leaf</i> . Elongated leaves that curl upward and inward. Usually male and female sterile.	(Cox, 1985)
<i>Creb-2</i>		<i>Cucumber mosaic virus resistance</i> . A single dominant gene for resistance to this cucumovirus in Yamatouri.	(Daryono et al., 2010)
<b>culcrv</b>		<b><i>cucurbit leaf crumple virus resistance</i>. A single recessive gene for resistance to this geminivirus transmitted by whitefly in PI 313970.</b>	(McCreight et al., 2008)
<b>Cvy-1</b>		<b>Cucumber vein yellowing resistance. Cvy-1 (1) controlling resistance in PI 164323. The recessive allele cvy-2 present in HSD 2458 controls the tolerance and the allele Cvy-3, present in Ouzbeque 2, controls the highly susceptible type of symptoms.</b>	(Pitrat et al., 2012)
<b>Cys</b>	-	<b><i>Cucurbit yellow stunting disorder virus resistance</i>. One dominant gene for resistance to this crinivirus in TGR-1551. A single recessive gene in PI 313970 for resistance to CYSDV.</b>	(Lopez-Sese and Gomez-Guillamon, 2000) McCreight and Wintermantel, 2011
<i>dc-1</i>	-	<i>Dacus cucurbitae-1</i> resistance. One of two complementary recessive genes for resistance to the melon fruitfly. See <i>dc-2</i> .	(Sambandam and Chelliah, 1972)
<i>dc-2</i>	-	<i>Dacus cucurbitae-2</i> resistance. One of two complementary recessive genes for resistance to the melon fruitfly. See <i>dc-1</i> .	(Sambandam and Chelliah, 1972)

<i>dl</i>	-	<b>dissected leaf. Highly indented leaves in URSS 4.</b>		(Dyutin, 1967)
<i>dl<sup>v</sup></i>	<i>cl</i>	<b>dissected leaf Velich. First described as cut leaf in Cantaloup de Bellegarde. Allelic to <i>dl</i>.</b>		(Velich and Fulop, 1970)
<i>dl-2</i>	-	<i>dissected leaf-2</i> . First described as “hojas hendidas”.		(Esquinas Alcazar, 1975)
<i>dlet</i>	<i>dl</i>	<i>delayed lethal</i> . Reduced growth, necrotic lesions on leaves and premature death.		(Zink, 1990)
<i>Ec</i>	-	<b>Empty cavity. Carpels are separated at fruit maturity leaving a cavity; <i>Ec</i> in PI 414723, <i>ec</i> in Védtrantais.</b>	<b>III</b>	(Périn et al., 1999)
<i>ech</i>	-	<b>exaggerated curvature of the hook. Triple response of seedlings germinating in darkness in presence of ethylene; <i>ech</i> in PI 161375, <i>Ech</i> in Védtrantais.</b>	<b>I</b>	(Perin et al., 2002a)
<i>f</i>	-	<b>flava. Chlorophyll deficient mutant. Growth rate reduced in K 2005.</b>	<b>(8)</b>	(Pitrat et al., 1986)
<i>fas</i>	-	<b>fasciated stem, in Vilmorin 104.</b>		(Gabillard and Pitrat, 1988)
		<b>Fruit cracking resistance was explained with the genetic model E-0, incorporating two additive-dominance-epistasis major genes plus an additive-dominance-epistasis polygenic.</b>		(Qi et al., 2015)
<i>fe</i>	-	<b>fe (iron) inefficient mutant. Chlorotic leaves with green veins that turn green when adding iron in the nutrient solution.</b>		(Nugent and Bhella, 1988; Jolley et al., 1991)
<i>Fn</i>	-	<b>Flaccida necrosis. Semi-dominant gene for wilting and necrosis reactions to F pathotype of <i>Zucchini yellow mosaic virus</i>; <i>Fn</i> in Doublon, <i>fn</i> in Védtrantais).</b>	<b>(2) V</b>	(Risser et al., 1981)
<i>Fom-1</i>	<i>Fom<sub>1</sub></i>	<b><i>Fusarium oxysporum f.sp. melonis</i> resistance. Resistance to races 0 and 2 and susceptibility to races 1 and 1.2 of <i>Fusarium wilt</i>; <i>Fom-1</i> in Doublon, <i>fom-1</i> in Charentais T.</b>	<b>(5) IX</b>	(Risser, 1973)
<i>Fom-2</i>	<i>Fom<sub>1.2</sub></i>	<b><i>Fusarium oxysporum f.sp. melonis</i> resistance. Resistance to races 0 and 1 and susceptibility to races 2 and 1.2 of <i>Fusarium wilt</i>; <i>Fom-2</i> in CM 17187, <i>fom-2</i> in Charentais T.</b>	<b>(6) XI</b>	(Risser, 1973)
<i>Fom-3</i>	-	<b><i>Fusarium oxysporum f.sp. melonis</i> resistance. Same phenotype as <i>Fom-1</i> but segregates independently from <i>Fom-1</i>; <i>Fom-3</i> in Perlita FR, <i>fom-3</i> in Charentais T.</b>		(Zink and Gubler, 1985)
<i>fom1.2a</i>		<i>Fusarium oxysporum f.sp. melonis</i> resistance. Resistance to race 1.2 of <i>Fusarium wilt</i> ; <i>fom1.2a</i> in BIZ, <i>Fom1.2a</i> in PI 414723.	<b>II</b>	(Herman et al., 2008)
<i>fom-4</i>		<i>Fusarium oxysporum f.sp. melonis</i> resistance. Resistance to race 0 and 2 of <i>Fusarium wilt</i> , <i>fom-4</i> in Tortuga, likely associated with <i>Fom-1</i> .		(Oumouloud et al., 2010)
<i>Forc-1</i>		<i>Fusarium oxysporum f.sp. radices-cucumerinum</i> resistance. High level of resistance in Hemed.		(Elkabetz et al., 2016)
<i>forc-1</i>		<i>Fusarium oxysporum f.sp. radices-cucumerinum</i> resistance. High level of resistance in Hemed.		(Elkabetz et al., 2016)

<i>g</i>	-	<b><i>gynoecious</i>. Controls the presence of one (<i>g</i>) or two (<i>G</i>) types of flowers on one plant. Epistatic to <i>a</i>: <i>A_ G_</i> monoecious; <i>A_ gg</i> gynoeceous; <i>aa G_</i> andromonoecious; <i>aa gg</i> hermaphrodite.</b>		(Poole and Grimball, 1939)
<i>gf</i>	-	<b><i>green flesh</i> color. Recessive to salmon, <i>gf</i> in honeydew, <i>Gf</i> in Smiths' Perfect cantaloupe.</b>	VIII	(Hughes, 1948)
<i>gl</i>	-	<b><i>glabrous</i>. Trichomes lacking in Arizona glA.</b>	(3)	(Foster, 1963)
<i>gl-2</i>		<i>glabrous-2</i> . Complete absence of trichomes in the muskmelon line NSL73046.	VIII	(Zhu et al. 2018)
<i>gp</i>	-	<i>green petals</i> . Corolla leaf like in color and venation.		(Mockaitis and Kivilaan, 1965)
<i>Gs</i>	-	<i>Gelatinous sheath</i> around the seeds. Dominant to absence of gelatinous sheath.		(Ganesan, 1988)
<b><i>Gsb-1</i></b>	<b><i>Mc</i></b>	<b><i>Gummy stem blight</i> resistance-1. High degree of resistance to <i>Stagonosporopsis cucurbitacearum</i> (syn. <i>Didymella bryoniae</i> or <i>Mycosphaerella citrullina</i>) in PI 140471.</b>		(Prasad and Norton, 1967; Frantz and Jahn, 2004)
<i>Gsb-2</i>	<i>Mc-3</i>	<i>Gummy stem blight</i> resistance-2. High level of resistance to <i>Stagonosporopsis cucurbitacearum</i> (syn. <i>Didymella bryoniae</i> or <i>Mycosphaerella citrullina</i> ) in PI 157082, independent from <i>Gsb-1</i> , <i>Gsb-3</i> , <i>Gsb-4</i> and <i>gsb-5</i> .		(Zuniga et al., 1999; Frantz and Jahn, 2004)
<b><i>Gsb-3</i></b>	<b><i>Mc-4-</i></b>	<b><i>Gummy stem blight</i> resistance-3. High level of resistance to <i>Stagonosporopsis cucurbitacearum</i> (syn. <i>Didymella bryoniae</i> or <i>Mycosphaerella citrullina</i>) in PI 511890, independent from <i>Gsb-1</i>, <i>Gsb-2</i>, <i>Gsb-4</i> and <i>gsb-5</i>.</b>		(Zuniga et al., 1999; Frantz and Jahn, 2004)
<b><i>Gsb-4</i></b>	-	<b><i>Gummy stem blight</i> resistance-4. High level of resistance to <i>Stagonosporopsis cucurbitacearum</i> (syn. <i>Didymella bryoniae</i> or <i>Mycosphaerella citrullina</i>) in PI 482398, independent from <i>Gsb-1</i>, <i>Gsb-2</i>, <i>Gsb-3</i> and <i>gsb-5</i>.</b>		(Frantz and Jahn, 2004)
<b><i>gsb-5</i></b>	-	<b><i>gummy stem blight</i> resistance-5. High level of resistance to <i>Stagonosporopsis cucurbitacearum</i> (syn. <i>Didymella bryoniae</i> or <i>Mycosphaerella citrullina</i>) in PI 482399, independent from <i>Gsb-1</i>, <i>Gsb-2</i>, <i>Gsb-3</i> and <i>Gsb-4</i>.</b>		(Frantz and Jahn, 2004)
<i>Gsb-6</i>	<i>Mci, Mc-2</i>	<i>Mycosphaerella citrullina</i> resistance-2. Moderate degree of resistance to gummy stem blight in C-1 and C-8.		(Prasad and Norton, 1967)
<i>gyc</i>	-	<b><i>greenish yellow corolla</i>.</b>		(Zink, 1986)
<b><i>gy</i></b>	<b><i>n, M</i></b>	<b><i>gynomonoecious</i>. Interacts with <i>a</i> and <i>g</i> to produce stable gynoeceous plants (<i>A_ g g gy gy</i>) in WI 998.</b>		(Kenigsbuch and Cohen, 1987, 1990)
<b><i>h</i></b>	-	<b><i>halo</i> cotyledons. Yellow halo on the cotyledons, later turning green.</b>	(4) II	(Nugent and Hoffman, 1974)
<i>Imy</i>	-	<i>Interveinal mottling and yellowing</i> resistance. Resistance to a complex of viruses, in PI 378062.		(Hassan et al., 1998)
<i>jf</i>	-	<i>juicy flesh</i> . Segregates discretely in a monogenic ratio in segregating generations.		(Chadha et al., 1972)

<i>L</i>	-	<i>Lobed</i> leaf. Dominant on non-lobed, linked with <i>Acute leaf apex L</i> in Maine Rock, <i>l</i> in P.V. Green.		(Ganesan and Sambandam, 1985)
<i>Liy</i>	-	<b>Lettuce infectious yellows virus resistance. One dominant gene for resistance to this crinivirus in PI 313970.</b>		(McCreight, 2000)
<i>lmi</i>	-	<b>long mainstem internode. Affects internode length of the main stem but not of the lateral ones in 48764.</b>	<b>(8)</b>	(McCreight, 1983b)
<i>Ls</i>	-	Resistance to the leafminer <i>Liriomyza sativae</i> . The plant BAGMEL 56-R was selected as a new source of resistance.		(Celin et al., 2017b)
<i>Lt</i>	-	<b>Liriomyza trifolii (leafminer) resistance in Nantais Oblong.</b>		(Dogimont et al., 1999)
<i>M-Pc-5</i>	-	<i>Modifier of Pc-5</i> . Gene <i>Pc-5</i> for downy mildew resistance is dominant in presence of <i>M-Pc-5</i> , recessive in the absence of <i>M-Pc-5</i> .		(Angelov and Krasteva, 2000)
<i>Mca</i>	-	<i>Macrocalyx</i> . Large, leaf like structure of the sepals in staminate and hermaphrodite flowers; <i>Mca</i> in Makuwa, <i>mca</i> in Annamalai.		(Ganesan and Sambandam, 1979)
<i>mdw1</i>		<i>Mutant dwarf 1</i> . A recessive gene in the mutant line PNU-D1 ( <i>cantalupensis</i> ).	VII	(Hwang et al., 2014)
<i>Me</i>	-	<i>Mealy</i> flesh texture. Dominant to crisp flesh; <i>Me</i> in <i>C. callosus</i> , <i>me</i> in Makuwa.		(Ganesan, 1988)
<i>me-2</i>	-	<b>mealy flesh texture-2 in PI 414723.</b>		(Périn et al., 1999)
<b>Mnr-1</b>	<b>Mnr1</b>	<b>Melon necrotic resistance 1. One of two dominant genes for resistance to Melon necrotic spot virus (MNSV) located at 19 cM from <i>nsv</i>; Mnr-1 in Doublon, <i>mnr-1</i> in ANC-42.</b>	<b>XII</b>	(Mallor Gimenez et al., 2003)
<b>Mnr-2</b>	<b>Mnr2</b>	<b>Melon necrotic resistance 2. One of two dominant genes for resistance to Melon necrotic spot virus (MNSV) independent from Mnr-1; Mnr-2 in Doublon, <i>mnr-2</i> in ANC-42.</b>		(Mallor Gimenez et al., 2003)
<i>ms-1</i>	<i>ms<sup>1</sup></i>	<b>male sterile-1. Indehiscent anthers with empty pollen walls in tetrad stage.</b>	<b>(3)</b>	(Bohn and Whitaker, 1949)
<i>ms-2</i>	<i>ms<sup>2</sup></i>	<b>male sterile-2. Anthers indehiscent, containing mostly empty pollen walls, growth rate reduced.</b>	<b>(6) XI</b>	(Bohn and Principe, 1964)
<i>ms-3</i>	<i>ms-L</i>	<b>male sterile-3. Waxy and translucent indehiscent anthers, containing two types of empty pollen sacs.</b>	<b>(12) VII</b>	(McCreight and Elmstrom, 1984)
<i>ms-4</i>	-	<b>male sterile-4. Small indehiscent anthers. First male flowers abort at bud stage in Bulgaria 7.</b>	<b>(9)</b>	(Lozanov, 1983)
<i>ms-5</i>	-	<b>male sterile-5. Small indehiscent anthers. Empty pollen in Jivaro, Fox.</b>	<b>(13)</b>	(Lecouviour et al., 1990)
<i>Mt</i>	-	<i>Mottled</i> rind pattern. Dominant to uniform color. Epistatic with <i>Y</i> (not expressed in <i>Y<sub>-</sub></i> ) and <i>st</i> ( <i>Mt<sub>-</sub> st st</i> and <i>Mt<sub>-</sub> St<sub>-</sub></i> mottled; <i>mt mt st st</i> striped, <i>mt mt St<sub>-</sub></i> uniform); <i>Mt</i> in Annamalai, <i>mt</i> in Makuwa.		(Ganesan, 1988)
<i>mt-2</i>	-	<b>mottled rind pattern in PI 161375.</b>	<b>II</b>	(Périn et al., 1999)

<i>Mu</i>	-	<i>Musky</i> flavor (olfactory). Dominant on mild flavor; <i>Mu</i> in <i>C. melo callosus</i> , <i>mu</i> in Makuwa or Annamalai.		(Ganesan, 1988)
<i>Mvd</i>	-	<i>Melon vine decline</i> resistance in Pat 81. Semi-dominant gene for partial resistance to <i>Acremonium cucurbitacearum</i> and <i>Monosporascus cannonballus</i> .		(Iglesias et al., 2000)
<i>My</i>	-	<b>Melon yellows virus resistance. Semi-dominant gene for partial resistance to this crinivirus, in Nagata Kin Makuwa.</b>		(Esteva and Nuez, 1992; Nuez et al., 1999)
<i>n</i>	-	<b>nectarless. Nectaries lacking in all flowers of 40099.</b>		(Bohn, 1961)
<i>Nm</i>	-	<b>Necrosis with Morocco strains of Watermelon mosaic virus, a potyvirus; Nm in Védrañtais, nm in Ouzbèque.</b>		(Quiot-Douine et al., 1988)
<i>nsv</i>	-	<b>Melon necrotic spot virus resistance. A single recessive gene for resistance to this carmovirus in Gulfstream, Planters Jumbo.</b>	<b>(7) XII</b>	(Coudriet et al., 1981)
<i>O</i>	-	<b>Oval fruit shape. Dominant to round, associated with <i>a</i>.</b>		(Wall, 1967)
<i>Org-1</i>	-	<i>Organogenic</i> response for <i>in vitro</i> shoot regeneration. Partially dominant. Interacts with an additive model with <i>Org-2</i> .		(Molina and Nuez, 1996)
<i>Org-2</i>	-	<i>Organogenic</i> response for <i>in vitro</i> shoot regeneration. Partially dominant. Interacts with an additive model with <i>Org-1</i> .		(Molina and Nuez, 1996)
<i>Org-3</i>	-	<i>Organogenic</i> response for <i>in vitro</i> regeneration. Dominant allele for high response in BU-12/3, recessive allele in PMR 45 or Ananas Yokneam. Probably different from <i>Org-1</i> and <i>Org-2</i> .		(Galperin et al., 2003)
<i>p</i>	-	<b>pentamerous. Five carpels and stamens; recessive to trimerous; in Casaba.</b>	<b>XII</b>	(Rosa, 1928)
<i>Pa</i>	-	<b>Pale green foliage. PaPa plants are white (lethal); Papa are yellow; in 30567.</b>	<b>(3)</b>	(McCreight and Bohn, 1979)
<i>Pc-1</i>	-	<b><i>Pseudoperonospora cubensis</i> resistance. One of two complementary incompletely dominant genes for downy mildew resistance in PI 124111. See <i>Pc-2</i>.</b>		(Cohen et al., 1985; Thomas et al., 1988)
<i>Pc-2</i>	-	<b><i>Pseudoperonospora cubensis</i> resistance. One of two complementary incompletely dominant genes for downy mildew resistance in PI 124111). See <i>Pc-1</i>.</b>		(Cohen et al., 1985; Thomas et al., 1988)
<i>Pc-3</i>	-	<b><i>Pseudoperonospora cubensis</i> resistance. Partial resistance to downy mildew in PI 414723.</b>		(Epinat and Pitrat, 1989)
<i>Pc-4</i>	-	<b><i>Pseudoperonospora cubensis</i> resistance. One of two complementary genes for downy mildew resistance in PI 124112. Interacts with <i>Pc-1</i> or <i>Pc-2</i>.</b>		(Kenigsbuch and Cohen, 1992)
<i>Pc-5</i>	-	<i>Pseudoperonospora cubensis</i> resistance. One gene in Line 5-4-2-1 which interacts with <i>M-Pc-5</i> in the susceptible line K15-6; <i>Pc-5</i> is dominant in presence of <i>M-Pc-5</i> , recessive in the absence of <i>M-Pc-5</i> .		(Angelov and Krasteva, 2000)
<i>pH</i>	-	<b>pH (acidity) of the mature fruit flesh. Low pH value in PI 414723 dominant to high pH value in Dulce.</b>	<b>VIII</b>	(Danin-Poleg et al., 2002)

<i>pin</i>	-	<i>pine-seed</i> shape in PI 161375.	III	(Perin et al., 2002a)
<i>Pm-2</i>	<i>Pm</i> <sup>2</sup> <i>Pm-C</i> ?	<i>Powdery mildew</i> resistance-2. Interacts with <i>Pm-1</i> ; Resistance to race 2 of <i>Podosphaera xanthii</i> in PMR 5 with <i>Pm-1</i> .		(Bohn and Whitaker, 1964)
<i>Pm-3</i>	<i>Pm</i> <sup>3</sup>	<i>Powdery mildew</i> resistance-3. Resistance to race 1 of <i>Podosphaera xanthii</i> in PI 124111.	(7)	(Harwood and Markarian, 1968a and b)
<i>Pm-4</i>	<i>Pm</i> <sup>4</sup>	<i>Powdery mildew</i> resistance-4. Resistance to <i>Podosphaera xanthii</i> in PI 124112.		(Harwood and Markarian, 1968a and b)
<i>Pm-5</i>	<i>Pm</i> <sup>5</sup>	<i>Powdery mildew</i> resistance-5. Resistance to <i>Podosphaera xanthii</i> in PI 124112.		(Harwood and Markarian, 1968a and b)
<i>Pm-6</i>	-	<i>Powdery mildew</i> resistance-6. Resistance to <i>Podosphaera xanthii</i> race 2 in PI 124111.		(Kenigsbuch and Cohen, 1989)
<i>Pm-7</i>	-	<i>Powdery mildew</i> resistance-7. Resistance to <i>Podosphaera xanthii</i> race 1 in PI 414723.		(Anagnostou et al., 2000)
<i>Pm-8</i>		<i>Powdery mildew</i> resistance-8. Resistance to <i>Podosphaera xanthii</i> race pxCh1 in PI 134198.		(Liu et al., 2010)
<i>Pm-E</i>	-	<i>Powdery mildew</i> resistance-E. Interacts with <i>Pm-C</i> in PMR 5 for <i>Golovinomyces cichoracearum</i> resistance.		(Epinat et al., 1993)
<i>Pm-F</i>	-	<i>Powdery mildew</i> resistance-F. Interacts with <i>Pm-G</i> in PI 124112 for <i>Golovinomyces cichoracearum</i> resistance.		(Epinat et al., 1993)
<i>Pm-G</i>	-	<i>Powdery mildew</i> resistance-G. Interacts with <i>Pm-F</i> in PI 124112 for <i>Golovinomyces cichoracearum</i> resistance.		(Epinat et al., 1993)
<i>Pm-H</i>	-	<i>Powdery mildew</i> resistance-H. Resistance to <i>Golovinomyces cichoracearum</i> and susceptibility to <i>Podosphaera xanthii</i> in Nantais oblong.		(Epinat et al., 1993)
<i>Pm-R</i>	-	<i>Powdery mildew</i> resistance-R. Resistance to <i>Podosphaera xanthii</i> races 1, 2, and 5 in TGR-1551.	V	(Yuste-Lisbona et al., 2011b)
<i>pm-S</i>		<i>powdery mildew</i> resistance-S. Resistance to <i>Podosphaera xanthii</i> race S in PI 313970. Recessive to susceptibility in Top Mark.		(McCreight and Coffey, 2011)
<i>Pm-w</i>	<i>Pm-B</i> ?	<i>Powdery mildew</i> resistance-w. Resistance to <i>Podosphaera xanthii</i> race 2 in WMR 29.	(2) V	(Pitrat, 1991)
<i>Pm-x</i>	-	<i>Powdery mildew</i> resistance-x. Resistance to <i>Podosphaera xanthii</i> in PI 414723.	(4) II	(Pitrat, 1991)
<i>Pm-y</i>	-	<i>Powdery mildew</i> resistance-y. Resistance to <i>Podosphaera xanthii</i> in VA 435.	(7) XII	(Pitrat, 1991)
<i>Pm-z</i>		<i>Powdery mildew</i> resistance-z. Resistance to <i>Podosphaera xanthii</i> races 1 and 2US in PI 313970.		(McCreight, 2003)
<i>PmV.1</i>	-	<i>Powdery mildew</i> resistance V.1. Resistance to <i>Podosphaera xanthii</i> races 1, 2 and 3 in PI 124112.	V	(Perchepied et al., 2005b)

<i>PmXII.1</i>		<b>Powdery mildew resistance XII.I. Resistance to <i>Podosphaera xanthii</i> races 1, 2 and 5 and to <i>Golovinomyces cichoracearum</i> race 1 in PI 124112.</b>	<b>XII</b>	(Perchepped et al., 2005b)
<i>PMRI</i>		<b>Powdery mildew resistance to <i>Podosphaera xanthii</i> race 1 in leaves of MR-1 with an epistatic effect on the recessive gene <i>pmrs</i>.</b>	<b>XII</b>	(Cui et al., 2022a)
<i>pmrs</i>		<b>powdery mildew resistance to <i>Podosphaera xanthii</i> race 1 in stem of MR-1. Recessive to susceptibility in MR-1.</b>	<b>X</b>	(Cui et al., 2022a)
<i>Prv<sup>2</sup></i>	-	<b><i>Papaya Ringspot virus</i> resistance<sup>2</sup>. Allele at the same locus as <i>Prv<sup>1</sup></i> but different reaction with some strains of the virus; in 72-025, which was derived from PI 180283. Recessive to <i>Prv<sup>1</sup></i>.</b>	<b>(5) IX</b>	(Webb, 1979; Pitrat and Lecoq, 1983)
<i>Prv-2</i>	-	<b><i>Papaya Ringspot virus</i> resistance-2. Relationship with <i>Prv</i> is unknown; in PI 124112.</b>		(McCreight and Fashing-Burdette, 1996)
<i>r</i>	-	<b>red stem. Red pigment under epidermis of stems, especially at nodes, and reddish or tan seed color; in PI 157083.</b>	<b>(3)</b>	(Bohn, 1968; McCreight and Bohn, 1979)
<i>ri</i>	-	<i>ridge</i> . Ridged fruit surface, recessive to ridgeless. ( <i>ri</i> in C68, <i>Ri</i> in Pearl).		(Takada et al., 1975)
<i>Rn</i>	<i>N</i>	<i>Rind netting</i> . Netted fruit surface, regardless of the degree of netting; <i>Rn</i> in B12 dominant to smooth, non-netted rind, <i>rn</i> in PI 414723.		(Herman et al., 2008)
<i>s</i>	-	<i>sutures</i> . Presence of vein tracts on the fruit (« sutures »); recessive to ribless.		(Bains and Kang, 1963)
<i>s-2</i>	-	<b><i>sutures-2</i> on the fruit rind of PI 161375. Relationship with <i>s</i> is unknown.</b>	<b>XI</b>	(Périn et al., 1999)
<i>Sfl</i>	<i>S</i>	<i>Subtended floral leaf</i> . The floral leaf bearing the hermaphrodite flowers is sessile, small and encloses the flower; <i>Sfl</i> in Makuwa, <i>sfl</i> in Annamalai.		(Ganesan and Sambandam, 1979)
<i>si-1</i>	<i>b</i>	<b><i>short internode-1</i>. Extremely compact plant habit (bush type) in UC Topmark Bush.</b>	<b>(1)</b>	(Denna, 1962)
<i>si-2</i>	-	<b><i>short internode-2</i>. Short internodes from 'birdnest' melon in Persia 202.</b>		(Paris et al., 1984)
<i>si-3</i>	-	<b><i>short internode-3</i>. Short internodes in Maindwarf.</b>		(Knavel, 1990)
<i>si-4</i>		<i>short internode-4</i> . Short internodes in mutant M406.	<b>VII</b>	(Yang et al., 2020b)
<i>slb</i>	<i>sb</i>	<b><i>short lateral branching</i>. Reduction of the elongation of the lateral branches, in LB-1.</b>		(Ohara et al., 2001)
<i>So</i>	-	<i>Sour</i> taste. Dominant to sweet.		(Kubicki, 1962)
<i>So-2</i>	-	<b><i>Sour</i> taste-2. Relationship with <i>So</i> is unknown, in PI 414723.</b>		(Périn et al., 1999)
<i>sp</i>	-	<i>spherical</i> fruit shape. Recessive to obtuse; dominance incomplete.		(Lumsden, 1914; Bains and Kang, 1963)

<i>spk</i>	-	<b>speckled fruit epidermis; <i>spk</i> in PI 161375 and PI 414723, <i>Spk</i> in Védraçais.</b>	VII	(Perin et al., 2002a)
<i>sqmv</i>		<b>squash mosaic virus resistance. A single recessive gene for resistance to this Comovirus in China 51.</b>		(Provvidenti, 1998)
<i>st</i>	-	<i>striped epicarp</i> . Recessive to non-striped.		(Hagiwara and Kamimura, 1936)
<i>st-2</i>	<i>st</i>	<b>striped epicarp-2. Present in Dulce, recessive to non-striped in PI 414723. Relationship with <i>st</i> is unknown.</b>	XI	(Danin-Poleg et al., 2002)
<i>St-3</i>		<i>Striped epicarp</i> . Dominant to non-striped white rind. Present in X010 (green rind with stripes), dominant to white rind without stripes in M1-113.	IV	(Liu et al., 2019)
<i>suc</i>		<b>sucrose accumulation. Low sucrose level in Faqqous (<i>suc</i>), high sucrose in Noy Yizre'el (<i>Suc</i>). Incomplete recessivity.</b>		(Burger et al., 2002)
<i>v</i>	-	<b>virescent. Pale cream cotyledons and hypocotyls, and yellow green foliage, mainly young leaves.</b>		(Hoffman and Nugent, 1973)
<i>v-2</i>	-	<b>virescent-2.</b>		(Dyutin, 1979)
<i>v-3</i>	-	<b>virescent-3. White cotyledons which turn green, light green young leaves which are normal when they are older.</b>		(Pitrat et al., 1995)
<i>Vat</i>	-	<b>Virus aphid transmission resistance. Resistance to several viruses when transmitted by <i>Aphis gossypii</i>, in PI 161375.</b>	(2) V	(Pitrat and Lecoq, 1980)
<i>w</i>	-	<b>white color of mature fruit. Recessive to dark green fruit skin; <i>w</i> in honeydew, <i>W</i> in Smiths' Perfect cantaloupe.</b>		(Hughes, 1948)
<i>wf</i>	-	<b>white flesh. Recessive to salmon. <i>Wf</i> epistatic to <i>Gf</i>.</b>	IX	(Iman et al., 1972; Clayberg, 1992)
<i>Wi</i>	-	White color of <i>immature</i> fruit. Dominant to green.		(Kubicki, 1962)
<i>Wmr</i>	-	<b>Watermelon mosaic virus (formerly <i>Watermelon mosaic virus 2</i>) resistance. A single dominant gene, in PI 414723.</b>	II	(Gilbert et al., 1994)
<i>wmr-2</i>		<b>Watermelon mosaic virus (formerly <i>Watermelon mosaic virus 2</i>) resistance. A single recessive gene, in TGR-1551.</b>		(Diaz-Pendon et al., 2005)
<i>Wt</i>	-	<b>White testa. Dominant to yellow or tan seed coat color.</b>		(Hagiwara and Kamimura, 1936)
<i>Wt-2</i>	-	<b>White testa-2. Relationship with <i>Wt</i> unknown, in PI 414723.</b>	IV	(Périn et al., 1999)
<i>Y</i>	-	<b>Yellow epicarp. Dominant to white fruit skin.</b>		(Hagiwara and Kamimura, 1936)
<i>yg</i>	-	<b>yellow green leaves. Reduced chlorophyll content.</b>	(6) XI	(Whitaker, 1952)
<i>yg<sup>w</sup></i>	<i>lg</i>	<b>yellow green <i>Weslaco</i>. First described as <i>light green</i> in a cross Dulce x TAM-Uvalde. Allelic to <i>yg</i>.</b>		(Cox and Harding, 1986)
<i>yv</i>	-	<b>yellow virescence. Pale cotyledons; yellow green young leaves and tendrils; bright and yellow petals and yellow stigma; etiolated; older leaves becoming green.</b>	1	(Zink, 1977)

<i>yv-2</i>	<i>yv-X</i>	<b><i>yellow virescence-2</i></b> . Young leaves yellow green, old leaves normal green	<b>(5) IX</b>	(Pitrat, 1991)
<b><i>Zym</i></b>	<b><i>Zym-1</i></b>	<b><i>Zucchini Yellow Mosaic</i></b> virus resistance. Resistance to pathotype 0 of this potyvirus in PI 414723.	<b>(4) II</b>	(Pitrat and Lecoq, 1984)
<b><i>Zym-2</i></b>	-	<b><i>Zucchini Yellow Mosaic</i></b> potyvirus resistance. One of three complementary genes (see <i>Zym</i> and <i>Zym-3</i> ) for resistance to this potyvirus in PI 414723.		(Danin Poleg et al., 1997)
<b><i>Zym-3</i></b>	-	<b><i>Zucchini Yellow Mosaic</i></b> potyvirus resistance. One of three complementary genes (see <i>Zym</i> and <i>Zym-2</i> ) for resistance to this potyvirus in PI 414723.		(Danin Poleg et al., 1997)
<i>cyt-Yt</i>	-	<i>cytoplasmic yellow tip</i> . Chlorophyll deficient mutant with yellow young leaves, turning green when becoming older. Maternally inherited.		(Ray and McCreight, 1996)

<sup>z</sup>Genes maintained by the curators in the INRAE Centre for Vegetable Germplasm (CRB-Leg) (Salinier et al., 2022; [https://www6.paca.inrae.fr/gafl\\_eng/Vegetable-Germplasm-Centre](https://www6.paca.inrae.fr/gafl_eng/Vegetable-Germplasm-Centre)) or very common in collections (like *andromonoecious* or *white testa*) are written in **bold**. Genes that have been apparently lost or not maintained by curators, or have uncertain descriptions are written normally.

<sup>y</sup>The number in brackets refers to linkage groups to which the genes belong according to Pitrat (1991), Roman numbers refer to linkage groups according to Périn et al. (2002a) and correspond to chromosome numbers according to Garcia-Mas et al. (2012).

**Table 2. Quantitative traits loci for pest and pathogen resistances, flowering and fruit related traits and other traits, including description of the quantitative trait, number of QTL reported, respective parental lines, and references.**

Description of the quantitative trait, parental lines of the cross used	References
<p><b><i>Aphis gossypii</i> resistance</b></p> <ul style="list-style-type: none"> <li>Four additive and two couples of epistatic QTL affecting behaviour and biotic potential of <i>Aphis gossypii</i> in the cross Védreantais x PI 161375 (RILs).</li> </ul>	(Boissot et al., 2010)
<p><b><i>Bemisia tabaci</i> resistance</b></p> <ul style="list-style-type: none"> <li>Two QTL affecting the biotic potential of the whiteflies in the cross Védreantais x PI 161375 (RILs).</li> </ul>	(Boissot et al., 2010)
<p><b>Cucumber mosaic virus resistance.</b></p> <ul style="list-style-type: none"> <li>Seven QTL are involved in resistance to three different CMV strains in the cross Védreantais x PI 161375 (RILs).</li> <li>A single QTL required for controlling CMV P9 and P104.82 strains in the cross Piel de Sapo x PI 161375 (LG XII).</li> <li>One major QTL in LG XII (cmvqw12.1) and two minor QTL in LG III (cmvqw3.1) and LG X (cmvqw10.1) for resistance to CMV strains M6 and TL in the cross Védreantais x PI 161375 (DHLd and near-isogenic lines).</li> </ul>	(Dogimont et al., 2000) (Essafi et al., 2009) (Guiu-Aragones et al., 2014)
<p><b>Cucurbit chlorotic yellows virus (CCYV) resistance</b></p> <ul style="list-style-type: none"> <li>A single QTL in the cross of two susceptible accessions ('Harukei No. 3' and 'AnMP-5') x "JP 138332".</li> </ul>	(Kawazu et al., 2018)
<p><b>Cucurbit yellow stunting disorder virus (CYSDV) resistance</b></p> <ul style="list-style-type: none"> <li>Two QTL based on disease reaction phenotype and virus titer in the cross TGR-1551 x Bola de Oro.</li> <li>Two QTL in a cross of 'Top Mark' with PI 313970, a major one on chr. 5 and a second on chr. 3.</li> </ul>	(Perez-de-Castro et al., 2020) (Tamang et al., 2021)
<p><b>Tomato leaf curl New Delhi virus resistance</b></p> <ul style="list-style-type: none"> <li>Three genomic regions are controlled ToLCNDV by a major QTL located in chromosome 11.</li> </ul>	(Saez et al., 2017)
<p><b>Watermelon mosaic virus resistance</b></p> <ul style="list-style-type: none"> <li>One major QTL (<i>wmv</i>) on the linkage group (LG) XI close to the microsatellite marker CMN04_35.</li> <li>Three minor QTL for WMV resistance in chromosomes 4, 5, and 6 in addition to the major one.</li> </ul>	(Palomares-Rius et al., 2011) (Perez-de-Castro et al., 2019)
<p><b><i>Alternaria cucumerina</i> resistance</b></p> <ul style="list-style-type: none"> <li>Two QTL of variation in lesion area in a cross between <i>Alternaria</i>-resistant parent MR-1 and the susceptible parent Ananas Yokneum.</li> </ul>	(Daley et al., 2017)
<p><b><i>Podosphaera xanthii</i> resistance</b></p> <ul style="list-style-type: none"> <li>Two major QTL in the cross Védreantais x PI 124112, <i>PmV.1</i> in the linkage group V which confers resistance to <i>P. xanthii</i> races 1, 2, and 3 and <i>PmXII.1</i> in the linkage group XII, which confers resistance to <i>P. xanthii</i> races 1, 2 and 5 and to <i>Golovinomyces cichoracearum</i> race 1.</li> <li>Two QTL for resistance to powdery mildew described in the cross TGR-1551 x Bola de Oro, a major one, dominant (LG V) and a minor one, recessive (LG VIII).</li> <li>Two linked loci in linkage group II, one conferring resistance to races 1 and 5 (denominated <i>Pm-x1,5</i>), and the second to race 3 (denominated <i>Pm-x3</i>), located 5.1 cM apart from the cross of PI 414723 x Védreantais.</li> </ul>	(Perchepied et al., 2005b) (Yuste-Lisbona et al., 2011b) (Fazza et al., 2013)

<ul style="list-style-type: none"> <li>• A major effective QTL on chr. 12, named <i>BPm12.1</i>, was identified in cross MR-1 x Top Mark.</li> <li>• Resistance to Px1A in 'Edisto 47' was controlled by two dominant genes mapped on LGII and LGV and resistance to Px1B was controlled by one dominant gene in a cross 'Edisto 47' x 'Queen'.</li> <li>• Powdery mildew resistance in MR-1 leaves was linked to a dominant gene (<i>PMRI</i>) on chr. 12, whereas stem resistance was under the control of a recessive gene (<i>pmrs</i>) on chr. 10, with the dominant gene having an epistatic effect on the recessive gene.</li> </ul>	<p>(Li et al., 2017)</p> <p>(Ning et al., 2014)</p> <p>(Cui et al., 2022a)</p>
<p><b><i>Pseudoperonospora cubensis</i> resistance</b></p> <ul style="list-style-type: none"> <li>• A major QTL for resistance to downy mildew described in the cross Védraçais x PI 124112.</li> <li>• Nine QTL in the cross MR-1 x Ananas Yok'neam, two major ones on chr. 10 and 8.</li> </ul>	<p>(Perchepped et al., 2005b)</p> <p>(Toporek et al., 2021)</p>
<p><b>Flowering-related traits</b></p> <ul style="list-style-type: none"> <li>• Ten QTL of flowering-related traits were detected, which explained 2.16–19.34% of the phenotypic variance. <i>mft2.1</i> and <i>fft2.1</i> were located in the same region, between CmSSR07071 and CmSSR07102. By gene annotation, 36 candidate genes were detected in this region, 26 of which were annotated.</li> </ul>	<p>(Wang et al., 2021)</p>
<p><b>Ovary shape and other ovary traits</b></p> <ul style="list-style-type: none"> <li>• Six QTL for ovary length, eight QTL for ovary width and six QTL for the ratio ovary length/ovary width described in the cross Védraçais x PI 161375 (RILs).</li> <li>• Five QTL for ovary shape in the cross Piel de Sapo x PI 161375 (NILs).</li> <li>• Resequencing analysis for ovary-related traits exhibited that two distinct parental lines (M1-32 female and X090 male) covered 97.48% and 96.02% of reference genome, and total 302,684 major SNPs yielded 3519 CAPS loci. An F<sub>2</sub> mapping population of 156 individuals was genotyped for genetic linkage mapping with novel 149 SNP-CAPS markers, and spanning total 4072 cM distance and 27.32 cM in average b/w adjacent markers on 12 chromosomes.</li> </ul>	<p>(Perin et al., 2002b)</p> <p>(Eduardo et al., 2007)</p> <p>(Amanullah et al., 2020)</p>
<p><b>Stigma color</b></p> <ul style="list-style-type: none"> <li>• A major QTL on chr. 6 and a minor on chr. 8 for controlling stigma color in a cross MR-1 (with green stigmas) x 'M1-32' (with yellow stigmas).</li> </ul>	<p>(Qiao et al., 2021)</p>
<p><b>Fruit traits</b></p> <ul style="list-style-type: none"> <li>• 31 QTL for fruit quality and fruit morphological traits in a cross of a Group <i>Flexuosus</i> genotype x a Group <i>Cantalupensis</i> genotype. A small segment of LG8 explained most of the phenotypic variation for yield. 8 new QTL for fruit shape, total fruit weight per plant, soluble solids concentration, flesh color, ovary shape and seed cell diameter and a locus for chlorosis were mapped.</li> <li>• Major QTL for fruit diameter and flesh thickness were identified on LG5 and LG11. 4 QTL responsible for netting width of fruit rind were co-localized with the QTL for netting density.</li> <li>• QTL for fruit size in chromosomes 6 and 11, fruit shape in chromosome 7 and 11, flesh color in chromosomes 2, 8 and 9, sucrose content and delayed climacteric behavior in chromosomes 5 and 10.</li> </ul>	<p>(Ramamurthy and Waters, 2015)</p> <p>(Wang et al., 2016)</p> <p>(Perpina et al., 2016)</p>
<p><b>Carotenoid content in mature fruit</b></p> <ul style="list-style-type: none"> <li>• Eight QTL for beta-carotene content distributed in four LG in the cross USDA 846-1 x Top Mark (RILs).</li> <li>• Three QTL for beta-carotene content in the cross Chinese line Q 3-2-2 (white flesh) x Top Mark (F<sub>2</sub>-F<sub>3</sub>).</li> <li>• Two QTL for total carotenoid content, two for beta-carotene, two for phytoene, one for alpha-carotene, and one for lutein described in the cross PI 414723 x Dulce (RI).</li> </ul>	<p>(Cuevas et al., 2008)</p> <p>(Cuevas et al., 2009)</p> <p>(Harel-Beja et al., 2010)</p>

<p><b>Earliness</b></p> <ul style="list-style-type: none"> <li>• Nine QTL described in the cross Piel de Sapo x PI 161375 (F<sub>2</sub> and DHLs).</li> <li>• Three QTL for early fruit maturity in the cross Chinese line Q 3-2-2 x Top Mark (F<sub>2</sub>-F<sub>3</sub>).</li> </ul>	<p>(Monforte et al., 2004) (Cuevas et al., 2009)</p>
<p><b>Ethylene production in fruit (climacteric crisis)</b></p> <ul style="list-style-type: none"> <li>• Four QTL described in the cross Védraçais x PI 161375 (RILs).</li> <li>• One QTL for ethylene production and climacteric response in the cross Piel de Sapo x PI 161375 (NILs), non-climacteric parental lines.</li> <li>• The QTL <i>ETHQV6.3</i> was detected on LG VI to induce climacteric ripening in the non-climacteric background (from Piel de Sapo and PI 161375).</li> <li>• <i>ETHQV6.3</i> likely corresponds <i>CmNAC-NOR</i>, encoding a NAC transcription factor that is closely related to the tomato <i>NOR</i> (non-ripening) gene.</li> <li>• A major QTL on chromosome 8, <i>ETHQV8.1</i>, sufficient to activate climacteric ripening in the cross Piel de Sapo x PI 161375</li> </ul>	<p>(Perin et al., 2002c) (Moreno et al., 2008) (Vegas et al., 2013) (Rios et al., 2017) (Pereira et al., 2020)</p>
<p><b>External color of the fruit</b></p> <ul style="list-style-type: none"> <li>• Four QTL described in the cross Piel de Sapo x PI 161375 (F<sub>2</sub> and DHLs).</li> <li>• Four QTL described in the cross Piel de Sapo x PI 161375 (NILs).</li> <li>• Thirteen QTL for skin color and 12 QTL for ground spot color using the three color components in the cross Piel de Sapo x PI 161375 (NILs).</li> </ul>	<p>(Monforte et al., 2004) (Eduardo et al., 2007) (Obando et al., 2008)</p>
<p><b>Fruit bitterness</b></p> <ul style="list-style-type: none"> <li>• Three QTL for bittener in a cross C68 (with non-bitter taste) x C69 (with bitter taste) in linkage groups II and V.</li> </ul>	<p>(Shang et al., 2020)</p>
<p><b>Fruit flesh color</b></p> <ul style="list-style-type: none"> <li>• Three QTL for orange flesh color described in the cross Piel de Sapo x PI 161375 (F<sub>2</sub> and DHLs).</li> <li>• Four QTL for fruit flesh color described in the cross Piel de Sapo x PI 161375 (NILs).</li> <li>• Sixteen QTL for flesh color and 10 QTL for juice color using the three color components in the cross Piel de Sapo x PI 161375 (NILs).</li> <li>• Three QTL for flesh color described in the cross PI 414723 x Dulce (RI).</li> </ul>	<p>(Monforte et al., 2004) (Eduardo et al., 2007) (Obando et al., 2008) (Harel-Beja et al., 2010)</p>
<p><b>Fruit content in ascorbic acid</b></p> <ul style="list-style-type: none"> <li>• One QTL in the in the cross Deltex x TGR-1551 (F<sub>2</sub>).</li> </ul>	<p>(Park et al., 2009a)</p>
<p><b>Fruit firmness</b></p> <ul style="list-style-type: none"> <li>• Two QTL for fruit firmness of the whole fruit in the cross PI 414723 x Dulce (RI).</li> <li>• QTL for fruit firmness identified using both genome-wide association study and biparental mapping. 11 SNPs across five (6, 8, 9, 11, and 12) chromosomes were found tightly linked to fruit firmness.</li> </ul>	<p>(Harel-Beja et al., 2010) (Nimmakayala et al., 2016)</p>
<p><b>Fruit flesh aroma profile</b></p> <ul style="list-style-type: none"> <li>• <i>Ester 3-hydroxy-2,4,4-trimethyl-pentyl 2-methylpropanoate</i>: Two QTL in the cross Piel de Sapo x PI 161375 (NILs).</li> <li>• <i>(Z,Z)-3,6 nonadiena</i>, responsible for the cucumber-like aroma: One QTL in the cross Piel de Sapo x PI 161375 (NILs).</li> <li>• <i>Octanal</i>: One QTL in the cross Piel de Sapo x PI 161375 (NILs).</li> </ul>	<p>(Obando-Ulloa et al., 2010)</p>
<p><b>Fruit flesh color</b></p> <ul style="list-style-type: none"> <li>• Three QTL for orange flesh color described in the cross Piel de Sapo x PI 161375 (F<sub>2</sub> and DHLs).</li> <li>• Four QTL for fruit flesh color described in the cross Piel de Sapo x PI 161375 (NILs).</li> <li>• Sixteen QTL for flesh color and 10 QTL for juice color using the three color components in the cross Piel de Sapo x PI 161375 (NILs).</li> <li>• Three QTL for flesh color described in the cross PI 414723 x Dulce (RI).</li> </ul>	<p>(Monforte et al., 2004) (Eduardo et al., 2007) (Obando et al., 2008) (Harel-Beja et al., 2010)</p>

<ul style="list-style-type: none"> <li>• A major gene for flesh color in a cross between light green ‘Tam Dew’ and orange fleshed ‘Dulce’. <i>CmOr</i>, a melon <i>Or</i> homolog, was described for the <i>gf</i> locus.</li> </ul>	(Tzuri et al., 2015)
<b>Fruit flesh firmness</b> <ul style="list-style-type: none"> <li>• Five QTL for flesh firmness in the cross Piel de Sapo x PI 161375 (NILs).</li> </ul>	(Moreno et al., 2008)
<b>Fruit flesh organic acid profile in mature fruit</b> <ul style="list-style-type: none"> <li>• Twenty-one QTL for organic acids in the cross Piel de Sapo x PI 161375 (NILs).</li> </ul>	(Obando-Ulloa et al., 2009)
<b>Fruit pedicel length</b> <ul style="list-style-type: none"> <li>• A major QTL controlling fruit pedicel length, <i>CmFpl3.1</i>, located on chr. 3.</li> </ul>	(Cui et al., 2022b)
<b>Fruit rind traits</b> <ul style="list-style-type: none"> <li>• Three QTL for stripes, three QTL for sutures in the cross PI 414723 x Dulce (RI).</li> </ul>	(Harel-Beja et al., 2010)
<b>Fruit shape</b> <ul style="list-style-type: none"> <li>• Four QTL for fruit length, 5 QTL for fruit width and 6 QTL for the ratio fruit length/fruit width described in the cross Védreantais x PI 161375.</li> <li>• Four QTL for fruit length, one for fruit width and two for the ratio fruit length: fruit width described in the cross Védreantais x PI 414723, which are common to both crosses.</li> <li>• Eight QTL for fruit shape described in the cross Piel de Sapo x PI 161375 (F<sub>2</sub> and DHLs).</li> <li>• Eleven QTL for fruit length, 10 QTL for fruit width and 15 QTL for the ratio fruit length/fruit width described in the cross Piel de Sapo x PI 161375 (NILs).</li> <li>• Two QTL for fruit length, 2 QTL for fruit width and QTL for the ratio fruit length/fruit width described in the PI 414723 x Dulce (RI).</li> <li>• QTL for fruit shape co-localized with OFP family members.</li> <li>• Five QTL for fruit length, 2 for fruit diameter, 3 for fruit shape in the cross Piel de Sapo x PI 124112.</li> <li>• A major QTL for fruit shape corresponding to <i>CmACS7</i> in chromosome 2.</li> </ul>	(Perin et al., 2002b) (Perin et al., 2002b) (Monforte et al., 2004) (Eduardo et al., 2007; Fernandez-Silva et al., 2010) (Harel-Beja, 2010) (Monforte et al., 2014) (Diaz et al., 2014) (Boualem et al., 2022)
<b>Fruit weight</b> <ul style="list-style-type: none"> <li>• Six QTL described in the cross Piel de Sapo x PI 161375 (F<sub>2</sub> and DHLs).</li> <li>• Eleven QTL described in the cross Piel de Sapo x PI 161375 (NILs).</li> <li>• QTL for fruit weight co-localized frequently with members of the CNR/FW2.2 and KLUH/FW3.2 families</li> </ul>	(Monforte et al., 2004) (Eduardo et al., 2007) (Monforte et al., 2014)
<b>Postharvest life traits</b> <ul style="list-style-type: none"> <li>• Three QTL involved in reduced postharvest losses and 11 with a detrimental effect on fruits after storage in the cross Piel de Sapo x PI 161375 (NILs).</li> </ul>	(Fernandez-Trujillo et al., 2007)
<b>Sensory traits</b> <ul style="list-style-type: none"> <li>• Thirty-two QTL including global appreciation, sweetness, sourness in the cross Piel de Sapo x PI 161375 (NILs).</li> </ul>	(Obando-Ulloa et al., 2009)

<p><b>Sugar content of fruit flesh in mature fruit</b></p> <ul style="list-style-type: none"> <li>• Five QTL for soluble solid content described in the cross Piel de Sapo x PI 161375 (F<sub>2</sub> and DHLs).</li> <li>• QTL for sucrose, total sucre soluble in the cross TAM Dulce x TGR-1551 (F<sub>2</sub>).</li> <li>• Fifteen QTL for soluble solid content in the cross Piel de Sapo x PI 161375 (NILs).</li> <li>• Twenty-seven QTL for sugars, eight for fructose, six for glucose, four for sucrose, nine for sucrose equivalents in the cross Piel de Sapo x PI 161375 (NILs).</li> <li>• Six QTL for sucrose, total sucre soluble in the cross Deltex x TGR-1551 (F<sub>2</sub>).</li> <li>• Six QTL for sucrose, total sucre soluble in the cross PI 414723 x Dulce (RI).</li> <li>• Sweet trait-related QTL located on chromosomes 6, 10, 11 and 12; sour trait-related QTL on chromosomes 2, 3, 4, 5, 9 and 12 in Fengwei melons and its parents Shouxing as the female and Xinguowei as the male parent.</li> <li>• Sugar content QTL located on chromosomes 4, 5 and 7 in a cross of Piel de Sapo x Songwhan Charmi and other segregating populations.</li> </ul>	<p>(Monforte et al., 2004)</p> <p>(Sinclair et al., 2006)</p> <p>(Eduardo et al., 2007)</p> <p>(Obando-Ulloa et al., 2009)</p> <p>(Park et al., 2009a)</p> <p>(Harel-Beja et al., 2010)</p> <p>(Zhang et al., 2016)</p> <p>(Argyris et al., 2017)</p>
<p><b>Root growth and architecture</b></p> <ul style="list-style-type: none"> <li>• Seventeen QTL for root traits in the cross Piel de Sapo x PI 161375 (NILs).</li> </ul>	<p>(Fita et al., 2008)</p>
<p><b>Trichomes</b></p> <ul style="list-style-type: none"> <li>• An oligenic model for the inheritance of the character with an important additive component and strong epistatic relationships between loci. The character is controlled by one major QTL, <i>tric11</i>.</li> </ul>	<p>(Palomeras-Rius et al., 2016)</p>
<p><b>Yield-related traits</b></p> <ul style="list-style-type: none"> <li>• Four QTL for primary branch number, five QTL for fruit number per plant, four QTL for fruit weight per plant, two QTL for average weight per fruit and one QTL for percentage of mature fruit per plot in the cross USDA 846-1 x Top Mark (RILs).</li> </ul>	<p>(Zalapa et al., 2007)</p>

**Table 3. List of transgenics developed in melon for quality, biotic and abiotic stress-related traits (modified from Kesh and Kaushik, 2021).**

Traits improved	Transgene description	Transformation method	References
<i>Pest/Disease resistance</i>			
<i>Aphis gossypii</i>	CC-NBS-LRR gene, named <i>Vat</i>	<i>Agrobacterium tumefaciens</i>	(Dogimont et al., 2014)
CMV resistance	CP gene or CMV	<i>Agrobacterium tumefaciens</i>	(Yoshioka et al., 1992)
CMV resistance	CP gene of CMV-WL	<i>Agrobacterium tumefaciens</i>	(Gonsalves et al., 1994)
CMV resistance	Polyribozyme against CMV	<i>Agrobacterium tumefaciens</i>	(Plages, 1997)
ZYMV resistance	ZYMV coat protein	<i>Agrobacterium tumefaciens</i>	(Yalcin-Mendi et al., 2004)
ZYMV resistance	CP gene	<i>Agrobacterium tumefaciens</i>	(Wu et al., 2009)
Resistance against ZYMV and WMV	CP gene of ZYMV, WMV and CMV	-	(Clough and Hamm, 1995)
Potyvirus resistance	ZYMV-CP gene	<i>Agrobacterium tumefaciens</i>	(Fang and Grumet, 1993)
Potyvirus resistance	Polyribozyme	-	(Huttner et al., 2001)
Potyvirus resistance	CP genes of ZYMV and PRSV-W	<i>Agrobacterium tumefaciens</i>	(Wu et al., 2010)
Downy mildew resistance	<i>eR</i> genes <i>At1</i> and <i>At2</i>	<i>Agrobacterium tumefaciens</i>	(Taler et al., 2004)
Fungal disease resistance	<i>Chitinase</i> and $\beta$ - <i>Glucanase</i> genes	<i>Agrobacterium tumefaciens</i>	(Akbari et al., 2013)
Fusarium wilt resistance	Antisense vector		(Li et al., 2019)
Resistance against glufosinate ammonium-based herbicides.	<i>Bar</i> gene	ZYMV-AGII (Potyvirus based vector)	(Shiboleth et al., 2001)
<i>Flower and fruit quality traits</i>			
Sex expression	ACS synthase	<i>Agrobacterium tumefaciens</i>	(Papadopoulou et al., 2005)
Bisexual and female flowers	<i>CmACS-7</i>	<i>Agrobacterium tumefaciens</i>	(Zhang et al., 2014)
Early flowering	<i>CmFT</i>	<i>Agrobacterium-mediated</i>	(Zhang and Zhang, 2020)
Fruit development and sucrose content	<i>MAI1</i> (acid invertase gene)	<i>Agrobacterium tumefaciens</i>	(Yu et al., 2008)
Ripening behaviour	SAMase (S-adenosylmethionine hydrolase)	<i>Agrobacterium tumefaciens</i>	(Clendennen et al., 1999)
Ripening behavior	ACC oxidase gene	<i>Agrobacterium tumefaciens</i>	(Silva et al., 2004)
Reduced ethylene production	ACC Oxidase gene	<i>Agrobacterium tumefaciens</i>	(Guis et al., 2000)
Reduced ethylene production	<i>pAP4</i> gene	<i>Agrobacterium tumefaciens</i>	(Nora et al., 2001)
Improved shelf life	ACC oxidase gene	<i>Agrobacterium tumefaciens</i>	(Ayub et al., 1996; Nuñez-Palenius et al., 2006)
Aroma	Two ADH genes	<i>Agrobacterium tumefaciens</i>	(Kocaman et al., 2016)
Aroma	<i>Cm-AAT (1, 3 and 4)</i>	<i>Agrobacterium tumefaciens</i>	(Izgu et al., 2016)
Gene escape	ZYMV resistance	<i>Agrobacterium tumefaciens</i>	(Yalcin-Mendi et al., 2010)
<i>Abiotic stress tolerance</i>			
Salt tolerance	<i>HAL1</i> gene	<i>Agrobacterium tumefaciens</i>	(Bordas et al., 1997; Serrano et al., 1999)

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