

# The Genes of Watermelon

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**Abstract.** Watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai] is a major vegetable crop in the world, accounting for 6.8% of the world area devoted to vegetable crops. Watermelon is a useful vegetable crop for genetic research because of its small genome size, and the many available gene mutants. The watermelon genes were originally organized and summarized in 1944, and have been expanded and updated periodically. However, the action of some watermelon genes has not been described clearly in some cases. Also, the interaction of multiple gene loci that control similar traits needs to be described more clearly. Finally, it is necessary to identify the inbred lines having each published gene mutant, for use as type lines in studies of gene action, allelism, and linkage. The objective of this work was to update the gene list, identify the cultivar or line having each gene mutant, and collect seeds of the lines for use by interested researchers. In addition, the gene descriptions were expanded and clarified, information on gene interactions was added, and errors in naming or citing previously described genes were corrected. New genes that have not previously been described (*cr*, *Ctr*, *dw-3*, *ms-2*, *Ti*, *ts* and *zym-FL*) were added to the list, for a total of 163 watermelon gene mutants.

Watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai) is a major cucurbit crop that accounts for 6.8% of the world area devoted to vegetable crops (FAO, 2002). Watermelon is grown for its fleshy, juicy, and sweet fruit. Mostly eaten fresh, they provide a delicious and refreshing dessert especially in hot weather. The watermelon has high lycopene content in the red-fleshed cultivars: 60% more than tomato. Lycopene has been classified as useful in the human diet for prevention of heart attacks and certain types of cancer.

Watermelon is native to central Africa where it was domesticated as a source of water, a staple food crop, and an animal feed. It was cultivated in Africa and the Middle East for >4000 years, then introduced to China around 900 AD, and finally brought to the New World in the 1500s. There are 1.3 million ha of watermelon grown in the world, with China and the Middle Eastern countries the major consumers. China is the largest watermelon producer, with 68.9% of the total production. The other major watermelon producing countries are Turkey, Iran, Egypt, United States, Mexico, and Korea (FAO, 2002). In the United States, watermelon is used fresh as a dessert, or in salads. U.S. production is concentrated in Florida, California, Texas, and Georgia (USDA, 2002), increasing from 1.2 Mt in 1980 to 3.9 Mt in 2002, with a farm value of \$329 million (USDA, 2002).

Watermelon is a useful crop species for genetic research because of its small genome size, and the many available gene mutants. Genome size of watermelon is 424 million base pairs. DNA sequence analysis revealed high conservation useful for comparative genomic analysis with other plant species, as well as within the Cucurbitaceae. Like some of the other cultivated cucurbits, watermelon

has much genetic variability in seed and fruit traits. Genetic investigations have been made for some of those, including seed color, seed size, fruit shape, rind color, rind pattern, and flesh color.

This is the latest version of the gene list for watermelon. The watermelon genes were originally organized and summarized by Poole (1944). The list and updates of genes for watermelon have been expanded and published by Robinson et al. (1976), the Cucurbit Gene List Committee (1979, 1982, and 1987), Henderson (1991 and 1992), Rhodes and Zhang (1995), and Rhodes and Dane (1999). This current gene list provides an update of the known genes of watermelon, with 163 total mutants grouped into seed and seedling mutants, vine mutants, flower mutants, fruit mutants, resistance mutants, protein (isozyme) mutants, DNA (RFLP and RAPD) markers, and cloned genes.

This gene list has been modified from previous lists in that we have 1) added or expanded the description of the phenotypes of many of the gene mutants, 2) added descriptions for phenotypes of interacting gene loci, 3) identified the type lines that carry each form of each gene, 4) identified the gene mutant lines that are in the curator collections, and 5) added genes that have not previously been described: *cr* (El-Hafez et al., 1981), *Ctr* (Provvidenti, 1992), *dw-3* (Hexun et al., 1998), *ms-2* (Dyutin, and Sokolov, 1990), *Ti* (Tanaka et al., 1995), *ts* (Zhang et al., 1994a), and *zym-FL* (Provvidenti, 1991). We had intended to include a review of gene linkage, but few reports were found except for sets of molecular markers in wide crosses of *Citrullus*. Finally, we attempted to correct some of the errors in gene descriptions or references from previous lists.

## Gene Mutants

*Seed and seedling mutants.* Three major genes control seed coat color: *r* (Poole et

al., 1941), *t* (McKay, 1936), and *w* (Poole et al., 1941) for red, tan, and white seed coat, respectively. The genes interact to produce six phenotypes: black (*RR TT WW*); clump (*RR TT ww*); tan (*RR tt WW*); white with tan tip (*RR tt ww*); red (*rr tt WW*); and white with pink tip (*rr tt ww*). A fourth gene, *d* was suggested by Poole et al. (1941) as a modifier, producing black dotted seed coat when dominant for *r*, *t*, and *w* but having no effect on other genotypes.

The genes (*s*) and (*l*) for short and long seed length (sometimes called small and large seed size) control seed size, with *s* epistatic to *l* (Poole et al., 1941). The genotype *LLSS* gives medium size, *llSS* gives long, and *LLss* or *llss* gives short seeds. The *Ti* gene for tiny seed was reported by Tanaka et al. (1995). Tiny seed from 'Sweet Princess' was dominant over medium-size seed and controlled by a single dominant gene. The small seed gene behaved in a manner different from Poole's medium-size seed cultivar. Tanaka et al. (1995) suggested that the *Ti* gene was different from the *s* and *l* genes. Unfortunately, the origin of short and long seed genes was not described in Poole's paper.

Tomato seed is shorter and narrower than the short seeded genotype, *llss* (width × length: 2.6 × 4.2 mm). It is controlled by the *ts* (Zhang et al., 1994a) gene, with genotype *LL ss tsts*. Cracked seed coat *cr* (El-Hafez et al., 1981) is inherited as a single gene that is recessive to noncracked seed coat. Egusi seed *eg* (Gusmini et al., 2003) has fleshy pericarp covering the seeds. After washing and drying, the seeds are difficult to distinguish from normal.

*Vine mutants.* Several genes control leaf or foliage traits of watermelon. Nonlobed leaf (*nl*) has the entire leaf rather than the lobed leaf type of the typical watermelon (Mohr, 1953). Seedling leaf variegation *slv* (Provvidenti, 1994) causes a variegation resembling virus infection on seedlings. It is linked or pleiotropic with *Ctr* for cool temperature resistance. The yellow leaf (*Yl*) gene results in yellow leaves, and is incompletely dominant to green leaves (Warid and Abd-El-Hafez, 1976). Delayed green leaf *dg* (Rhodes, 1986) causes pale green cotyledons and leaves for the first few nodes, with later leaves developing the normal green color. Inhibitor of delayed green leaf (*i-dg*) makes leaves normal green even when they have *dgdg* genotype (Rhodes, 1986). The juvenile albino *ja* (Zhang et al., 1996b) gene causes reduced chlorophyll in seedling tissues, as well as leaf margins and fruit rind when plants are grown under short day conditions. The dominant gene *Sp* (Poole, 1944) causes round yellow spots to form on cotyledons, leaves and fruit, resulting in the fruit pattern called moon and stars.

So far, four dwarf genes of watermelon have been identified that affect stem length and plant habit: *dw-1* (Mohr, 1956) and *dw-1<sup>s</sup>* (Dyutin and Afanas'eva, 1987) are allelic, and *dw-1*, *dw-2* (Liu and Loy, 1972), and *dw-3* (Hexun et al., 1998) are non-allelic. Dwarf-1 plants have short internodes due to fewer and shorter cells than the normal plant type. Plants with *dw-1<sup>s</sup>* have vine length intermediate between normal and dwarf, and the hypocotyls were somewhat

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Table 1. The genes of watermelon.

Gene	Synonym	Character
<i>a</i>	---	<i>andromonoecious</i> ; recessive to monoecious; <i>a</i> from 'Angeleno' (black seeded); <i>A</i> from cultivars 'Conqueror' and 'Klondike'.
<i>Aco-1</i>	---	<i>Aconitase-1</i> .
<i>Aco-2</i>	---	<i>Aconitase-2</i> .
<i>Adh-1</i>	---	<i>Alcohol dehydrogenase-1</i> ; one of five codominant alleles, each regulating one band
<i>Adh-1<sup>1</sup></i>	---	<i>Alcohol dehydrogenase-1<sup>1</sup></i> ; one of five codominant alleles, each regulating one band; found in <i>C. lanatus</i> var. <i>citroides</i> and <i>C. colocynthis</i> .
<i>Adh-1<sup>2</sup></i>	---	<i>Alcohol dehydrogenase-1<sup>2</sup></i> ; one of five codominant alleles, each regulating one band; found in <i>C. lanatus</i> var. <i>citroides</i> and <i>C. colocynthis</i> .
<i>Adh-1<sup>3</sup></i>	---	<i>Alcohol dehydrogenase-1<sup>3</sup></i> ; one of five codominant alleles, each regulating one band; found in <i>Praecitrullus fistulosus</i> .
<i>Adh-1<sup>4</sup></i>	---	<i>Alcohol dehydrogenase-1<sup>4</sup></i> ; one of five codominant alleles, each regulating one band; found in <i>Acanthosicyos naudinianus</i> .
<i>Af</i>	---	<i>Aulacophora faveicollis</i> resistance; resistance to the red pumpkin beetle; dominant to susceptibility; <i>Af</i> from SI.72 and SI.98 inbreds; <i>af</i> from 'Sugar Baby'.
<i>Aps-1</i>	<i>Acph-A</i>	<i>Acid phosphatase-1</i> .
<i>Aps-2<sup>1</sup></i>	---	<i>Acid phosphatase-2<sup>1</sup></i> ; one of two codominant alleles, each regulating one band; found in <i>C. lanatus</i> and <i>C. colocynthis</i> .
<i>Aps-2<sup>2</sup></i>	---	<i>Acid phosphatase-2<sup>2</sup></i> ; one of two codominant alleles, each regulating one band; found in <i>Acanthosicyos naudinianus</i> .
<i>Ar-1</i>	<i>B Gc</i>	<i>Anthracnose resistance to races 1 and 3 of Glomerella cingulata</i> var. <i>orbiculare</i> ( <i>Colletotrichum lagenarium</i> ); <i>Ar-1</i> from 'Africa 8'*; 'Africa 9'*; and 'Africa 13'* and 'Charleston Gray'*; <i>ar-1</i> from 'Iowa Belle 476', 'Iowa Belle 487'* and N.C.9-2, N.C.11, and 'New Hampshire Midget'*.
<i>Ar-2<sup>1</sup></i>	---	<i>Anthracnose resistance to race 2 of Colletotrichum lagenarium</i> ; <i>Ar-2-1</i> from W695 citron* and PI 189225, PI 271775, PI 271779, and PI 299379**; <i>ar-2-1</i> from 'Allsweet', 'Charleston Gray', and 'Florida Giant'; resistance in <i>Citrullus colocynthis</i> is due to other dominant factors; resistance from R309***; susceptibility from 'New Hampshire Midget'.
<i>B</i>	<i>Y</i>	<i>Yellow flesh</i> ; <i>Wf</i> is epistatic to <i>B</i> ( <i>Y</i> renamed <i>B</i> by Henderson); <i>WfWfBB</i> or <i>WfWfbb</i> white fleshed; <i>wfwfBB</i> yellow fleshed; <i>wfwfbb</i> red fleshed; flesh color segregated into 12 white, 3 yellow and 1 red in the F <sub>2</sub> ; <i>B</i> from breeding line V.No.3 and <i>b</i> from V.No.1.
<i>C</i>	---	<i>Canary yellow flesh</i> ; dominant to pink; <i>i</i> inhibitory to <i>C</i> , resulting in red flesh; in the absence of <i>i</i> , <i>C</i> is epistatic to <i>Y</i> ; <i>CC</i> from 'Honey Cream'*; <i>cc</i> from 'Dove'*; <i>CCYYI-C I-C</i> from 'Yellow Baby' F1** and 'Yellow Doll' F1**; <i>cc y<sup>o</sup> I-C I-C</i> from 'Tendersweet Orange Flesh'*; <i>cc yy I-C I-C</i> from 'Golden Honey'*; <i>cc YY i-C i-C</i> from 'Sweet Princess'*.
<i>cr</i>	---	<i>cracked seed coat</i> ; recessive to <i>Cr</i> (non-cracked) seed coat; <i>cr</i> from 'Leeby' and <i>Cr</i> from 'Kaho' and 'Congo'.
<i>Ctr</i>	---	<i>Cool temperature resistance</i> ; <i>Ctr</i> from line PP261-1 (a single plant selection of PI 482261 from Zimbabwe); <i>ctr</i> from 'New Hampshire Midget'; resistant to leaf mosaic injury when grown at air temperature below 20°C.
<i>d</i>	---	<i>dotted seed coat</i> ; black dotted seeds when dominant for color genes <i>r</i> , <i>t</i> , and <i>w</i> ; <i>d</i> is a specific modifier of black seed coat color wherein <i>RR TT WW DD</i> is solid black and <i>RR TT WW dd</i> is dotted black seed coat; <i>d</i> from 'Klondike' and 'Hope Giant'; <i>D</i> from 'Winter Queen'.
<i>db</i>	---	<i>Resistance to gummy stem blight</i> caused by <i>Didymella bryoniae</i> ; <i>db</i> from PI 189225; <i>Db</i> from 'Charleston Gray'.
<i>dg</i>	---	<i>delayed green</i> ; cotyledons and young leaves are initially pale green but later develop chlorophyll; first reported to be hypostatic to <i>I-dg</i> ; more recent evidence indicates a simple recessive; <i>dg</i> from breeding line 'Pale 90'; <i>Dg</i> from 'Allsweet'.
<i>Dia-1</i>	---	<i>Diaphorase-1</i>
<i>dw-1</i>	---	<i>dwarf-1</i> ; short internodes, due to fewer and shorter cells than normal forms; allelic to <i>dw-1<sup>1</sup></i> ; <i>dw-1</i> from 'Bush Desert King' (also, 'Bush Charleston Gray', 'Bush Jubilee', 'Sugar Bush'); <i>Dw-1</i> from 'Sugar Baby' and 'Vine Desert King'.
<i>dw-1<sup>1</sup></i>	---	<i>short vine</i> ; allelic to <i>dw-1</i> ; vine length intermediate between normal and dwarf; hypocotyl somewhat longer than normal vine and considerably longer than dwarf; <i>dw-1<sup>1</sup></i> recessive to normal; <i>dw-1<sup>1</sup></i> from 'Somali Local' (All-Union Research Institute of Plant Growing No.4641).
<i>dw-2</i>	---	<i>dwarf-2</i> ; short internodes, due to fewer cells; <i>dw-2</i> from inbred line WB-2; <i>Dw-2</i> from 'Sugar Baby' and 'Vine Desert King'.
<i>dw-3</i>	---	<i>dwarf-3</i> ; dwarf with fewer leaf lobes (intermediate between normal leaf and non-lobed leaf); <i>dw-3</i> from 'Dwarf Male-Sterile Watermelon (DMSW)'; <i>Dw-3</i> from 'Changhui', 'Fuyandagua', and 'America B'.
<i>e</i>	<i>t</i>	<i>explosive rind</i> ; thin, tender rind, bursting when cut; <i>e</i> from 'California Klondike'; <i>E</i> from 'Thurmond Gray'.
<i>eg</i>	---	<i>egusi seed</i> ; seeds with fleshy pericarp; <i>eg</i> from PI 490383 selection NCG-529 and PI 560006; <i>Eg</i> from 'Calhoun Gray' and 'Charleston Gray'.
<i>Est-1</i>	---	<i>Esterase-1</i> ; one of six codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Est-1<sup>1</sup></i>	---	<i>Esterase-1<sup>1</sup></i> ; one of six codominant alleles, each regulating one band; found in <i>C. lanatus</i> var. <i>citroides</i> and <i>C. colocynthis</i> .
<i>Est-1<sup>2</sup></i>	---	<i>Esterase-1<sup>2</sup></i> ; one of six codominant alleles, each regulating one band; found in <i>C. colocynthis</i> .
<i>Est-1<sup>3</sup></i>	---	<i>Esterase-1<sup>3</sup></i> ; one of six codominant alleles, each regulating one band; found in <i>Praecitrullus fistulosus</i> .
<i>Est-1<sup>4</sup></i>	---	<i>Esterase-1<sup>4</sup></i> ; one of six codominant alleles, each regulating one band; found in <i>C. ecirrhosus</i> .
<i>Est-1<sup>5</sup></i>	---	<i>Esterase-1<sup>5</sup></i> ; one of six codominant alleles, each regulating one band; found in <i>Acanthosicyos naudinianus</i> .
<i>Est-2</i>	---	<i>Esterase-2</i> ; one of five codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Est-2<sup>1</sup></i>	---	<i>Esterase-2<sup>1</sup></i> ; one of five codominant alleles, each regulating one band; found in <i>C. colocynthis</i> .
<i>Est-2<sup>2</sup></i>	---	<i>Esterase-2<sup>2</sup></i> ; one of five codominant alleles, each regulating one band; found in <i>C. colocynthis</i> .
<i>Est-2<sup>3</sup></i>	---	<i>Esterase-2<sup>3</sup></i> ; one of five codominant alleles, each regulating one band; found in <i>Praecitrullus fistulosus</i> .
<i>Est-2<sup>4</sup></i>	---	<i>Esterase-2<sup>4</sup></i> ; one of five codominant alleles, each regulating one band; found in <i>Acanthosicyos naudinianus</i> .
<i>f</i>	---	<i>furrowed fruit surface</i> ; recessive to smooth; type inbreds not given; <i>f</i> like 'Stone Mountain' or 'Black Diamond'; <i>F</i> like 'Mickylee'.
<i>Fdp-1</i>	---	<i>Fructose 1,6 diphosphatase-1</i> .
<i>Fo-1</i>	---	<i>Fusarium wilt resistance for race 1</i> ; dominant gene for resistance to race 1 of <i>Fusarium oxysporum</i> f. sp. <i>niveum</i> ; <i>Fo-1</i> from 'Calhoun Gray' and 'Summit'; <i>fo-1</i> from 'New Hampshire Midget'.
<i>For-1</i>	---	<i>Fructose 1,6 diphosphatase-1</i> .
<i>Fwr</i>	---	<i>Fruit fly resistance caused by Dacus cucurbitae</i> ; dominant to susceptibility; <i>Fwr</i> from breeding lines J 18-1 and J 56-1; <i>fwr</i> from 'New Hampshire Midget', 'Bykovski', 'Red Nectar' and breeding line 'J 20-1'.
<i>g</i>	<i>d</i>	<i>light green fruit rind pattern</i> ; light green fruit recessive to dark green ( <i>G</i> ) and striped green ( <i>g</i> ); <i>g</i> from 'Thurmond Gray' and <i>G</i> from 'California Klondike'.
<i>g<sup>s</sup></i>	<i>d<sup>s</sup></i>	<i>striped green fruit rind pattern</i> ; recessive to dark green but dominant to light green skin; <i>g<sup>s</sup></i> from 'Golden Honey'; <i>G</i> from 'California Klondike'.
<i>Gdh-1</i>	---	<i>Glutamate dehydrogenase-1</i> ; isozyme located in cytosol.
<i>Gdh-2</i>	---	<i>Glutamate dehydrogenase-2</i> ; isozyme located in plastids.
<i>gf</i>	---	<i>light green flower color</i> ; <i>gf</i> from 'KW-695' and 'Dalgona'; <i>Gf</i> from Korean watermelon accession 'SS-4'.
<i>gms</i>	<i>ms<sub>g</sub></i>	<i>glabrous male sterile</i> ; foliage lacking trichomes; male sterile caused by chromosome desynapsis (named glabrous male sterile by Robinson*); <i>gms</i> from 'Sugar Baby' irradiated with gamma rays.
<i>go</i>	<i>c</i>	<i>golden yellow color of older leaves and mature fruit</i> ; (named golden by Robinson*); <i>go</i> from 'Royal Golden'; <i>Go</i> from 'NC 34-9-1' and 'NC 34-2-1'.
<i>Got-1</i>	---	<i>Glutamate oxaloacetate transaminase-1</i> ; one of four codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Got-1<sup>1</sup></i>	---	<i>Glutamate oxaloacetate transaminase-1<sup>1</sup></i> ; one of four codominant alleles, each regulating one band; found in <i>C. colocynthis</i> and <i>Praecitrullus fistulosus</i> .
<i>Got-1<sup>2</sup></i>	---	<i>Glutamate oxaloacetate transaminase-1<sup>2</sup></i> ; one of four codominant alleles, each regulating one band; found in <i>C. lanatus</i> var. <i>citroides</i> .
<i>Got-1<sup>3</sup></i>	---	<i>Glutamate oxaloacetate transaminase-1<sup>3</sup></i> ; one of four codominant alleles, each regulating one band; found in <i>Acanthosicyos naudinianus</i> .
<i>Got-2</i>	---	<i>Glutamate oxaloacetate transaminase-2</i> ; one of five codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Got-2<sup>1</sup></i>	---	<i>Glutamate oxaloacetate transaminase-2<sup>1</sup></i> ; one of five codominant alleles, each regulating one band; found in <i>C. colocynthis</i> .
<i>Got-2<sup>2</sup></i>	---	<i>Glutamate oxaloacetate transaminase-2<sup>2</sup></i> ; one of five codominant alleles, each regulating one band; found in <i>C. ecirrhosus</i> .
<i>Got-2<sup>3</sup></i>	---	<i>Glutamate oxaloacetate transaminase-2<sup>3</sup></i> ; one of five codominant alleles, each regulating one band; found in <i>Praecitrullus fistulosus</i> .

References <sup>a</sup>	Supplemental references <sup>c</sup>	Available <sup>b</sup>
Rosa, 1928	Porter, 1937; Poole, 1944	C
Navot et al., 1990	---	M
Navot et al., 1990	---	M
Navot and Zamir 1986, 1987; Zamir et al., 1984	---	M
Navot and Zamir 1986, 1987; Zamir et al., 1984	---	M
Navot and Zamir 1986, 1987; Zamir et al., 1984	---	M
Navot and Zamir 1986, 1987; Zamir et al., 1984	---	M
Navot and Zamir 1986, 1987; Zamir et al., 1984	---	M
Vashishta and Choudhury, 1972	---	?
Navot et al., 1990; Navot and Zamir 1986, 1987; Zamir et al., 1984	---	M
Navot et al., 1990; Navot and Zamir 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir 1986, 1987	---	M
Layton 1937*	Hall et al., 1960; Robinson et al., 1976; Winstead et al., 1959**	C
Winstead et al., 1959*	Love and Rhodes, 1988***, 1991; Sowell et al., 1980**; Suvanprakorn and Norton, 1980	P
Shimotsuama, 1963	Henderson, 1992	?
Poole, 1944*	Henderson et al., 1998**	C
El-Hafez et al., 1981	---	?
Provvidenti, 1992	Provvidenti, 2003	P
Poole et al., 1941	Poole, 1944; Kanda, 1951	C
Norton, 1979	---	P
Rhodes, 1986	---	?
Navot et al., 1990	---	M
Mohr, 1956	Liu and Loy, 1972	C
Dyutin and Afanas'eva, 1987	---	?
Liu and Loy, 1972	Mohr and Sandhu, 1975	?
Hexun et al., 1998	---	?
Porter, 1937	Poole, 1944	?
Gusmini et al., 2003	---	C
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Poole, 1944	---	?
Navot et al., 1990; Navot and Zamir, 1986	---	M
Henderson et al., 1970	Netzer and Weintall, 1980	C
Navot et al., 1990	---	M
Khandelwal and Nath, 1978	---	?
Weetman, 1937	Poole, 1944; Porter, 1937	?
Weetman, 1937	Poole, 1944	C
Navot and Zamir, 1986	---	M
Navot et al., 1990; Navot and Zamir, 1986	---	M
Kwon and Dane, 1999	---	?
Watts, 1962, 1967	Robinson et al., 1976*; Ray and Sherman, 1988	?
Barham, 1956	Robinson et al., 1976*	C
Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984	---	M

Table 1 (continued). The genes of watermelon.

Gene	Synonym	Character
<i>Got-2<sup>d</sup></i>	---	<i>Glutamate oxaloacetate transaminase-2<sup>d</sup></i> ; One of five codominant alleles, each regulating one band; found in <i>Acanthosicyos naudinianus</i> .
<i>Got-3</i>	---	<i>Glutamate oxaloacetate transaminase-3</i> .
<i>Got-4</i>	---	<i>Glutamate oxaloacetate transaminase-4</i> .
<i>hsp-70</i>	---	<i>heat shock protein 70</i> ; one gene presequence 72-kDa hsp70 is modulated differently in glyoxomes and plastids.
<i>i-dg</i>	---	<i>inhibitor of delayed green</i> ; Epistatic to <i>dg</i> ; <i>I-dg I-dg dgdg</i> plants are pale green; and <i>i-dg i-dg dgdg</i> plants are normal; <i>dg</i> from breeding line Pale 90; <i>Dg</i> from 'Allsweet'; <i>i-dg</i> gene was lost when advanced inbreds were made.
<i>ldh-1</i>	---	<i>Isocitrate dehydrogenase-1</i>
<i>i-C</i>	<i>i</i>	<i>inhibitor of canary yellow</i> , resulting in red flesh (renamed by Rhodes and Dane*); <i>CCYY I-C I-C</i> from 'Yellow Baby' F1 and 'Yellow Doll' F1; <i>cc y<sup>y</sup> I-C I-C</i> from 'Tendersweet Orange Flesh'; <i>cc yy I-C I-C</i> from 'Golden Honey'; <i>cc YY i-C i-C</i> from 'Sweet Princess'.
<i>ja</i>	---	<i>juvenile albino</i> ; chlorophyll in seedlings, leaf margins, and fruit rind reduced when grown under short days; <i>ja</i> from 'Dixielee mutant' and 'G17AB' F2; <i>Ja</i> from 'Sweet Princess' and '20J57'.
<i>l</i>	---	<i>long (or large) seeds</i> ; interacts with <i>s</i> ; long recessive to medium or short; <i>LL SS</i> for medium, <i>ll SS</i> for long, and <i>LL ss</i> or <i>ll ss</i> for short seed; <i>ll SS</i> from 'Peerless'; <i>LL SS</i> from 'Klondike'; <i>LL ss</i> from 'Baby Delight'.
<i>Lap-1</i>	---	<i>Leucine aminopeptidase-1</i> .
<i>m</i>	---	<i>mottled skin</i> ; greenish white mottling of fruit skin; <i>m</i> from 'Iowa Belle' and <i>M</i> from 'Japan 4'.
<i>Mdh-1</i>	---	<i>Malic dehydrogenase-1</i> ; one of two codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Mdh-1<sup>1</sup></i>	---	<i>Malic dehydrogenase-1<sup>1</sup></i> ; one of two codominant alleles, each regulating one band; found in <i>Praecitrullus fistulosus</i> .
<i>Mdh-2</i>	---	<i>Malic dehydrogenase-2</i> ; one of three codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Mdh-2<sup>1</sup></i>	---	<i>Malic dehydrogenase-2<sup>1</sup></i> ; one of three codominant alleles, each regulating one band; found in <i>C. colocynthis</i> .
<i>Mdh-2<sup>2</sup></i>	---	<i>Malic dehydrogenase-2<sup>2</sup></i> ; one of three codominant alleles, each regulating one band; found in <i>Praecitrullus fistulosus</i> .
<i>Me-1</i>	---	<i>Malic enzyme-1</i> ; one of three codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Me-1<sup>1</sup></i>	---	<i>Malic enzyme-1<sup>1</sup></i> ; one of three codominant alleles, each regulating one band; found in <i>Praecitrullus fistulosus</i> .
<i>Me-1<sup>2</sup></i>	---	<i>Malic enzyme-1<sup>2</sup></i> ; one of three codominant alleles, each regulating one band; found in <i>C. colocynthis</i> .
<i>Me-2</i>	---	<i>Malic enzyme-2</i> .
<i>ms-1</i>	<i>ms</i>	<i>male sterile</i> ; plants with small, shrunken anthers and aborted pollen; <i>ms-1</i> from 'Nongmei 100'; <i>Ms-1</i> from most cultivars, e.g. 'Allsweet'.
<i>ms-dw</i>	<i>ms<sup>dw</sup></i>	<i>male sterile, dwarf</i> ; <i>ms-dw</i> from 'Dwarf Male-Sterile Watermelon (DMSW)'; <i>Ms-dw</i> from 'Changhui', 'Fuyandangua', and 'America B'.
<i>ms-2</i>	---	<i>male sterile with high seed productivity</i> ; <i>ms-2</i> from 'Kamyzyakskii'; <i>Ms-2</i> from cultivars like 'Allsweet'.
<i>nl</i>	---	<i>nonlobed leaves</i> ; leaves lack the typical lobing; incomplete dominance; (named nonlobed by Robinson*); <i>nl</i> from spontaneous mutation of 'Black Diamond'.
<i>O</i>	---	<i>Elongate fruit</i> ; incompletely dominant to spherical, so that <i>Oo</i> is oval; <i>O</i> from 'Long Iowa Belle'; <i>o</i> from 'Round Iowa Belle', 'China 23', 'Japan 4', and 'Japan 6'.
<i>p</i>	---	<i>pencilled lines on skin</i> ; inconspicuous stripes; greenish-white mottling* (called pencilled by Robinson**); recessive to netted fruit; <i>p</i> from 'Long Iowa Belle' and <i>P</i> from 'Japan 6'.
<i>Pgd-1</i>	<i>6 Pgdh-1</i>	<i>6-Phosphogluconate dehydrogenase-1</i> ; one of three codominant alleles, each regulating one plastid band; found in <i>C. lanatus</i> .
<i>Pgd-1<sup>1</sup></i>	<i>6 Pgdh-1<sup>1</sup></i>	<i>6-Phosphogluconate dehydrogenase-1<sup>1</sup></i> ; one of three codominant alleles, each regulating one plastid band; found in <i>Praecitrullus fistulosus</i> .
<i>Pgd-1<sup>2</sup></i>	<i>6 Pgdh-1<sup>2</sup></i>	<i>6-Phosphogluconate dehydrogenase-1<sup>2</sup></i> ; one of three codominant alleles, each regulating one plastid band; found in <i>Acanthosicyos naudinianus</i> .
<i>Pgd-2</i>	<i>6 Pgdh-2</i>	<i>6-Phosphogluconate dehydrogenase-2</i> ; one of five codominant alleles, each regulating one cytosolic band; found in <i>C. lanatus</i> .
<i>Pgd-2<sup>1</sup></i>	<i>6 Pgdh-2<sup>1</sup></i>	<i>6-Phosphogluconate dehydrogenase-2<sup>1</sup></i> ; one of five codominant alleles, each regulating one cytosolic band; found in <i>C. ecirrhosus</i> .
<i>Pgd-2<sup>2</sup></i>	<i>6 Pgdh-2<sup>2</sup></i>	<i>6-Phosphogluconate dehydrogenase-2<sup>2</sup></i> ; one of five codominant alleles, each regulating one cytosolic band; found in <i>Praecitrullus fistulosus</i> .
<i>Pgd-2<sup>3</sup></i>	<i>6 Pgdh-2<sup>3</sup></i>	<i>6-Phosphogluconate dehydrogenase-2<sup>3</sup></i> ; one of five codominant alleles, each regulating one cytosolic band; found in <i>C. colocynthis</i> .
<i>Pgd-2<sup>4</sup></i>	<i>6 Pgdh-2<sup>4</sup></i>	<i>6-Phosphogluconate dehydrogenase-2<sup>4</sup></i> ; one of five codominant alleles, each regulating one cytosolic band; found in <i>Acanthosicyos naudinianus</i> .
<i>Pgi-1</i>	---	<i>Phosphoglucoisomerase-1</i> ; one of three codominant alleles, each regulating one plastid band; found in <i>C. lanatus</i> .
<i>Pgi-1<sup>1</sup></i>	---	<i>Phosphoglucoisomerase-1<sup>1</sup></i> ; one of three codominant alleles, each regulating one plastid band; found in <i>C. colocynthis</i> .
<i>Pgi-1<sup>2</sup></i>	---	<i>Phosphoglucoisomerase-1<sup>2</sup></i> ; one of three codominant alleles, each regulating one plastid band; found in <i>Acanthosicyos naudinianus</i> .
<i>Pgi-2</i>	---	<i>Phosphoglucoisomerase-2</i> ; one of six codominant alleles, each regulating one cytosolic band; found in <i>C. lanatus</i> .
<i>Pgi-2<sup>1</sup></i>	---	<i>Phosphoglucoisomerase-2<sup>1</sup></i> ; one of six codominant alleles, each regulating one cytosolic band; found in <i>C. lanatus</i> and <i>C. colocynthis</i> .
<i>Pgi-2<sup>2</sup></i>	---	<i>Phosphoglucoisomerase-2<sup>2</sup></i> ; one of six codominant alleles, each regulating one cytosolic band; found in <i>C. ecirrhosus</i> .
<i>Pgi-2<sup>3</sup></i>	---	<i>Phosphoglucoisomerase-2<sup>3</sup></i> ; one of six codominant alleles, each regulating one cytosolic band; found in <i>Praecitrullus fistulosus</i> .
<i>Pgi-2<sup>4</sup></i>	---	<i>Phosphoglucoisomerase-2<sup>4</sup></i> ; one of six codominant alleles, each regulating one cytosolic band; found in <i>C. lanatus</i> var. <i>citroides</i> .
<i>Pgi-2<sup>5</sup></i>	---	<i>Phosphoglucoisomerase-2<sup>5</sup></i> ; one of six codominant alleles, each regulating one cytosolic band; found in <i>Acanthosicyos naudinianus</i> .
<i>Pgm-1</i>	---	<i>Phosphoglucomutase-1</i> ; one of four codominant alleles, each regulating one plastid band; found in <i>C. lanatus</i> .
<i>Pgm-1<sup>1</sup></i>	---	<i>Phosphoglucomutase-1<sup>1</sup></i> ; one of four codominant alleles, each regulating one plastid band; found in <i>C. colocynthis</i> .
<i>Pgm-1<sup>2</sup></i>	---	<i>Phosphoglucomutase-1<sup>2</sup></i> ; one of four codominant alleles, each regulating one plastid band; found in <i>Acanthosicyos naudinianus</i> .
<i>Pgm-1<sup>3</sup></i>	---	<i>Phosphoglucomutase-1<sup>3</sup></i> ; one of four codominant alleles, each regulating one plastid band; found in <i>Praecitrullus fistulosus</i> .
<i>Pgm-2</i>	---	<i>Phosphoglucomutase-2</i> ; one of four codominant alleles, each regulating one cytosolic band; found in <i>C. lanatus</i> .
<i>Pgm-2<sup>1</sup></i>	---	<i>Phosphoglucomutase-2<sup>1</sup></i> ; one of four codominant alleles, each regulating one cytosolic band; found in <i>Acanthosicyos naudinianus</i> .
<i>Pgm-2<sup>2</sup></i>	---	<i>Phosphoglucomutase-2<sup>2</sup></i> ; one of four codominant alleles, each regulating one cytosolic band; found in <i>C. lanatus</i> .
<i>Pgm-2<sup>3</sup></i>	---	<i>Phosphoglucomutase-2<sup>3</sup></i> ; one of four codominant alleles, each regulating one cytosolic band; found in <i>Praecitrullus fistulosus</i> .
<i>pm</i>	---	<i>powdery mildew susceptibility</i> ; susceptibility to <i>Sphaerotheca fuliginea</i> is recessive; <i>pm</i> from PI 269677; <i>Pm</i> from 'Sugar Baby' and most cultivars.
<i>Prx-1</i>	---	<i>Peroxidase-1</i> ; one of seven codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Prx-1<sup>1</sup></i>	---	<i>Peroxidase-1<sup>1</sup></i> ; one of seven codominant alleles, each regulating one band; found in <i>C. colocynthis</i> .
<i>Prx-1<sup>2</sup></i>	---	<i>Peroxidase-1<sup>2</sup></i> ; one of seven codominant alleles, each regulating one band; found in <i>Praecitrullus fistulosus</i> .
<i>Prx-1<sup>3</sup></i>	---	<i>Peroxidase-1<sup>3</sup></i> ; one of seven codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Prx-1<sup>4</sup></i>	---	<i>Peroxidase-1<sup>4</sup></i> ; one of seven codominant alleles, each regulating one band; found in <i>C. ecirrhosus</i> .
<i>Prx-1<sup>5</sup></i>	---	<i>Peroxidase-1<sup>5</sup></i> ; one of seven codominant alleles, each regulating one band; found in <i>C. lanatus</i> and <i>C. colocynthis</i> .
<i>Prx-1<sup>6</sup></i>	---	<i>Peroxidase-1<sup>6</sup></i> ; one of seven codominant alleles, each regulating one band; found in <i>Acanthosicyos naudinianus</i> .
<i>Prx-2</i>	---	<i>Peroxidase-2</i> .
<i>Prx-3</i>	---	<i>Peroxidase-3</i> .
<i>r</i>	---	<i>red seed coat</i> ; genes <i>r</i> , <i>t</i> and <i>w</i> interact to produce seeds of different colors; black from 'Klondike' ( <i>RR TT WW</i> ); clump from 'Sun Moon and Stars' ( <i>RR TT ww</i> ); tan from 'Baby Delight' ( <i>RR tt WW</i> ); white with tan tip from 'Pride of Muscatine' ( <i>RR tt ww</i> ); red from citron ( <i>rr tt WW</i> ); white with pink tip from 'Peerless' ( <i>rr tt ww</i> ).
<i>s</i>	---	<i>short (or small) seeds</i> ; epistatic to <i>l</i> ; long recessive to medium or short; <i>LL SS</i> for medium, <i>ll SS</i> for long, and <i>LL ss</i> or <i>ll ss</i> for short seed; <i>ll SS</i> from 'Peerless'; <i>LL SS</i> from 'Klondike'; <i>LL ss</i> from 'Baby Delight'.
<i>Sat</i>	---	<i>Serine acetyltransferase</i> ; catalyzes the formation of O-acetylserine from serine and acetyl-CoA.
<i>Skdh-1</i>	---	<i>Shikimic acid dehydrogenase-1</i> .
<i>Skdh-2</i>	---	<i>Shikimic acid dehydrogenase-2</i> ; one of six codominant alleles, each regulating one band.
<i>Skdh-2<sup>1</sup></i>	---	<i>Shikimic acid dehydrogenase-2<sup>1</sup></i> ; one of six codominant alleles, each regulating one band; found in <i>C. colocynthis</i> .



Table 1 (continued). The genes of watermelon.

Gene	Synonym	Character
<i>Skdh-2<sup>2</sup></i>	---	<i>Shikimic acid dehydrogenase-2<sup>2</sup></i> ; one of six codominant alleles, each regulating one band; found in <i>C. colocynthis</i> .
<i>Skdh-2<sup>3</sup></i>	---	<i>Shikimic acid dehydrogenase-2<sup>3</sup></i> ; one of six codominant alleles, each regulating one band; found in <i>Acanthosicyos naudinianus</i> .
<i>Skdh-2<sup>4</sup></i>	---	<i>Shikimic acid dehydrogenase-2<sup>4</sup></i> ; one of six codominant alleles, each regulating one band; found in <i>C. ecirrhosus</i> .
<i>Skdh-2<sup>5</sup></i>	---	<i>Shikimic acid dehydrogenase-2<sup>5</sup></i> ; one of six codominant alleles, each regulating one band; found in <i>Praecitrullus fistulosus</i> .
<i>slv</i>	---	<i>seedling leaf variegation</i> ; conferred by a single recessive gene in PI 482261; linked or pleiotropic with a dominant allele for resistance to cool temperature injury (20°C for greenhouse-grown plants); <i>slv</i> from PI 482261 (resistant to ZYMV-FL); <i>Slv</i> from 'New Hampshire Midget'.
<i>Sod-1</i>	---	<i>Superoxide dismutase-1</i> ; one of three codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Sod-1<sup>1</sup></i>	---	<i>Superoxide dismutase-1<sup>1</sup></i> ; one of three codominant alleles, each regulating one band; found in <i>C. colocynthis</i> .
<i>Sod-1<sup>2</sup></i>	---	<i>Superoxide dismutase-1<sup>2</sup></i> ; one of three codominant alleles, each regulating one band; found in <i>Acanthosicyos naudinianus</i> .
<i>Sod-2</i>	---	<i>Superoxide dismutase-2</i> ; one of two codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Sod-2<sup>1</sup></i>	---	<i>Superoxide dismutase-2<sup>1</sup></i> ; one of two codominant alleles, each regulating one band; found in <i>Acanthosicyos naudinianus</i> .
<i>Sod-3</i>	---	<i>Superoxide dismutase-3</i> ; one of two codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Sod-3<sup>1</sup></i>	---	<i>Superoxide dismutase-3<sup>1</sup></i> ; one of two codominant alleles, each regulating one band; found in <i>Praecitrullus fistulosus</i> .
<i>Sp</i>	---	<i>Spotted cotyledons, leaves and fruit</i> ; dominant to uniform foliage and fruit color; <i>Sp</i> from 'Sun, Moon and Stars'* and 'Moon and Stars'*; <i>sp</i> from 'Allsweet'.
<i>Spr-1</i>	---	<i>Seed protein-1</i> .
<i>Spr-2</i>	---	<i>Seed protein-2</i> .
<i>Spr-3</i>	---	<i>Seed protein-3</i> .
<i>Spr-4</i>	<i>Sp-4</i>	<i>Seed protein-4</i> .
<i>Spr-5</i>	<i>Sp-5</i>	<i>Seed protein-5</i> .
<i>su</i>	<i>Bi, su<sup>Bi</sup></i>	<i>suppressor of bitterness</i> ; ( <i>su</i> named by Robinson*); non-bitter fruit; <i>su</i> from 'Hawkesbury'; <i>Su</i> from bitter-fruited mutant of 'Hawkesbury'; bitterness in <i>C. colocynthis</i> is due to <i>Su Su</i> genotype.
<i>t</i>	<i>b<sup>t</sup></i>	<i>tan seed coat</i> ; genes <i>r</i> , <i>t</i> and <i>w</i> interact to produce seeds of different colors; black from 'Klondike' ( <i>RR TT WW</i> ); clump from 'Sun Moon and Stars' ( <i>RR TT ww</i> ); tan from 'Baby Delight' ( <i>RR tt WW</i> ); white with tan tip from 'Pride of Muscatine' ( <i>RR tt ww</i> ); red from citron ( <i>rr tt WW</i> ); white with pink tip from 'Peerless' ( <i>rr tt ww</i> ).
<i>Ti</i>	---	<i>Tiny seed</i> ; dominant over medium seed ( <i>ti</i> ); <i>Ti</i> from 'Sweet Princess'; <i>ti</i> from 'Fujihikari'.
<i>tl</i>	<i>bl</i>	<i>tendrillless</i> (formerly called <i>branchless</i> *), after 4th or 5th node, vegetative axillary buds are transformed into flower buds and leaf shape is altered; <i>tl</i> from 'Early Branchless'; <i>Tl</i> from breeding lines 'G17AB', 'ASS-1', 'YF91-1-2', and S173 breeding line.
<i>Tpi-</i>	---	<i>Triosephosphatase isomerase-1</i> . one of four codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Tpi-1<sup>1</sup></i>	---	<i>Triosephosphatase isomerase-1<sup>1</sup></i> ; one of four codominant alleles, each regulating one band; found in <i>C. colocynthis</i> .
<i>Tpi-1<sup>2</sup></i>	---	<i>Triosephosphatase isomerase-1<sup>2</sup></i> ; one of four codominant alleles, each regulating one band; found in <i>Praecitrullus fistulosus</i> .
<i>Tpi-1<sup>3</sup></i>	---	<i>Triosephosphatase isomerase-1<sup>3</sup></i> ; one of four codominant alleles, each regulating one band; found in <i>Acanthosicyos naudinianus</i> .
<i>Tpi-2</i>	---	<i>Triosephosphatase isomerase-2</i> ; one of three codominant alleles, each regulating one band; found in <i>C. lanatus</i> .
<i>Tpi-2<sup>1</sup></i>	---	<i>Triosephosphatase isomerase-2<sup>1</sup></i> ; one of three codominant alleles, each regulating one band; found in <i>Acanthosicyos naudinianus</i> .
<i>Tpi-2<sup>2</sup></i>	---	<i>Triosephosphatase isomerase-2<sup>2</sup></i> ; one of three codominant alleles, each regulating one band; found in <i>Praecitrullus fistulosus</i> .
<i>ts</i>	<i>tss</i>	<i>tomato seed</i> ; seeds smaller than short ( <i>LLss</i> or <i>llss</i> ), almost the size of a tomato seed; <i>ts</i> from tomato seed Sugar Baby mutant; <i>Ts</i> from 'Gn-1'.
<i>Ure-1</i>	---	<i>Urease-1</i> .
<i>w</i>	---	<i>white seed coat</i> ; genes <i>r</i> , <i>t</i> and <i>w</i> interact to produce seeds of different colors; black from 'Klondike' ( <i>RR TT WW</i> ); clump from 'Sun Moon and Stars' ( <i>RR TT ww</i> ); tan from 'Baby Delight' ( <i>RR tt WW</i> ); white with tan tip from 'Pride of Muscatine' ( <i>RR tt ww</i> ); red from citron ( <i>rr tt WW</i> ); white with pink tip from 'Peerless' ( <i>rr tt ww</i> ).
<i>Wf</i>	<i>W</i>	<i>White flesh</i> ; (named white flesh by Robinson*); <i>Wf</i> is epistatic to <i>B</i> ( <i>Y</i> renamed <i>B</i> by Henderson**); <i>WfWf BB</i> or <i>WfWf bb</i> white fleshed; <i>wfwf BB</i> yellow fleshed; <i>wfwf bb</i> red fleshed; <i>B</i> from breeding line V.No.3 and <i>b</i> from V.No.1; flesh color segregated into 12 white, 3 yellow and 1 red in the F2.
<i>y</i>	<i>rd</i>	<i>yellow flesh</i> ; recessive to red flesh; <i>y</i> from 'Golden Honey'; <i>Y</i> from 'Angeleno' (black seeded).
<i>y<sup>o</sup></i>	---	<i>orange flesh</i> ; allelic to <i>y</i> ; <i>Y</i> (red flesh) is dominant to <i>y<sup>o</sup></i> (orange flesh) and <i>y</i> (salmon yellow flesh); <i>y<sup>o</sup></i> (orange flesh) is dominant to <i>y</i> (salmon yellow flesh); <i>cc y<sup>o</sup> I-C I-C</i> from 'Tendersweet Orange Flesh'; <i>cc yy I-C I-C</i> from 'Golden Honey'; <i>cc YY i-C i-C</i> from 'Sweet Princess'.
<i>Yl</i>	<i>Y</i>	<i>Yellow leaf</i> ; incompletely dominant to green leaf ( <i>yl</i> ); ( <i>Y</i> renamed <i>Yl</i> by Henderson*). <i>yl</i> from 'Congo'; <i>Yl</i> from 'Yellow Skin'.
<i>zym-FL</i>	<i>zym</i>	<i>Resistance to zucchini yellow mosaic virus (ZYMV-FL)</i> ; resistance is specific to the Florida strain; <i>zym-FL</i> from PI 482322, PI 482299, PI 482261, and PI 482308.

\*Asterisks on cultigens and associated references indicate the source of information for each.

<sup>1</sup>C = mutant available from Cucurbit Genetics Cooperative watermelon gene curator; M = molecular marker or isozyme; P = mutants are available as standard cultivars or accessions from the plant introduction collection; ? = availability not known; L = mutant has been lost.

longer than normal vine and considerably longer than dwarf. The *dw-1<sup>s</sup>* is recessive to normal plant type. Plants with *dw-2* have short internodes due to fewer cells than the normal type, and plants with *dw-3* have leaves with fewer lobes than the normal leaf.

The golden yellow mutant is controlled by the single recessive gene *go*, where the stem and older leaves are golden yellow (Barham, 1956). The gene *go* was from 'Royal Golden'. One benefit of the *go* gene is that the fruit become golden yellow as they mature, possibly useful as a maturity indicator. The gene *tl* (formerly called *branchless*, *bl*) results in tendrillless branches after the 5th or 6th node (Rhodes et al., 1999 and Zhang et al., 1996a). Also, plants have half the number of branches of the normal plant type, vegetative meristems gradually become floral, tendrils and vegetative buds are replaced by flowers (with a large percentage being perfect), and growth becomes determinate.

**Flower mutants.** The andromonoecious gene *a* (Rosa, 1928) controls monoecious (*AA*) vs. andromonoecious (*aa*) sex expression in watermelon. Andromonoecious plants have both staminate and perfect flowers, and appears to be the wild type. Light green flower color is controlled by the single recessive gene, *gf* (Kwon and Dane, 1999).

Four genes for male sterility have been reported. Glabrous male sterile (*gms*) is unique, with sterility associated with glabrous foliage (Watts, 1962 and 1967). A second male sterile *ms-1* (Zhang and Wang, 1990) produces plants with small, shrunken anthers and aborted pollen. A third male sterile mutant appeared simultaneously with dwarfism, and the dwarf gene was different from the three known dwarf genes. It was named male sterile dwarf (*ms-dw*) by Huang et al. (1998). All male sterile genes reduce female fertility as well. These mutants have been used in hybrid production, but have not been as successful as hoped, since they

often have low seed yield. A new, spontaneous male sterile mutant (*ms-2*) with high normal seed set has been identified, and will be more useful for hybrid production (Dyutin, and Sokolov, 1990).

**Fruit mutants.** Considerable attention has been given to genes affecting fruit type in watermelon. A single recessive gene *su* (Chambliss et al., 1968) eliminates bitterness in fruit of *C. lanatus*, and appears to be the same as the dominant gene (*Su*) for bitter flavor in the fruit of the colocynth (*Citrullus colocynthis*).

Fruit shape is controlled by a single, incompletely dominant gene, resulting in fruit that are elongate (*OO*), oval (*Oo*), or spherical (*oo*) (Weetman, 1937). A single gene controls furrowed fruit surface *f* (Poole, 1944) that is recessive to smooth (*F*). Explosive rind (*e*) causes the fruit rind to burst or split when cut (Porter, 1937). The non-explosive genotype (*EE*) would be important to improve shipping ability for marketing.

References <sup>c</sup>	Supplemental references <sup>c</sup>	Available <sup>c</sup>
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Provvidenti, 1994	---	P
Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987; Zamir et al., 1984	---	M
Navot and Zamir, 1987	---	M
Navot and Zamir, 1987	---	M
Navot and Zamir, 1987	---	M
Navot and Zamir, 1987	---	M
Poole, 1944*	Rhodes, 1986**	C
Navot and Zamir, 1986	---	M
Navot and Zamir, 1986	---	M
Navot and Zamir, 1986	---	M
Navot et al., 1990; Navot and Zamir, 1986	---	M
Navot et al., 1990; Navot and Zamir, 1986	---	M
Chambliss et al., 1968	Robinson et al., 1976*	?
McKay, 1936	Poole et al., 1941	?
Tanaka et al., 1995	---	?
Rhodes et al., 1999; Zhang et al., 1996a	Lin, Tong, Wang, Zhang and Rhodes, 1992*	?
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot et al., 1990; Navot and Zamir, 1986, 1987	---	M
Navot and Zamir, 1987	---	M
Navot and Zamir, 1987	---	M
Navot and Zamir, 1987	---	M
Zhang et al., 1994a	Zhang, 1996	C
Navot and Zamir, 1987	---	M
Poole et al., 1941	---	?
Shimotsuma, 1963	Robinson et al., 1976*; Henderson, 1992**	?
Porter, 1937	Poole, 1944; Henderson, 1989; Henderson et al., 1998	C
Henderson, 1989; Henderson et al., 1998	Poole, 1944; Porter, 1937	C
Warid and Abd-El-Hafez, 1976	Henderson, 1991*	?
Provvidenti, 1991	---	P

Thirteen mutants have been identified that affect fruit color either in the skin or flesh. A single gene determines the intensity of green color of the fruit skin, with solid light green (*g*) skin color recessive to solid dark green (*G*) (Weetman, 1937). Green striped skin is controlled by a single gene *g<sup>s</sup>* (Weetman, 1937) that is recessive to dark green, but dominant to light green. The symbol *g<sup>s</sup>* for this gene was proposed, although there are narrow, medium, and wide striped patterns that were not explained by qualitative genes so far. Another type of striping of the fruit skin is where the stripes are very narrow and inconspicuous. The trait is controlled by a single recessive gene inherited independently of *g<sup>s</sup>*, called pencilled lines *p* (Weetman, 1937). The greenish white mottling of the fruit skin is controlled by the single recessive gene *m* (Weetman, 1937), resulting in gray types, such as 'Iowa Belle' and 'Charleston Gray'. The gene *Sp* produces spotted fruit, making interesting effects as found on the cultivar 'Moon and Stars' (Poole, 1944).

Watermelon flesh color is controlled by

several genes to produce red, orange, salmon yellow, canary yellow, or white. Genes conditioning flesh colors are *B* (Shimotsuma, 1963), *C* (Poole, 1944), *i-C* (Henderson et al., 1998), *Wf* (Shimotsuma, 1963), *y* (Porter, 1937) and *y<sup>o</sup>* (Henderson, 1989 and Henderson et al. 1998). Canary yellow (*C*) is dominant to red flesh (*c*). Red flesh (*Y*) is dominant to salmon yellow (*y*). Orange flesh (*y<sup>o</sup>*) is a member of multiple allelic system at that locus, where *Y* (red flesh) is dominant to both *y<sup>o</sup>* (orange flesh) and *y* salmon yellow (salmon yellow), and *y<sup>o</sup>* (orange flesh) is dominant to *y* (salmon yellow). In a separate study, two loci with epistatic interaction controlled white, yellow and red flesh. Yellow flesh (*B*) is dominant to red flesh. The gene *Wf* is epistatic to *B*, so genotypes *WfWfBB* or *WfWfbb* were white fleshed, *wfwfBB* was yellow fleshed, and *wfwfbb* was red fleshed. Canary yellow flesh is dominant to red, and *i-C* inhibitory to *C*, resulting in red flesh. In the absence of *i-C*, *C* is epistatic to *Y*.

Golden yellow was inherited as a single recessive gene *go* (Barham, 1956) derived from 'Royal Golden' watermelon. The immature

fruit had a dark green rind which becomes more golden yellow as the fruit matures. The stem and older leaves also become golden yellow, and the flesh color changes from pink to red.

**Resistance mutants.** Resistance to race 1 (and 3) of anthracnose (*Colletotrichum lagenarium* formerly *Glomerella cingulata* var. *orbiculare*) is controlled by a single dominant gene *Ar-1* (Layton 1937). Resistance to race 2 of anthracnose is also controlled by a single dominant gene *Ar-2<sup>1</sup>* (Winstead et al., 1959). Resistance to race 1 of *Fusarium oxysporum* f. sp. *niveum* is controlled by a single dominant gene *Fo-1* (Henderson et al., 1970). Gummy stem blight, caused by *Didymella bryoniae* (Auersw.) Rehm, is inherited by a recessive gene *db* (Norton, 1979). Most watermelons are resistant to races of *Sphaerotheca fuliginea* present in the U.S., but a single recessive gene *pm* (Robinson et al., 1975) for susceptibility to powdery mildew was found in the plant introduction, PI 269677. A high level of resistance to zucchini yellow mosaic virus was found in four landraces of *Citrullus lanatus*, but was specific to the Florida strain of the virus.

Resistance was conferred by a single recessive gene *zym-FL* (Provvidenti, 1991).

Genes for insect resistance have been reported in watermelon. Fruit fly (*Dacus cucurbitae*) resistance was controlled by a single dominant gene *Fwr* (Khandelwal and Nath, 1978), and red pumpkin beetle (*Aulacophora faveicollis*) resistance was controlled by a single dominant gene *Af* (Vashishta and Choudhury, 1972).

Stress resistance has been found in watermelon. Seedlings grown at temperatures below 20 °C often develop a foliar mottle and stunting. A persistent low temperature is conducive to more prominent foliar symptoms, malformation, and growth retardation. The single dominant gene *Ctr* provided cool temperature resistance (Provvidenti, 1992).

#### Literature Cited

- Arumuganathan, K., and E.D. Earle. 1991. Nuclear DNA content of some important plants. *Plant Mol. Bio. Rpt.* 9:208–218.
- Barham, W.S. 1956. A study of the Royal Golden watermelon with emphasis on the inheritance of the chlorotic condition characteristic of this variety. *Proc. Amer. Soc. Hort. Sci.* 67:487–489.
- Chambliss, O.L., H.T. Erickson, and C.M. Jones. 1968. Genetic control of bitterness in watermelon fruits. *Proc. Amer. Soc. Hort. Sci.* 93:539–546.
- Cucurbit Gene List Committee. 1979. New genes for the Cucurbitaceae. *Cucurbit Genet. Coop. Rpt.* 2:49–53.
- Cucurbit Gene List Committee. 1982. Update of cucurbit gene list and nomenclature rules. *Cucurbit Genet. Coop. Rpt.* 5:62–66.
- Cucurbit Gene List Committee. 1987. Gene list for watermelon. *Cucurbit Genet. Coop. Rpt.* 10:106–110.
- Dyutin, K.E. and E.A. Afanas'eva. 1987. Inheritance of the short vine trait in watermelon. *Cytol. Genet. (Tsitologiya i Genetika)* 21:71–73.
- Dyutin, K.E. and S.D. Sokolov. 1990. "Spontaneous mutant of watermelon with male sterility." *Cytol. Genet. (Tsitologiya i Genetika)* 24:56–57.
- El-Hafez, A.A.A., A.K. Gaafer, and A.M.M. Allam. 1981. Inheritance of flesh color, seed coat cracks and total soluble solids in watermelon and their genetic relations. *Acta Agron. Acad. Hungaricae* 30:82–86.
- FAO. 2002. Agricultural statistics for 2002. Food Agr. Org. United Nations, Rome. <http://apps.fao.org/page/collections?subset=agriculture>.
- Gusmini, G., T.C. Wehner, and R.L. Jarret. 2003. Inheritance of 'Egusi' seed-type in watermelon (*Citrullus lanatus* var. *lanatus*). *J. Hered.* (in press).
- Hall, C.V., S.K. Dutta, H.R. Kalia, and C.T. Rogerson. 1960. Inheritance of resistance to the fungus *Colletotrichum lagenarium* (Pass.) Ell. and Halst. in watermelons. *Proc. Amer. Soc. Hort. Sci.* 75:638–643.
- Henderson, W.R. 1989. Inheritance of orange flesh color in watermelon. *Cucurbit Genet. Coop. Rpt.* 12:59–63.
- Henderson, W.R. 1991. Gene list for watermelon. *Cucurbit Genet. Coop. Rpt.* 14:129–138.
- Henderson, W.R. 1992. Corrigenda to the 1991 watermelon gene list (CGC 14:129–137). *Cucurbit Genet. Coop. Rpt.* 15:110.
- Henderson, W.R., S.F. Jenkins, Jr., and J.O. Rawlings. 1970. The inheritance of Fusarium wilt resistance in watermelon, *Citrullus lanatus* (Thunb.) Mansf. *J. Amer. Soc. Hort. Sci.* 95:276–282.
- Henderson, W.R., G.H. Scott, and T.C. Wehner. 1998. Interaction of flesh color genes in watermelon. *J. Hered.* 89:50–53.
- Huang, H., X. Zhang, Z. Wei, Q. Li, and X. Li. 1998. Inheritance of male-sterility and dwarfism in watermelon [*Citrullus lanatus* (Thunb.) Matsum. and Nakai]. *Scientia Hort.* 74:175–181.
- Kanda, T. 1951. The inheritance of seed-coat colouring in the watermelon. *Jpn. J. Genet.* 7:30–48.
- Khandelwal, R.C. and P. Nath. 1978. Inheritance of resistance to fruit fly in watermelon. *Can. J. Genet. Cytol.* 20:31–34.
- Kwon, Y.S. and F. Dane. 1999. Inheritance of green flower color (*gf*) in watermelon (*Citrullus lanatus*). *Cucurbit Genet. Coop. Rpt.* 22:31–33.
- Layton, D.V. 1937. The parasitism of *Colletotrichum lagenarium* (Pass.) Ells. and Halst. Iowa Agr. Expt. Sta. Ann. Bul. 223.
- Lin, D., T. Wang, Y. Wang, X. Zhang, and B.B. Rhodes. 1992. The effect of the branchless gene *bl* on plant morphology in watermelon. *Cucurbit Genet. Coop. Rpt.* 15:74–75.
- Liu, P.B.W. and J.B. Loy. 1972. Inheritance and morphology of two dwarf mutants in watermelon. *J. Amer. Soc. Hort. Sci.* 97:745–748.
- Love, S.L. and B.B. Rhodes. 1988. Single gene control of anthracnose resistance in *Citrullus?* *Cucurbit Genet. Coop. Rpt.* 11:64–67.
- Love, S.L. and B.B. Rhodes. 1991. R309, a selection of *Citrullus colocynthis* with multigenic resistance to *Colletotrichum lagenarium* race 2. *Cucurbit Genet. Coop. Rpt.* 14:92–95.
- McKay, J.W. 1936. Factor interaction in *Citrullus*. *J. Hered.* 27:110–112.
- Mohr, H.C. 1953. A mutant leaf form in watermelon. *Proc. Assn. S. Agr. Workers* 50:129–130.
- Mohr, H.C. 1956. Mode of inheritance of the bushy growth characteristics in watermelon. *Proc. Assn. S. Agr. Workers* 53:174.
- Mohr, H.C. and M.S. Sandhu. 1975. Inheritance and morphological traits of a double recessive dwarf in watermelon, *Citrullus lanatus* (Thunb.) Mansf. *J. Amer. Soc. Hort. Sci.* 100:135–137.
- Navot, N., M. Sarfatti, and D. Zamir. 1990. Linkage relationships of genes affecting bitterness and flesh color in watermelon. *J. Hered.* 81:162–165.
- Navot, N. and D. Zamir. 1986. Linkage relationships of 19 protein coding genes in watermelon. *Theor. Appl. Genet.* 72:274–278.
- Navot, N. and D. Zamir. 1987. Isozyme and seed protein phylogeny of the genus *Citrullus* (Cucurbitaceae). *Plant Syst. Evol.* 156:61–67.
- Netzer, D. and C. Weintall. 1980. Inheritance of resistance to race 1 of *Fusarium oxysporum* f. sp. *niveum*. *Plant Dis.* 64:863–854.
- Norton, J.D. 1979. Inheritance of resistance to gummy stem blight in watermelon. *HortScience* 14:630–632.
- Pasha, M.A.S.S. 1998. Numerical and chemical approaches to taxonomy and relationships., p. 19–32. In: N.M. Nayyar and T.A. More (eds.). *Cucurbits*. Science Publ., New Hampshire.
- Perkins-Veazie, P., J.K. Collins, S.D. Pair, and W. Roberts. 2001. Lycopene content differs among red-fleshed watermelon cultivars. *J. Sci. Food Agr.* 81:983–987.
- Poole, C.F. 1944. Genetics of cultivated cucurbits. *J. Hered.* 35:122–128.
- Poole, C.F. and P.C. Grimball. 1945. Interaction of sex, shape, and weight genes in watermelon. *J. Agr. Res.* 71:533–552.
- Poole, C.F. P.C. Grimball, and D.R. Porter. 1941. Inheritance of seed characters in watermelon. *J. Agr. Res.* 63:433–456.
- Porter, D.R. 1937. Inheritance of certain fruit and seed characters in watermelons. *Hilgardia* 10:489–509.
- Provvidenti, R. 1991. Inheritance of resistance to the Florida strain of zucchini yellow mosaic virus in watermelon. *HortScience* 26(4):407–408.
- Provvidenti, R. 1992. Cold resistance in accessions of watermelon from Zimbabwe. *Cucurbit Genet. Coop. Rpt.* 15:67–68.
- Provvidenti, R. 1994. Inheritance of a partial chlorophyll deficiency in watermelon activated by low temperatures at the seedling stage. *HortScience* 29(9):1062–1063.
- Provvidenti, R. 2003. Naming the gene conferring resistance to cool temperatures in watermelon. *Cucurbit Genet. Coop. Rpt.* 26 (in press).
- Ray, D.T. and J.D. Sherman. 1988. Desynaptic chromosome behavior of the *gms* mutant in watermelon. *J. Hered.* 79:397–399.
- Rhodes, B.B. 1986. Genes affecting foliage color in watermelon. *J. Hered.* 77:134–135.
- Rhodes, B. and X. Zhang. 1995. Gene list for watermelon. *Cucurbit Genet. Coop. Rpt.* 18:69–84.
- Rhodes, B. and F. Dane. 1999. Gene list for watermelon. *Cucurbit Genet. Coop. Rpt.* 22:61–74.
- Rhodes, B.B., X.P. Zhang, V.B. Baird, and H. Knapp. 1999. A tendrillless mutant in watermelon: Phenotype and inheritance. *Cucurbit Genet. Coop. Rpt.* 22:28–30.
- Robinson, R.W., H.M. Munger, T.W. Whitaker and G.W. Bohn. 1976. Genes of the Cucurbitaceae. *HortScience* 11:554–568.
- Robinson, R.W., R. Provvidenti and J.W. Shail. 1975. Inheritance of susceptibility to powdery mildew in the watermelon. *J. Hered.* 66:310–311.
- Rosa, J.T. 1928. The inheritance of flower types in *Cucumis* and *Citrullus*. *Hilgardia* 3:233–250.
- Saito, K., K. Inoue, R. Fukushima, and M. Noji. 1997. *Gene* 189:57–63.
- Shimotsuma, M. 1963. Cytogenetical studies in the genus *Citrullus*. VII. Inheritance of several characters in watermelons. *Jpn. J. Breed.* 13:235–240.
- Sowell, Jr., G., B.B. Rhodes, and J.D. Norton. 1980. New sources of resistance to watermelon anthracnose. *J. Amer. Soc. Hort. Sci.* 105:197–199.
- Suvanprakorn, K. and J.D. Norton. 1980. Inheritance of resistance to anthracnose race 2 in watermelon. *J. Amer. Soc. Hort. Sci.* 105:862–865.
- Tanaka, T., S. Wimol, and T. Mizutani. 1995. Inheritance of fruit shape and seed size of watermelon. *J. Jpn. Soc. Hort. Sci.* 64(3):543–548.
- U.S. Department of Agriculture. 2002. Agricultural statistics. USDA, National Agr. Stat. Serv., Wash., D.C., <http://www.usda.gov/nass/pubs/agr02/acro02.htm>.
- Vashishta, R.N. and B. Choudhury. 1972. Inheritance of resistance to red pumpkin beetle in muskmelon, bottle gourd and watermelon. *Proc. 3rd Intl. Symp. Sub-Trop. Hort.* 1:75–81.
- Warid, A. and A.A. Abd-El-Hafez. 1976. Inheritance of marker genes of leaf color and ovary shape in watermelon, *Citrullus vulgaris* Schrad. *Libyan Sci. J.* 6A:1–8.
- Watts, V.M. 1962. A marked male-sterile mutant in watermelon. *Proc. Amer. Soc. Hort. Sci.* 81:498–505.
- Watts, V.M. 1967. Development of disease resistance and seed production in watermelon stocks carrying the *msg* gene. *Proc. Amer. Soc. Hort. Sci.* 91:579–583.
- Weetman, L.M. 1937. Inheritance and correlation of shape, size, and color in the watermelon, *Citrullus vulgaris* Schrad. Iowa Agr. Expt. Sta. Res. Bul. 228:222–256.
- Wimmer, B., F. Lottspeich, I. van der Klei, M. Veenhuis, and C. Gietl. 1997. The glyoxysomal and plastid molecular chaperones (70-kDa heat shock protein) of watermelon cotyledons are encoded by a single gene. *Proc. Natl. Acad. Sci. USA* 94:13624–13629.
- Winstead, N.N., M.J. Goode, and W.S. Barham. 1959. Resistance in watermelon to *Colletotrichum lagenarium* races 1, 2, and 3. *Plant Dis. Rptr.* 43:570–577.
- Zamir, D., N. Navot, and J. Rudich. 1984. Enzyme polymorphism in *Citrullus lanatus* and *C. colocynthis* in Israel and Sinai. *Plant Syst. Evol.* 146:163–170.
- Zhang, X.P. and M. Wang. 1990. A genetic male-sterile (*ms*) watermelon from China. *Cucurbit Genet. Coop. Rpt.* 13:45.
- Zhang, X.P. B.B. Rhodes, and M. Wang. 1994a. Genes controlling watermelon seed size. *Cucurbitaceae '94: Evaluation and enhancement of cucurbit germplasm*, p. 144–147. In: G. Lester and J. Dunlap. (eds.). ASHS Press, Alexandria, Va.
- Zhang, X.P., H.T. Skorupska, and B.B. Rhodes. 1994b. Cytological expression in the male sterile *ms* mutant in watermelon. *J. Hered.* 85:279–285.
- Zhang, X.P. 1996. Inheritance of seed size from diverse crosses in watermelon. *Cucurbit Genet. Coop. Rpt.* 19:67–69.
- Zhang, X.P., B. B. Rhodes, V. Baird, and H. Skorupska. 1996a. A tendrillless mutant in watermelon: phenotype and development. *HortScience* 31(4):602 (abstr.).
- Zhang, X.P., B.B. Rhodes, and W.C. Bridges. 1996b. Phenotype, inheritance and regulation of expression of a new virescent mutant in watermelon: juvenile albino. *J. Amer. Soc. Hort. Sci.* 121(4):609–615.