

The Genes of *Capsicum*

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Abstract. Pepper (*Capsicum* spp.) is one of the most cultivated vegetable and spice crops in the world. *Capsicum* genetics have been extensively studied, but the most recent *Capsicum* gene list was published more than a decade ago. Since then, new genes have been described. This updated gene list provides detailed descriptions of genes, including the genes' characteristics, the genetic background of the mutants/lines, action mechanisms of genes, gene interactions, molecular markers, and chromosome localization when available. This new list includes 292 genes for morphological traits; physiological traits; sterility; and resistance to diseases, nematodes, and herbicides, which includes the 92 genes that have not been previously described.

Pepper (*Capsicum* spp.) is one of the most cultivated vegetable and spice crops worldwide, and plays an important role as a constituent in many of the world food industries (Bosland and Votava, 2000). Peppers were one of the first plants to be domesticated and cultivated in the western hemisphere. The small-fruited wild forms of peppers—chiltepins—are still found growing wild in Arizona and Texas in the United States. World pepper production in 2004 reached 1.65 million ha with more than 24 million metric tons harvested (FAO, 2005). China is the world's largest producer, with more than 33% of the total production area and nearly 50% of total world production (FAO, 2005).

Capsicum is native to the tropical and subtropical Americas and may comprise up to 30 species, among which the five major cultivated species are *C. annuum* L., *C. frutescens* L., *C. chinense* Jacq., *C. baccatum* L., and *C. pubescens* Ruiz and Pavon (Bosland, 1992). Worldwide, *C. annuum* is the most cultivated and economically important species, and includes both sweet and hot fruits in myriad shapes and sizes.

Most *Capsicum* species are diploid ($2n = 2x = 24$), but there are a few species for which the genome is $2n = 2x = 32$. *Capsicum* has a large genome, with the 2C DNA content ranging from 7.65 pg/nucleus in *C. annuum* to 9.72 pg/nucleus in *C. pubescens*, and with

a general mean of 8.42 pg/nucleus (Belletti et al., 1998). These values correspond to the 1c genome size of 3.691 (*C. annuum*), 4.690 (*C. pubescens*), and 4.063 (general mean) Mbp. *C. annuum* genome is about three to four times the size of the tomato (*Solanum lycopersicum* L.) genome (Arumuganathan and Earle, 1991).

Capsicum genes have been studied since Webber, in 1912, investigated the inheritance of several traits (cited in Boswell, 1937). Other early contributions to *Capsicum* genetics were made by Atkins and Sherrard (1915) of England, Deshpande (1933) of India, Ikeno (1913, 1917) of Japan, and Halsted (1918) and Dale (1929, 1931) of the United States (all cited in Boswell, 1937). In 1933, Matsuura summarized pepper genetics, from 1910 to 1929, that consisted of 12 characters without designating any gene symbols (cited in Boswell, 1937). Boswell (1937) reviewed the inheritance of 16 characters in pepper, of which seven gene symbols were recorded for seven different traits (purple foliage and stem color, intense purple foliage and stem color, red mature fruit color, blunt fruit apex, bulged fruit base, pendent fruit position, and non-clasping fruit calyx). After Boswell's work, inheritance studies in pepper gained more interest and included more important traits associated with greater importance of pepper production worldwide, as well as more induced or spontaneous mutants being obtained.

From the late 1980s, more efforts to tag the identified genes with molecular markers, and to clone and characterize the genes were undertaken (Lefebvre et al., 1995). Paran and colleagues (2004) used data from six individual maps from the United States, Israel, and France to construct an integrated genetic map of *Capsicum* including six distinct progenies and 2262 genetic markers covering 1832 cM. Many markers and quantitative trait loci (QTLs) are linked with important traits, and the *pun-1* gene, which causes heat

in the fruit, was successfully cloned (Stewart et al., 2005).

Lippert and associates (1965) compiled the first *Capsicum* gene list containing 50 genes, and proposed the basic rules for *Capsicum* gene nomenclature and symbolism according to the Report of the Committee on Genetic Symbols and Nomenclature. Later, Lippert and associates (1966) increased the list to 75 genes (cited in Daskalov and Poulos, 1994). Daskalov (1973) presented, in Bulgarian, a gene list with nearly 90 genes. For the benefit of pepper breeders, Greenleaf (1986) produced a gene list considered important to pepper breeding that was adapted from the gene lists of Lippert and associates (1965, 1966), and proposed several new gene symbols. The *Capsicum* and Eggplant Newsletter Editorial Board (CENL) (1994) proposed the rules for gene nomenclature of *Capsicum* to assist in standardizing and articulating the gene symbols. Based on these rules, Daskalov and Poulos (1994) compiled a list of the known genes, reassigned several gene symbols, and standardized other confusing symbols.

The gene list updated here has been modified and updated from previous lists, especially the gene list of Daskalov and Poulos (1994). The current gene list contains detailed descriptions of the gene mutants and gene lines as well as the genetic background (cultivars or accessions, and species). If known, we have also added the acting mechanisms and characteristics of genes and gene interactions. In addition, molecular markers and the chromosome localization of genes have been added.

In addition to the genes listed by Daskalov and Poulos (1994), 92 new genes have been added to this gene list. The gene symbols proposed are in accordance to the rules for gene nomenclature of *Capsicum* for those characters that have been examined for inheritance (CENL, 1994). An attempt was made to correct errors in the gene symbols or descriptions from previous lists. This gene list (Table 1) presents the 292 known genes of *Capsicum*, including morphological traits, physiological traits, sterility, and resistance to diseases, nematodes, and herbicides.

Gene Nomenclature for *Capsicum*

The basic rules for *Capsicum* gene nomenclature have been proposed by Lippert and associates (1965), and adopted by Daskalov (1973), Csillery (1980a, 1983), Greenleaf (1986), Daskalov and Poulos (1994), and then updated by the CENL Committee for *Capsicum* Gene Nomenclature (1994). In brief, the rules for assigning gene symbols adopted from others are that genes are symbolized by a maximum of three italicized Roman letters. The first letter of the symbol should be the same as that for the gene name, which should describe a characteristic feature of the mutant type in a minimum of adjectives or nouns in English or Latin. When the mutant is dominant, the first letter of the symbol is capitalized; if the mutant is

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Table 1. The genes of *Capsicum*.

| Preferred symbol | Synonym | Character | References |
|---|-----------------|--|--|
| <i>A</i> | <i>F</i> | <i>Anthocyanin</i> ; the incompletely dominant gene for anthocyanin color in the foliage, flower, and immature fruit | Lippert et al., 1965; Odland, 1960; Peterson, 1959 |
| <i>al-1</i> to <i>al-8</i> | <i>b, s</i> | <i>Anthocyanin-less</i> ; prevents purple color on the stem, fruits, and in plants; nodes, green; anthers, yellow; only <i>al5</i> shows a slight purplish marking along the lines of dehiscence; lack of purple spots on immature fruits; in some genotypes, and especially in cold and rainy weather, purple spots on the nodes and immature fruits may be observed; epistatic to <i>A</i> , <i>As</i> , and <i>Asf</i> ; nonallelic; <i>al6</i> and <i>al7</i> found in <i>C. chinense</i> , <i>al8</i> found in <i>C. chacoense</i> ; linkage found between <i>al2</i> and <i>mos2</i> | Cook, 1961b; Csillery, 1980a, 1983, 1984; Daskalov, 1973a, b; Daskalov and Poulos, 1994; Greenleaf, 1986; Odland, 1960 |
| <i>Anr-1*</i> | | <i>Anthracnose resistance</i> ; resistance of <i>C. annuum</i> cv. Chungryong to <i>C. dematium</i> | Park et al., 1992 |
| <i>Anr-2*</i> , <i>Anr-3*</i> , <i>Anr-4*</i> | | Resistance to <i>C. gloeosporioides</i> in <i>C. annuum</i> , <i>Anr2</i> in 'BGH3077'; two genes <i>Anr3</i> and <i>Anr4</i> in 'BGH2850' and 'BGH5085' | Fernandes and Ribeiro, 1998 |
| <i>Anr-5*</i> | | <i>Anthracnose resistance</i> ; resistance to <i>C. capsici</i> in the line '83-168' | Lin et al., 2002 |
| <i>anv</i> | | <i>Angustifolia variegada</i> ; elliptical cotyledons, long and narrow leaves | Daskalov and Poulos, 1994 |
| <i>Ap**</i> | <i>AP</i> | <i>The pointed shape of the fruit apex</i> ; dominant to the indented shape | Ishikawa et al., 1998 |
| <i>As</i> | <i>P</i> | <i>Anthocyanin on style</i> ; purple in the absence of <i>A</i> or <i>Asf</i> | Lippert et al., 1965 |
| <i>Asf</i> | <i>W</i> | <i>Anthocyanin on style and filament</i> ; purple in the absence of <i>A</i> . | Lippert et al., 1965; Odland, 1960 |
| <i>aur</i> | | <i>Aurea</i> ; golden cotyledons and leaves | Daskalov and Poulos, 1994 |
| <i>B</i> | | <i>Beta-carotene</i> ; high beta-carotene content in mature fruits; interacts with <i>t</i> | Lippert et al., 1965 |
| <i>bc*</i> | | <i>Beta-carotene</i> ; high beta-carotene content conferred by preventing hydroxylation of beta-carotene to beta-cryptoxanthin; mutant from 'Pasardzhishka Kapia' | Chalukova et al., 1993; Daskalov et al., 1995 |
| <i>bl</i> | | <i>Branchless</i> ; plants grow normally to the stage of first stem bifurcation, then stem development stops; found in PI 169113 | Bergh and Lippert, 1964 |
| <i>brl</i> | | <i>Braquitica latifoliata</i> ; shortened stem internodes; leaf blades wide, large, round, and dark green with short, thickened petioles | Daskalov and Poulos, 1994 |
| <i>Bs-1</i> | | <i>Bacterial spot</i> resistance; hypersensitive resistance in PI 163192 to race 2 of <i>X. campestris</i> pv. <i>vesicatoria</i> | Cook and Stall, 1963 |
| <i>Bs-2</i> | | <i>Bacterial spot</i> resistance; hypersensitive resistance in PI 260435 to both race 1 and race 2 of <i>X. campestris</i> pv. <i>Vesicatoria</i> | Hibberd et al., 1987 |
| <i>Bs-3</i> | | <i>Bacterial spot</i> resistance; hypersensitive resistance in PI 271322 to race 1 of <i>X. campestris</i> pv. <i>vesicatoria</i> | Hibberd et al., 1987 |
| <i>Bs-4*</i> | | <i>Bacterial spot</i> resistance; hypersensitive resistance in PI 235047(<i>C. pubescens</i>) to race 6 of <i>X. campestris</i> pv. <i>vesicatori</i> . | Sahin and Miller, 1997, 1998 |
| <i>bs-5*</i> , <i>bs-6*</i> | | <i>Bacterial spot</i> resistance; nonhypersensitive resistance in ECW-12346 to race 6 of <i>X. campestris</i> pv. <i>vesicatoria</i> | Jones et al., 2002 |
| <i>bv</i> | <i>mutant-2</i> | <i>Bushy variegated</i> ; plants with creamy white apical leaves spotted with small green areas; extensive lateral shoot development provides a bushy appearance | Cook, 1962; Lippert et al., 1964 |
| <i>Bzt</i> | | <i>Bentazon tolerance</i> ; confers a high level of tolerance to herbicide bentazon in <i>C. annuum</i> cv. 'Santaka'; modifying genes may affect the <i>Bzt</i> gene in 'Bohemian Chilli' | Fery and Harrison, 1990; Wolff et al., 1992 |
| <i>c-1</i> | <i>c</i> | <i>Carotenoid pigment inhibitors</i> ; reduce 10% in red color of mature fruits; <i>c1</i> and <i>c2</i> reduced pigmentation of y^+ and y by the inhibition of beta-carotene | Hernandez and Smith, 1985; Lippert et al., 1965 |
| <i>c-2</i> | <i>c1</i> | <i>Carotenoid pigment inhibitors</i> ; much stronger red color reduction than <i>c1</i> | Hernandez and Smith, 1985; Lippert et al., 1965 |
| <i>ca</i> | | <i>Canoe</i> ; margins of cotyledons and leaves are rolled upward by hyponasty; weak and tumbling stem | Csillery, 1980a |
| <i>call</i> | | <i>Callus proliferations</i> ; tiny wartlike structures scattered on cotyledon, stem, and leaf; more pronounced on the abaxial surface | Csillery, 1983 |
| <i>ce</i> | <i>e</i> | <i>Calyx enclosed</i> ; calyx-enclosed fruit base; loci <i>ce</i> and <i>fb</i> are linked at 4.7 cM | Miller and Fineman, 1938 |

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Table 1. (Continued) The genes of *Capsicum*.

| Preferred symbol | Synonym | Character | References |
|-----------------------------|-------------|--|--|
| <i>cf-1</i> | <i>cf</i> | <i>Closed flower</i> ; petals remain attached to one another at anthesis; allelic to the gene governing the closed-flower trait in nine Hungarian mutants; found in 'UFBG 8209-1' | Subramanya and Ozaki, 1984; Zewdie and Bosland, 2001 |
| <i>cf-2*</i> | | <i>Closed flower</i> ; calyx enlarged covering half portion of the corolla, which remains rolled and never opens; plant dwarf and bushy with many branches; most flowers with protruded style; allelism to <i>cf1</i> unknown | Pathak et al., 1983a |
| <i>cfs</i> | | <i>Conditional female sterile</i> ; vigorous plants with compact habits; normal developed flowers containing fertile pollen grains; obtained from an M ₂ population of the cv. 'Borjana' | Daskalov and Mihailov, 1988 |
| <i>chl</i> | | <i>Chlorina</i> ; greenish yellow variegation or chlorophyll deficiency | Lippert et al., 1965 |
| <i>ci</i> | | <i>Compound inflorescences</i> ; dichasial structure formed with repeated branching as in a pseudo umbel at the end of the sympodia | Csillery, 1983 |
| <i>cl</i> | <i>g</i> | <i>Chlorophyll retainer</i> ; in mature fruit; combines with <i>y</i> * (red) or <i>y</i> (yellow) to produce brown and olive green mature fruit color, respectively | Hurtado-Hernandez and Smith, 1985; Shiffriss and Pilovsky, 1992; Smith, 1950 |
| <i>cm*</i> | | <i>Cucumber mosaic virus (CMV) resistance</i> ; resistance to CMV in 'Perennial' | Singh and Thakur, 1977 |
| <i>ct</i> | | <i>Compact</i> ; controls the extent of lateral axillary shoot development before the first bifurcation; plants have more numerous and erect axillary shoots at maturity, and are about half as tall as normal, but internodes are not as short as in dwarfs | McCammon and Honma, 1984; Shiffriss and Hakim, 1977 |
| <i>cur*</i> | | <i>Curved leaf</i> ; leaves have curved leaf blades with long petioles; fewer branches, flowers, and fruits; seed set poor; induced from 'PC 1' | Aniel Kumar et al., 2001 |
| <i>cy</i> | | <i>Chappy</i> ; at maturity the exocarp is covered with transversally oriented, small suberized cracks | Csillery, 1983 |
| <i>div</i> | | <i>Diversa</i> ; deformed leaves, yellow-green virescent leaves | Daskalov and Poulos, 1994 |
| <i>dm</i> | <i>sl</i> | <i>Diminished morphology</i> ; extremely small (2 cm in length, 1 cm in width) leaves with normal shape; main stem before the first cyme has 18 to 20 internodes; equally tiny stem and flowers; moderate water stress causes wilting as in <i>sd</i> | Csillery, 1983; Daskalov and Poulos, 1994 |
| <i>Dms</i> | | <i>Dominant genetic male sterility</i> ; mutation from <i>ms5</i> | Daskalov and Poulos, 1994 |
| <i>ds</i> | | <i>Desynapsis</i> ; univalents occur at a high frequency despite regular pachytene pairing at diakinesis and metaphase I; causes a high degree of sterility; modifying genes may affect <i>ds</i> | Panda et al., 1987 |
| <i>dt</i> | | <i>Determinate growth</i> ; determinate growth habit; <i>Dt</i> and <i>Ct</i> condition indeterminate growth, and are epistatic to one another | McCammon and Honma, 1984 |
| <i>dtr</i> | <i>dt-1</i> | <i>Datura leaves</i> ; normal cotyledons; leaves are irregularly dentate like leaves of <i>Datura</i> spp. with maximal expression around the 10th leaf | Csillery, 1983; Daskalov and Poulos, 1994 |
| <i>dvg</i> | | <i>Deforme variegada</i> ; deformed and undulated green virescent variegated leaves | Daskalov and Poulos, 1994 |
| <i>dw-1</i> | | <i>Dwarf</i> ; plant height, 12 to 15 cm; very short internodes; very thick, curly, dark-green, glossy leaves; normal flowers; reduced female fertility; mutant in 'Zlaten Medal' | Daskalov, 1973b, 1974 |
| <i>dw-2</i> | | <i>Dwarf</i> ; 15 to 20 cm in height; short internodes; thick, dark-green leaves; mutant in 'Zlaten Medal' | Daskalov, 1974 |
| <i>dw-3</i> | <i>dw1</i> | <i>Dwarf</i> ; 10 to 15 cm height; found in the interspecific hybridization between <i>C. baccatum</i> and <i>C. annuum</i> | Csillery, 1980a |
| <i>dw-4</i> | <i>dw2</i> | <i>Dwarf</i> ; 8 to 10 cm in height, shorter than <i>dw3</i> ; found in the interspecific hybridization between <i>C. frutescens</i> and <i>C. annuum</i> | Csillery, 1983 |
| <i>dw-5*</i> | | <i>Dwarf</i> ; induced mutant in the Italian variety 'Friariello' | Restaino, 1991 |
| <i>dw-6*</i> , <i>dw-7*</i> | | <i>Dwarf</i> ; controlled by two complementary dominant genes; found in the interspecific hybridization between <i>C. annuum</i> and <i>C. chinense</i> | Yazawa et al., 1991 |
| <i>dw-8*</i> | | <i>Dwarf</i> ; 10 to 20 cm height; reduced size of leaf, flowers, fruits, and seeds; mutant from 'PC 1' | Aniel Kumar et al., 2001 |
| <i>ef*</i> | | <i>Early flowering</i> ; flowering 20 to 25 d earlier than 'PC 1'; seed set poor; induced from 'PC 1' | Aniel Kumar et al., 2001 |
| <i>ep*</i> | | <i>Elongated petiole</i> ; narrow and long petiole; irregular flower opening; induced from 'PC 1' | Aniel Kumar et al., 2001 |

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Table 1. (Continued) The genes of *Capsicum*.

| Preferred symbol | Synonym | Character | References |
|-----------------------|-------------------------------------|--|---|
| <i>fa</i> | | <i>Fasciculation</i> ; compact, bushy plants with determinate tendency, short internodes; flowers and fruits borne in clusters; minor genes involved in the expression of fasciculation | Greenleaf, 1986; Lippert et al., 1965; Van der Beek and Ltifi, 1990 |
| <i>fb</i> | <i>M_f</i> | <i>Fruit base nonbulging</i> ; nonbulged fruit base | Miller and Fineman, 1938 |
| <i>Fc</i> | | <i>Filament color</i> ; filament color in anthers | Prince et al., 1993 |
| <i>fcf**</i> | <i>fc</i> | <i>Fasciflora</i> ; female sterile plants with 27% to 55% pollen fertility, seedless fruits | Daskalov and Poulos, 1994 |
| <i>fems*</i> | | <i>Female and male sterility</i> ; pollen shrunken, containing no starch; many small fruits with no seeds; mutant in line '4526' | Martin and Crawford, 1951 |
| <i>fi-1</i> | <i>mutant-1, fi</i> | <i>Filiform</i> ; threadlike leaves, blossom irregularities; female sterility | Cook, 1961b; Lippert et al., 1965 |
| <i>fi-2</i> | | <i>Filiform</i> ; similar to <i>fi1</i> ; narrow cotyledons and leaves (3–4 mm); threadlike petals; carpels usually not fused to pistil except in particularly small fruited varietal background; incomplete female sterile | Csillery, 1980a |
| <i>fl*</i> | | <i>Folded leaf</i> ; leaves folded upward, giving boat-shaped appearance; prominent in seedlings; partially fertile; induced from 'PC 1' | Aniel Kumar et al., 2001 |
| <i>flc</i> | | <i>Flaccid</i> ; cotyledons and leaves exhibit flaccid condition; the mutant has a normal leaf phenotype, but under typical field and greenhouse conditions it becomes flaccid; induced mutant from 'Keystone Resistant Giant No. 3' | Bosland, 2002 |
| <i>flf*</i> | | <i>Flowerless plant</i> ; profuse vegetative growth, induced from 'PC 1' | Aniel Kumar et al., 2001 |
| <i>Flv</i> | | <i>Flavi</i> ; yellow-green leaves, shorter and less vigorous plants | Daskalov and Poulos, 1994 |
| <i>fms</i> | | <i>Functional male sterility</i> ; degenerated corolla; shriveling stamens develop incomplete anther and stigma; anthers closed by longer calyxes; mutant from 'Fudijian' | Yuan and Li, 2000 |
| <i>fr</i> | | <i>Frippy</i> ; leaf margins are marked by undulation | Csillery, 1980a |
| <i>fs</i> | | <i>Female sterile</i> ; complete female sterility with no other primary phenotypic effects; mature plants with a twiggy, multiflorous periphery; mutant from PI 159276 | Bergh and Lippert, 1964 |
| <i>fv</i> | | <i>Fan vein</i> ; veins of true leaves are branching like a fan; the leaf blade is often dissected, segments curled like tendrils, corolla, and other parts of the flower are irregularly reduced, but fruits may develop; found in <i>C. chacoense</i> | Csillery, 1980a |
| <i>gd</i> | | <i>Glossy diminutive</i> ; small leaves with an unusual, pale glossy appearance; plants vary from tiny to as large as one-sixth of the normal plant size; mutant from PI 159226 | Bergh and Lippert, 1964 |
| <i>gds</i> | | <i>General defense system</i> ; provides resistance to <i>Xanthomonas campestris</i> pv. <i>vesicatoria</i> in PI 163192; promotes cell growth and cell wall thickening | Csillery et al., 2004; Szarka and Csillery, 1995 |
| <i>Gi</i> | | <i>Graft incompatible</i> ; manifests when grafted to other <i>Solanaceae</i> | Lippert et al., 1965 |
| <i>H</i> | | <i>Hairy</i> or pubescent leaf surface; dominant gene; <i>H₁</i> is epistatic to <i>Sm₁</i> whereas <i>smsm</i> is epistatic to <i>hh</i> . | Holmes, 1934; Shuh and Fontenot, 1990 |
| <i>ht</i> | | <i>Hungarian tricolor</i> ; the basal one-fifth part of the fruit less pigmented, like <i>sw</i> before maturity, whereas more or less dark-green on top four-fifths portion; at full maturity a red-white-green fruit color results from the top to the calyx | Csillery, 1983 |
| <i>im</i> | | <i>Intermediate</i> ; purple color at intermediate maturity in originally nonpurple immature fruit; relation to <i>A</i> unknown. | Lippert et al., 1965 |
| <i>k</i> | | Easy pedicle detachment from node; related to flower and young fruit abscission | Uzo, 1984 |
| <i>L¹</i> | <i>L¹, l¹</i> | <i>Localization</i> ; localization of P ₀ strain of tobacco mosaic virus (TMV) in 'Bruinsma Wonder' and 'Verbeterde glas' | Boukema et al., 1980b; Holmes, 1934, 1937 |
| <i>L^{1c}</i> | | <i>Localization</i> ; localization of TMV resistance at high temperature; 'C' for 'Criollo de Moralos-334'; allelic at <i>L</i> locus | Daubeze et al., 1990 |
| <i>L²</i> | <i>L</i> | <i>Localization</i> ; localization of both P ₀ and P ₁ strains of TMV in <i>C. frutescens</i> cv. Tabasco | Boukema, 1980; Holmes, 1934, 1937 |

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Table 1. (Continued) The genes of *Capsicum*.

| Preferred symbol | Synonym | Character | References |
|---|-----------|---|--|
| L^{2g} | | <i>Localization</i> ; this allele in 'Greygo' behaves like the allele L^2 characteristic of 'Tabasco'; identity of the allele L^{2g} relative to L^2 is undetermined | Salamon et al., 2001 |
| L^3 | <i>Tm</i> | <i>Localization</i> ; localization of P ₀ , P ₁ , and P _{1,2} strains of TMV in <i>C. chinense</i> PIs | Boukema, 1980; van den Berkmortel, 1997 |
| L^4 | | <i>Localization</i> ; localization of P ₀ , P ₁ , P _{1,2} and P _{1,2,3} strain of TMV in <i>C. chacoense</i> accessions PI260429 and SA185; allelic series $L^4 > L^3 > L^2 > L^{1c} > L^1 > L^+$ | Boukema, 1984 |
| <i>ld*</i> | | <i>Leaf dimorphism</i> ; small, narrow, thin, light-green leaves at top of plant; long, broad, thick, dark-green leaves at lower portions of plant; induced from 'PC 1' | Aniel Kumar et al., 2001 |
| <i>lf*</i> | | <i>Late flowering</i> ; flower initiation 20 to 30 d later than in 'PC 1' | Aniel Kumar et al., 2001 |
| <i>lmr-1*</i> , <i>lmr-2*</i> , <i>lmr-3*</i> | | <i>Leveillula mildew resistance</i> ; three pairs of genes control the resistance to powdery mildew incited by <i>Leveillula taurica</i> (<i>Oidiopsis taurica</i>) in <i>C. annuum</i> 'H-V-12' | Shifriss et al., 1992 |
| <i>lov</i> | | <i>Loss of vesicle</i> ; nonpungency in <i>C. chinense</i> accession 'NMCA 30036' and 'PI 543190'; complementation with <i>pun1</i> results in pungency | Votava and Bosland, 2002 |
| <i>lsm</i> | | <i>Light-sensitive mosaic</i> ; green cotyledons in normal planting; when seeds germinate in light, cotyledons and leaves are variegated; stem and fruits may develop chlorophyll-less sections and stripes; loss of chlorophyll is related to the length of light exposure; 5 to 6 d of light exposure before the full expansion of the cotyledons is sufficient to produce plantlets like <i>xantha</i> | Csillery, 1980a |
| <i>lut-1</i> to <i>lut-18</i> | | <i>Lutescens</i> ; cotyledon and leaves are uniformly yellowish, lighter than normal green, however, distinct accessions may represent different intensities of color; nonallelism among <i>lut-1</i> to <i>lut-18</i> | Csillery, 1980a, 1983, 1985 |
| <i>lut-19*</i> | | <i>Lutescens</i> ; cotyledon and leaves are uniformly yellow-green; mutant from <i>C. annuum</i> ; allelism of <i>lut-19</i> and <i>lut-1</i> to <i>lut-18</i> unknown | Ma et al., 2001 |
| <i>m-1</i> | <i>m</i> | <i>Marbled</i> ; the first true leaf develops isolated zones of white, light-green, and normal green, suggesting a marbled appearance; the boundaries of the zones are distinct; leaves are puckered with irregular margins where marbling occurs | Lippert et al., 1964 |
| <i>m-2</i> | | <i>Marbled</i> ; all leaves have zones of white, light-green and green when grown in the greenhouse; when grown in the field, only the first true leaf has the marbled pattern; mutant found in 'Pasardjishka kapia 794' | Daskalov, 1974 |
| <i>m-3</i> | | <i>Marbled</i> ; marbled leaves well pronounced in the open field and the greenhouse; mutant plants are reduced in size; found in 'Zlaten Medal' | Daskalov, 1974 |
| <i>m-4</i> | | <i>Marbled</i> ; distinct green and white zones on foliage and immature fruits | Daskalov and Poulos, 1994 |
| <i>Me-1</i> | | <i>Meloidogyne</i> spp. resistance; <i>M. arenaria</i> , <i>M. incognita</i> , and <i>M. javanica</i> , resistance, but not to the 'Seville' isolate of <i>M. species</i> in 'PM 217' | Souza-Sobrinho et al., 2002 |
| <i>Me-2</i> | | <i>Meloidogyne</i> spp. resistance; resistant to <i>M. javanica</i> and the 'Seville' isolate of <i>M. species</i> in 'PM 217' | Souza-Sobrinho et al., 2002 |
| <i>Me-3</i> | | <i>Meloidogyne</i> spp. resistance; resistant to <i>M. incognita</i> , <i>M. javanica</i> , and most <i>M. arenaria</i> isolates (except <i>M. arenaria</i> Ain Toujdate isolate) in PI 322719 | Djian-Caporalino et al., 2001; Souza-Sobrinho et al., 2002 |
| <i>Me-4</i> | | <i>Meloidogyne</i> spp. resistance; resistant to <i>M. arenaria</i> Ain Taoujdate isolate in PI 322719 | Souza-Sobrinho et al., 2002 |
| <i>Me-5</i> | | <i>Meloidogyne</i> spp. resistance; resistant only to <i>M. javanica</i> in 'Yolo Wonder' | Souza-Sobrinho et al., 2002 |
| <i>Me-6</i> | | <i>Meloidogyne</i> spp. resistance; specifically resistance to <i>M. arenaria</i> and <i>M. javanica</i> (French population) in 'Yolo Wonder' | Djian-Caporalino, personal communication |
| <i>Me-7</i> | | <i>Meloidogyne</i> spp. resistance; conferring a high level of resistance to <i>M. arenaria</i> , <i>M. incognita</i> , and <i>M. javanica</i> in 'CM 334' | Pegard et al., 2005 |
| <i>Mech-1</i> , <i>Mech-2</i> | | <i>Meloidogyne chitwoodii</i> resistance; <i>Mech1</i> found in 'PM217'; <i>Mech2</i> found in 'CM 334' | Djian-Caporalino et al., 2004 |
| <i>MoA</i> | <i>B</i> | <i>Modifier of A</i> ; second locus for anthocyanin color, intensifies the purple color in the presence of <i>A</i> | Lippert et al., 1965 |

(Continued on next page)

Table 1. (Continued) The genes of *Capsicum*.

| Preferred symbol | Synonym | Character | References |
|-------------------------|-------------------|--|--|
| <i>Mf-1, Mf-2, Mf-3</i> | <i>M1, M2, M3</i> | <i>Multiple flowers per node</i> ; controls multiple flower expression; recessive homozygosity at any two loci is epistatic to the dominant allele present at the third locus | Daskalov and Poulos, 1994; Shuh and Fontenot, 1990 |
| <i>mos-1 to mos-52</i> | | <i>Mosaics</i> ; cotyledons are either normal or display mosaic variegation of the leaves; <i>mos-1 to mos-51</i> found in <i>C. annuum</i> , <i>mos-52</i> in <i>C. baccatum</i> , nonallelism among <i>mos-1 to mos-9</i> | Csillery, 1980a, 1983 |
| <i>ms-1</i> | | <i>Genic male sterility</i> ; anthers are small and shrunken, devoid of pollen grains; <i>ms-1</i> gene may be linked with one of the genes involved in pigmentation; mutant from 'All Big' | Shifriss and Frankel, 1969; Shifriss and Eidelman, 1987 |
| <i>ms-2</i> | | <i>Genic male sterility</i> ; shrunken anthers that release numerous, aborted pollen grains; mutant from 'California Wonder' | Shifriss and Rylski, 1972 |
| <i>ms-3</i> | | <i>Genic male sterility</i> ; shrunken anthers, in some cases only a very small amount of fertile and sterile pollens are formed; irradiation induced mutant from 'Pasardjishka Kapia 794' | Daskalov, 1968 |
| <i>ms-4</i> | | <i>Genic male sterility</i> ; anthers are not reduced severely, contain a small amount of fertile and sterile pollen grains; irradiation induced mutants from the variety 'Pasardjishka Kapia 794' | Daskalov, 1971, 1974 |
| <i>ms-5</i> | | <i>Cytoplasm male sterility</i> ; anthers are very severely reduced, contain no pollen grains in field; under greenhouse conditions certain plants may produce a small amount of fertile pollen grains; irradiation induced mutant from 'Kalinkov 800/7' | Daskalov, 1974 |
| <i>ms-6, ms-7, ms-8</i> | | <i>Genic male sterility</i> ; shrunken anthers with reduced anther sizes; sometimes only a very small amount of fertile pollens are formed; nonallelic among <i>ms-1 to ms-8</i> ; irradiation induced mutant from 'Zlaten Medal' | Daskalov, 1973b |
| <i>ms-9</i> | <i>mr9</i> | <i>Genic male sterility</i> ; γ -irradiation induced male sterile mutants | Daskalov and Poulos, 1994; Greenleaf, 1986 |
| <i>ms-10</i> | <i>mc-509</i> | <i>Genic male sterility</i> ; ethyl methansulphonate (EMS)-induced male sterile mutant; <i>ms-10</i> was found allelic to the <i>msk</i> allele isolated spontaneously in Korea | Daskalov and Poulos, 1994; Greenleaf, 1986; Shifriss, 1995 |
| <i>ms-11</i> | <i>mc-705</i> | <i>Genic male sterility</i> ; EMS-induced male sterile mutants | Daskalov and Poulos, 1994; Greenleaf, 1986 |
| <i>ms-12*</i> | | <i>Genic male sterility</i> ; small and shrunken anthers without pollen grains; postmeiotic breakdown of microspores; nonallelism to <i>ms-1</i> and <i>ms-2</i> ; allelism with Daskalov's <i>ms</i> -alleles unknown; mutant from 'Gambo' | Shifriss, 1973 |
| <i>ms-13*</i> | <i>ms</i> | <i>Genic male sterility</i> ; complete pollen sterility; the postmeiotic breakdown of microspores; mutant from 'CA452-1' | Meshram and Narkhede, 1982 |
| <i>ms-14*</i> | | <i>Genic male sterility</i> ; androecium transformed into petaloid structures; mutant from 'Kalyanpur selection' | Pathak et al., 1983b |
| <i>ms-15*</i> | <i>ms</i> | <i>Genic male sterility</i> ; anthers are dark blue, and reduced 50%; postmeiotic breakdown of the microspore during the formation of male gametes; mutant from 'CA-960' | Meshram et al., 1992 |
| <i>msc-1*</i> | | <i>Genic male sterility</i> ; spontaneous mutant found in China; allelism with <i>ms-1 to ms-15</i> , and <i>msk</i> unknown | Yang, 1981; Yang et al., 1994 |
| <i>msc-2*</i> | | <i>Genic male sterility</i> ; spontaneous mutant found in China from 'Ying Ge Bai Er'; allelism with <i>ms-1 to ms-15</i> , <i>msc-1</i> and <i>msk</i> unknown | Fan and Guo, 1994; Fan et al., 2004 |
| <i>msk</i> | | <i>Genic male sterility</i> ; spontaneous mutant in Korea | Shifriss, 1973 |
| <i>N</i> | | <i>Root-knot nematode resistance</i> ; resistance to <i>M. incognita</i> in 'Santaka' | Hare, 1957 |
| <i>nf</i> | | <i>Nonflowering</i> ; no flowering throughout the growing season | Pathak et al., 1985 |
| <i>nl*</i> | | <i>Narrow leaf</i> ; narrow leaves; reduced branches, flowers, and fruits; induced from 'PC 1' | Aniel Kumar et al., 2001 |
| <i>O</i> | | <i>Oblate fruit shape</i> ; fruit shape independent of fruit size; modifiers also affect fruit shape <i>A</i> , <i>O</i> , and <i>sw1</i> are linked, the linear order and the map distances are <i>A-6.5-O-18.8-sw1</i> | Peterson, 1959 |
| <i>P</i> | <i>D</i> | <i>Pointed fruit apex</i> ; incomplete dominant to blunt | Miller and Fineman, 1938; Lippert et al., 1965 |

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Table 1. (Continued) The genes of *Capsicum*.

| Preferred symbol | Synonym | Character | References |
|--------------------------|---|--|---|
| <i>pc-1, pc-2, pc-3</i> | | <i>Polycotyledons</i> ; cotyledon number is frequently three to four; the stem is fasciated; sometimes after three to four nodes a pseudo-dichotomous branching with unequally developing of shoots may occur; all three are nonallelic | Csillery, 1980a |
| <i>pec</i> | | <i>Petaloid calyx</i> ; the distal part of the calyx tube is transformed to a white corollalike tube and abscised after anthesis | Csillery, 1983 |
| <i>Ped**</i> | <i>PED</i> | <i>The acute shape of the fruit pedicle attachment</i> ; dominant to the bulged shape; reassignment for <i>PED</i> | Ishikawa et al., 1998 |
| <i>Pf</i> | | <i>Parthenocarpic fruit</i> ; fruit size reduced; ovules began to degenerate 2 d after flower opening, and completely degenerate after 5 d; pollen fertility highly reduced | Pathak et al., 1983c |
| <i>Pfo*</i> | | <i>Phytophthora capsici foliar resistance</i> ; resistance to foliar rot in 'CM 334' | Walker and Bosland, 1999; Sy et al., 2005 |
| <i>Pfr*</i> | <i>Fr</i> | <i>Phytophthora capsici fruit resistance</i> ; resistance to fruit rot in 'Waxy Globe'; reassignment for <i>Fr</i> | Saini and Sharma, 1978 |
| <i>Ph</i> | | <i>Procumbent hypocotyls</i> ; seedlings have a constriction below the cotyledonary node marked with a bright-green ring; at two to three leaf stage the hypocotyl bends down, the stem touching the ground; only the shoot tip turning upward; found in an interspecific hybrid between <i>C. chinense</i> and <i>C. annuum</i> | Csillery, 1980a |
| <i>pi</i> | <i>v</i> | <i>Plastid instability</i> ; green and white leaf variegation | Lippert et al., 1965 |
| <i>plut-1</i> | | <i>Pallid lutescens</i> ; pale-yellow leaf color | Csillery, 1985 |
| <i>Pn1</i> | | <i>Potyvirus necrotic</i> ; confers the system lethal necrotic response for specific resistance to PVY (0) in 'CM 334' | Dogimont et al., 1996 |
| <i>prp</i> | | <i>Proliferous plana</i> ; stamens are transformed into petals followed by equally transformed carpels, the latter form a closed structure, almost as a pistil, but inside the laminar structures are continuously formed petaloids and carpelloids | Csillery, 1983 |
| <i>Ps</i> | | <i>Pod separates easily from calyx</i> ; incomplete dominant; gene expressivity can be modified by genes controlling fruit shape | Greenleaf, 1986; Smith, 1951 |
| <i>Psr*</i> | | <i>Phytophthora stem rot resistance</i> ; resistance to stem rot in 'CM 334' | Sy et al., 2005 |
| <i>pun-1</i> | <i>c</i> | <i>Nonpungency</i> ; absence of capsaicinoids in fruit | Deshpande, 1935; Daskalov and Poulos, 1994 |
| <i>pvr-1</i> | <i>ef, ef¹, ef², ef³</i> | <i>Potyvirus resistance</i> ; locus for resistance to TEV and PepMoV in 'PI 152225' and 'PI 169236' | Boiteux et al., 1996; Greenleaf, 1956, 1986; Kyle and Palloix, 1997; Pasko et al., 1996; Zitter, 1972 |
| <i>pvr-1¹</i> | <i>pvr2¹, y^a, vy¹</i> | <i>Potyvirus resistance</i> ; resistance to PVY (0) in 'Yolo RP10' and 'Yolo Y' | Cook, 1961a; Gebre Selassie et al., 1983; Kang et al., 2005; Kyle and Palloix, 1997 |
| <i>pvr-1²</i> | <i>pvr2², ey^a, ef^a, vy²</i> | <i>Potyvirus resistance</i> ; resistance to PVY (1) and TEV from 'PI 264281' and 'SC46252', and bred into 'Florida VR2' | Cook and Anderson, 1959; Gebre Selassie et al., 1983; Kang et al., 2005; Kyle and Palloix, 1997 |
| <i>pvr-1³</i> | <i>pvr2³</i> | <i>Potyvirus resistance</i> ; polygenic resistance to PVY from 'Perennial' is a combination of QTLs including a major-effect gene mapped to the <i>pvr-2</i> locus; Ayme et al. (2004) propose to name <i>pvr-2³</i> the major-effect gene at the <i>pvr-2</i> locus | Ayme et al., 2004; Caranta et al., 1997a |
| <i>pvr-3</i> | <i>ey^{av}</i> | <i>Potyvirus resistance</i> ; monogenic resistance to PepMoV in 'Avelar' | Kyle and Palloix, 1997; Zitter and Cook, 1973 |
| <i>Pvr-4</i> | <i>cy2, Ry1-2, Pr4</i> | <i>Potyvirus resistance</i> ; resistance to PVY pathotypes 0, 1, and 1-2, and PepMov in 'CM 334' | Boiteux et al., 1996; Dogimont et al., 1996; Kyle and Palloix, 1997 |
| <i>pvr-5</i> | <i>pr5</i> | <i>Potyvirus resistance</i> ; resistance to PVY (0) in 'CM 334' | Caranta et al., 1999; Dogimont et al., 1996 |
| <i>pvr-6</i> | | <i>Potyvirus resistance</i> ; resistance to PVMV from 'Perennial'; complementary with <i>pvr-2</i> ; no detectable effect without <i>pvr-2</i> | Caranta et al., 1996 |
| <i>Pvr-7</i> | | <i>Potyvirus resistance</i> ; resistance to the PepMoV Florida (V1182) strain from <i>C. chinense</i> Jacq. 'PI159236-9093'; <i>Pvr-7</i> is tightly linked to <i>Pvr-4</i> with recombination frequencies of 0.012 to 0.016 | Grube et al., 2000 |
| <i>pvr-8</i> | | <i>Potyvirus resistance</i> ; resistance to PVY isolate P-62-81 (PVY-1) from 'CM 334' | Arnedo-Andres et al., 2004 |
| <i>R-1, R-2</i> | | <i>Purple flower color</i> ; needs comparison with <i>A</i> and <i>MoA</i> | Daskalov and Poulos, 1994 |
| <i>Riv</i> | | <i>Resistance to infection by virus</i> ; a dominant gene in 'Rama' controlling a quantitative effect (i.e., reduction of the probability of an effective multiplication of CMV in the leaves after mechanical inoculation); this gene also modifies the reaction to TMV in the presence of <i>L</i> gene | Pochard, 1982 |

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Table 1. (Continued) The genes of *Capsicum*.

| Preferred symbol | Synonym | Character | References |
|---|---|--|---|
| <i>rl-1</i> | | <i>Roundleaf</i> ; reduces the length of the leaf, but not the width, changing the length-to-width ratio from 1.5 to 1.24; mutant from 'Bighart' | Csillery, 1983; Greenleaf and Hearn, 1976 |
| <i>rl-2</i> | | <i>Roundleaf</i> ; leaf apex is markedly blunt | Csillery, 1980a, 1983 |
| <i>rl-3*</i> | | <i>Round leaf</i> ; leaf tip rounded; fewer branches, flowers and fruits; seed set very poor; induced from 'PC 1' | Aniel Kumar et al., 2001 |
| <i>Rsr-1*</i> , <i>Rsr-2*</i> | | <i>Ralstonia solanacearum</i> resistance; bacterial wilt resistance in 'Mie-Midori' shows incomplete dominance; at least two genes involved in resistance | Matsunaga et al., 1998 |
| <i>ru-1</i> , <i>ru-2</i> | | <i>Rugose</i> ; cotyledons fleshy and curved downward; mature leaves rugose or savoyed and appear darker green in the field | Csillery, 1983 |
| <i>S</i> | | <i>Soft juicy fruit</i> ; distinct from <i>Ps</i> | Greenleaf, 1986 |
| <i>sd</i> | | <i>Scabrous diminutive</i> ; plants similar to those of <i>gd</i> ; foliage with a uniform, fine-textured, surface roughness; found in PI 172768 | Bergh and Lippert, 1964 |
| <i>sel-1*</i> | | <i>Seedless</i> ; produces normal pollen, but ovaries are malformed and nonfunctional | Curtis and Scarchuk, 1948 |
| <i>sel-2*</i> | | <i>Seedless</i> ; placenta deformed; pericarp thick and fleshy; flowering significantly delayed | Proaram et al., 1990 |
| <i>sl-1</i> | <i>sl</i> | <i>Styleless</i> ; lacking normal style or stigma; incomplete female sterility | Bergh and Lippert, 1965 |
| <i>sl-2*</i> | | <i>Styleless</i> ; flowers devoid of style and stigma, ovary intact, no fruit set; female sterility; isolated from 'Kalyanpur Red' | Pathak et al., 1983a |
| <i>Sm</i> | | <i>Smooth leaf surface</i> ; interacts with <i>H</i> | Shuh and Fontenot, 1990 |
| <i>sm-1*</i> | | <i>Small leaf</i> ; leaves small; fewer flowers and fruits; seed set poor; partially sterile; induced from 'PC 1' | Aniel Kumar et al., 2001 |
| <i>sp</i> | | <i>Spinach</i> ; limited stem development, numerous large leaves developing just above ground level to form a dense whorl mass; flower buds; mutant found in PI 159280 | Bergh and Lippert, 1964 |
| (S) <i>rf-1</i> , <i>rf-2</i> | (S) <i>msms</i> | <i>Cytoplasmic male sterility</i> ; cytoplasmic male sterility controlled by two nuclear genes and the mutant cytoplasm S; the occurrence of the dominant alleles at both loci is necessary to restore pollen fertility; the influence of the mutant cytoplasm S is expressed only in the homozygously recessive constitution of the nuclear genes | Novac et al., 1971; Peterson, 1958; Shiffriss, 1997 |
| <i>Su</i> | | <i>Suppressor of indeterminate growth</i> ; suppressing the epistatic action of <i>Ct</i> | McCammon and Honma, 1984 |
| <i>sw₁</i> , <i>sw₂</i> , <i>sw_n</i> | <i>G₁</i> , <i>G₂</i> , etc | <i>Sulfury white immature fruit color</i> ; immature fruit color is conditioned by a series of genes; dominant alleles control various green shades; number of genes and gene action not clearly established | Daskalov and Poulos, 1994; Odland and Porter, 1938 |
| <i>t</i> | | <i>High beta-carotene</i> ; complementary with <i>B</i> | Lippert et al., 1965 |
| <i>tal*</i> | | <i>Tall</i> ; plant height, 65 to 80 cm; fewer branches, flowers and fruits; induced from 'PC 1' | Aniel Kumar et al., 2001 |
| <i>tl</i> | | <i>Taphrina leaf</i> ; leaves are deformed and rugose like peach leaves infected with <i>T. deformans</i> ; stems tend to prostrate | Csillery, 1983 |
| <i>tra</i> | | <i>Transition of fruit color</i> ; fruit color transition phenotype in the jalapeño cultivar 'NuMex Pinata' | Votava et al., 2000 |
| <i>Tsw</i> | | <i>Tomato spotted wilt virus resistance</i> ; resistance to TSWV in <i>C. chinense</i> PI 159236; highly effective against TSWV isolates | Boiteux and de Avila, 1994 |
| <i>tu</i> | | <i>Tube</i> ; cotyledons and leaves are rolled up like a tube, only the abaxial surface is exposed; relationship to <i>ca</i> not determined | Csillery, 1980a; Greenleaf, 1986 |
| <i>un</i> | | <i>Undulate</i> ; small dark-green leaves with undulated surface | Daskalov, 1973b |
| <i>up-1</i> , <i>up-2</i> | <i>p</i> , <i>u</i> | <i>Upright pedicle and fruit orientation</i> ; fruit and pedicle are upright | Lippert et al., 1965; Gopalakrishnan et al., 1990 |
| <i>vg^m</i> | | <i>Variiegated mottled</i> ; true leaves have yellow to light-green mottling; young leaves are intensely mottled to entirely yellow, particularly near the petiole; the allelic series <i>vg⁺</i> (<i>nonvariegated</i>) > <i>vg^m</i> > <i>vg^v</i> in descending order of dominance | Lippert et al., 1964 |
| <i>vg^v</i> | | <i>Variiegated virescent</i> ; small seedlings with yellow cotyledons; cotyledons rapidly develop green coloration, but true leaves uniformly yellow; the pattern of yellow new growth, turning nearly normal green with maturity, continued throughout the growth cycle; allelic recessive to <i>vg^m</i> | Lippert et al., 1964 |

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Table 1. (Continued) The genes of *Capsicum*.

| Preferred symbol | Synonym | Character | References |
|-------------------------|--------------|--|--|
| <i>vir-1</i> | <i>vir</i> | <i>Viridis</i> ; normal green cotyledons, true leaves yellowish green | Daskalov and Poulos, 1994; Lippert et al., 1965 |
| <i>vir-2</i> | <i>vir-a</i> | <i>Viridis</i> ; young leaves are yellowish, but later change to normal green; the mutant depends on 12-h day | Daskalov, 1973a; Daskalov and Poulos, 1994 |
| <i>wl-1</i> | <i>wl</i> | <i>Willow leaf</i> ; leaves are slim and narrow; practically female sterility | Bergh and Lippert, 1964 |
| <i>wl-2</i> | <i>wl-1</i> | <i>Willow leaf</i> ; cotyledons nearly normal; leaves narrow (8–12 mm in width); petals fused; corolla narrow and crimped | Csillery, 1980a |
| <i>xa-1 to xa-10</i> | | <i>Xantha</i> ; seedlings white to yellow; cotyledons expand, but plant dies in 10 to 15 d; <i>xa-1 to xa-8</i> found in <i>C. annum</i> , <i>xa-9</i> in <i>C. baccatum</i> , <i>xa-10</i> in <i>C. pubescens</i> ; relation among <i>xa-1 to xa-10</i> unknown | Csillery, 1980a, 1983; Lippert et al., 1965 |
| <i>xa2a, xa2b</i> | | <i>Xantha</i> ; similar to <i>xa-1</i> , but dominated by two complementary genes; relation to <i>xa-1 to xa-10</i> unknown | Lippert et al., 1965 |
| <i>y</i> | <i>r</i> | <i>Yellow mature fruit color</i> ; fruit color lemon yellow | Hurtado-Hernandes and Smith, 1985; Lippert et al., 1965; Smith, 1950 |
| <i>ya</i> | | <i>Yellow anther</i> ; yellow anthers, but with purple spots on the stem and fruits; found in ‘Zlaten Medal’ | Daskalov, 1974 |
| <i>yc</i> | | <i>Yellow cotyledon</i> ; yellow-white cotyledons, yellow-green leaves, yellow ovary; golden yellow immature fruits, light-red mature fruits | Daskalov and Poulos, 1994 |
| <i>Ys</i> | | <i>Yellow corolla spot</i> ; found in <i>C. baccatum</i> var. <i>pendulum</i> ; acts as a dominant gene in crosses with other species | Lippert et al., 1965 |
| <i>yt-1, yt-2, yt-3</i> | | <i>Yellow top</i> ; only the young, expanding leaves are yellow, turn green gradually; <i>yt-3</i> found in tetraploid of <i>C. annum</i> ; relation to <i>vir-2</i> unknown | Csillery, 1980a, 1983 |

*Proposed new gene symbols.

**Modified gene symbols that were previously published.

PED, peduncle; PVY, potato virus Y.

recessive, all letters of the gene symbol are in small letters. A gene symbol cannot be assigned to a character until supported by statistically valid segregating data (i.e., F₂ and BC populations). After validation by allelic tests, multiple alleles have the same symbol followed by a Roman letter or Arabic number superscript, and mimics may either have distinctive names and symbols, or the same gene symbol followed by a hyphen and a unique Arabic numeral or Roman letter. A modifying gene may have either a symbol for an appropriate name, such as intensifier, followed by a hyphen and the symbol of the allele affected, or a distinctive name. New gene symbols should not be assigned to preassigned symbols, nor should the same trait be described by more than one symbol. Priority in publication should be the primary criterion for establishing the preferred symbol when the same symbol has been inadvertently assigned to different genes or more than one symbol has been designated for the same gene or genes.

Genes Determining Morphological Traits

Plant height

Nine genes have been identified that affect plant height. Daskalov (1974) found two dwarf mutants, *dw-1* and *dw-2*, in ‘Zlaten Medal’. Csillery (1980b, 1983) reported two dwarf mutants from interspecific hybridizations—one from the interspecific hybridization between *C. baccatum* L. and *C. annum* L., and the other between *C. frutescens* L. and *C. annum*—and found that they were con-

ferred by *dw-3* and *dw-4*, respectively. Restaino (1991) identified a new dwarf mutant from the local Italian variety, ‘Friariello’, that was controlled by *dw-5*, and was suitable for protected cultivation with high plant density. Yazawa and coworkers (1991) in Japan observed that some cultivars of *C. annum* showed dwarfness in their interspecific hybrids with *C. chinense* no. 3341. This dwarfness was incited by an interaction between nuclear genes *dw-6* and *dw-7* from *C. annum* and the cytoplasm of *C. chinense*. The gene was linked 6 cM to the 610-bp RAPD marker amplified with SSU-2F (Inai et al., 1993; Yazawa et al., 1991). Aniel Kumar and colleagues (2001) found a recessive gene, *dw-8*, conferring the dwarf phenotype, and a recessive gene, *tal*, that was responsible for a tall mutant induced from *C. annum* cv. PC 1.

The genetic conclusions of the plant height mutants were reached by using the mutants and the normal varieties from which these mutants were obtained. Interestingly, Todorov (1992) found that with the Romanian dwarf *C. annum* variety *Buketon*, and the indeterminate, tall Bulgarian variety *Gorgled 6*, that plant height was controlled by two to three genes, with the environment having a stronger influence than genetic factors, suggesting additional genes may be involved in the genetic control of plant height.

Flaccid phenotypes

Four kinds of flaccid phenotypes have been described in *Capsicum*: diminished morphology (*dm*) (Csillery, 1983), scabrous diminutive (*sd*) (Bergh and Lippert, 1964),

spinach (*sp*) (Bergh and Lippert, 1964), and flaccidity (*flc*) (Bosland, 2002).

Branching habits

The *bl* gene responsible for branchless plants of PI 169113 was identified by Bergh and Lippert (1964). The ‘‘umbrella’’ branching in MSU 79-221 (*C. annum*) was controlled by three major recessive genes—*ct*, *dt*, and *fa*—and modifiers (McCammon and Honma, 1984). Both *dt* and *ct* control plant habit; *dt* conditions determinate growth, whereas *ct* determines the number of axillary shoots. The dominant alleles, *Dt* and *Ct*, control indeterminate growth and are epistatic to one another. The *fa* gene conditions the fasciculate or clustered fruit-bearing habit. The dominant suppressor gene, *Su*, suppresses the epistatic action of *Ct*.

Fasciculation

Fasciculation in pepper is expressed as a shortening of internodes, resulting in compact, bushy plants, and expressed as flowers and fruits borne on bunched, compounded nodes conferred by the recessive *fa* gene (Lippert et al., 1965). Van der Beek and Ltifi (1990) observed the variation in fasciculation, inferring that minor genes could be involved in the expression of fasciculation, operating in the presence of the *fa* gene. The *fa* gene showed tight linkage with a distance of 3.5 cM to the *dt* gene (Yang and Park, 1999).

Leaf Shape

Leaves with an undulate surface were conferred by the recessive gene *un* (Daskalov,

1973b). Zubrzycki and Pahlen (1974) identified recessive *anv* and *brl* genes responsible for two leaf mutants (cited by Daskalov and Poulos, 1994). Later, Csillery (1980b, 1983) reported morphological mutants of cotyledons and leaves [i.e., filiform (*fi*), willow leaf (*wl*), canoe (*ca*), tube (*tu*), fan vein (*fv*), round leaf (*rl-1*, *rl-2*), rugose (*ru-1*, *ru-2*), datura leaf (*dtr*), small leaf (*sl-1*), callus (*call*), frilly (*fr*), procumbent hypocotyl (*ph*) and polycotyledon (*pc-1*, *pc-2*, *pc-3*), and *TI*] responsible for the taphrina leaf mutant. Aniel Kumar and colleagues (2001) described eight kinds of leaf mutants [i.e., narrow leaf (*nl*), broad leaf (*bl*), small leaf (*sl2*), curved leaf (*cl*), folded leaf (*fl*), round leaf tip (*rl-3*), leaf dimorphism (*ld*), and elongated petiole (*ep*)] and determined that the mutant characters were controlled by single recessive genes. The allelism between *rl-1*, *rl-2*, and *rl-3* was not determined. The allelism between *sl-1* and *sl-2* was also not identified. Leaf pubescence (*HHSmSm*) was dominant over glabrous leaf (*hhsmsm*), and was controlled by two dominant genes: *H* and *Sm* (Shuh and Fontenot, 1990).

Color of plant parts

So far, color mutants of cotyledons, leaves, and stems have been described by Kormos and Kormos (1955) and Pahlen (1966) (cited by Daskalov and Poulos, 1994). Zubrzycki and Pahlen (1974) reported a mutant, *aur*, with golden cotyledons and leaves (cited by Daskalov and Poulos, 1994). Daskalov (1974) described a mutant, *ya*, with yellow anthers, but with purple spots on the stem and fruits. Later, Csillery (1980b, 1983) described color mutants of cotyledons, leaves, and stems, and showed that nine recessive genes (*xa-2* to *xa-10*) controlled the *xantha* mutants; 18 genes (*lut-1* to *lut-18*) conferred the *lutescens* (yellow-green) mutants; three genes (*yt-1*, *yt-2*, and *yt-3*) determined *yellow top* mutants; 52 genes (*mos-1* to *mos-52*) were responsible for the *mosaic* mutants; one gene (*lsm*), a *light-sensitive mosaic* mutant; and eight recessive genes (*al-1* to *al-8*), the *anthocyaninless* mutants. The *lut* genes are not allelic to each other, nor are the *mosaic* genes allelic among *mos-1* to *mos-9*. Recently, Ma coworkers (2001) in China reported a *lutescens* mutant conferred by gene *lut-19*. The allelism between *lut-19* and *lut-1* to *lut-18* was not investigated. Daskalov (1987) identified one *Flv* gene determining yellow-green leaves (cited by Daskalov and Poulos, 1994). The relationship between *lut* and *Flv* remains unknown.

An incompletely dominant gene, *A*, controls the anthocyanin color of stem, foliage, flowers, and immature fruits. The *A* gene is effective only in the presence of *al⁺*. In *AA* genotypes, the action of the *A* gene is intensified by a gene modifier, *MoA* (being ineffective alone). Additional genes for differential anthocyanin accumulation in flower (*R-1* and *R-2*), style (*As*), style and filament (*Asf*), and immature fruits (*F*) have been also reported. Odland (1960) found that the flower

colors were conditioned by three genes (*S*, *W*, and *A*). The *MoA* locus was localized to chromosome 11 by sharing a linkage with *L* that confers resistance to tobacco mosaic virus (TMV) (Ben Chaim et al., 2003). The *A* gene was assigned to chromosome 10 (Ben Chaim et al., 2003) and the gene *Fc* controlling the purple anther-filament color was assigned to chromosome 10 (Prince et al., 1993). The map position of *A* was identical to *Fc*, indicating that the two loci are allelic (Ben Chaim et al., 2003). A linkage of 6.5 cM between *A* and *O*, the gene that controls round fruit shape in *C. annuum*, was reported (Peterson, 1959) and recently verified (Ben Chaim et al., 2003). Ben Chaim and colleagues (2003) also reported that the *Fc* locus was linked to a major quantitative trait locus, *fs10.1*, for fruit shape index (ratio of fruit length to fruit width).

Variegated seedlings

Six types of variegated seedlings have been reported. Hagiwara and Oomura (1947) reported the *pi* gene was responsible for green and white leaf variegation (cited by Lippert et al., 1965). Cook (1962) showed that the *bv* gene was responsible for the bushy variegated mutant. Lippert and colleagues (1964) and Daskalov (1974, 1977) found four mutants with marbled leaves that were controlled by four genes: *m-1*, *m-2*, *m-3*, and *m-4* (cited by Daskalov and Poulos, 1994). The variegated mottled mutant and variegated virescent mutant were controlled by the *vg^m* and *vg^v* genes respectively (Lippert et al., 1964). The greenish yellow variegation mutant was conditioned by the *chl* gene (cited by Lippert et al., 1965), and Zubrzycki and Pahlen (1974) determined that the deformed and undulated green virescent variegated leaves were conferred by the gene *dvg* (cited by Daskalov and Poulos, 1994).

Flowers

Multiple flowers are controlled by three major dominant genes: *Mf-1*, *Mf-2*, and *Mf-3* (Shuh and Fontenot, 1990). The expression of multiple flowers occurs when *Mf-1* is present and either *Mf-2* or *Mf-3* is present. Recessive homozygosity at the *Mf-1* locus reduces the multiple-flower nodes despite dominant genes present at both *Mf-2* and *Mf-3*. Two genes affecting the time of flowering have been identified (Aniel Kumar et al., 2001): the gene *ef* for early flowering and the gene *lf* for late flowering. Pathak and associates (1985) found a nonflowering mutant that was controlled by a monogenic recessive gene *nf*. Two closed-flower mutants are conditioned by the *cf-1* and *cf-2* genes (Pathak et al., 1983; Subramanya and Ozaki, 1984).

Fruit shapes

Six genes have been identified to affect the characteristics of fruit shape. Deshpande (1933) described the dominant gene *P* for pointed fruit apex, the recessive gene *fb* for fruit base nonbulging, and the gene *ce* for calyx enclosed around fruit base (Daskalov and Poulos, 1994). The round fruit shape is

controlled by the major dominant gene *O* and other modifiers (Peterson, 1959), and recent molecular mapping studies confirm the existence of the major genes that control this trait (Ben Chaim et al., 2001, 2003; Rao and Paran, 2003). Upright fruit orientation is controlled by two recessive genes—*up-1* and *up-2*—that show specific dominant and recessive epistasis respectively (Gopalakrishnan et al., 1990; Lippert et al., 1965). Csillery (1983) identified the recessive gene, *cy*, responsible for the exocarp covered with transversally oriented, small suberized cracks at full fruit maturity. Ishikawa and coworkers (1998) reported the dominant *Ap* and *Ped* genes to condition the pointed shape of the fruit apex, and the acute shape of the fruit pedicle attachment respectively. The allelism between *Ap* and *P* is unknown. Parthenocarp is conferred by the *pf* gene from the variety 'Kalyanpur Chaman' (Pathak et al., 1983b).

Immature fruit color

Immature fruit color is conditioned by a series of alleles (Odland and Porter, 1938). The sulfur white, *sw₁*, locus controls the various white and green shades of the fruit. The lettuce or yellowish green color, *sw₂*, is dominant to the sulfury white, *sw₁*, and recessive to the cedar green, *sw₃*, whereas cedar green, *sw₃*, is dominant to sulfury white.

Mature fruit color

Early studies found that the mature yellow color of *Capsicum* fruits is recessive to red and controlled by a single gene *y* (yellow) (Boswell, 1937). Smith (1950) found that the brown color of ripe pepper fruit was the result of the combination of the normal red pigment and the retention of chlorophyll. The brown color is governed by two genes: *cl* for retention of chlorophyll and *y⁺* for red color. Hybridizations between red and white fruit varieties have shown that the mature fruit color is controlled by three genes: *c-1*, *c-2* and *y* (Hurtado-Hernandez and Smith, 1985). The *c-1* gene affects the amount, rather than the type, of carotenoids present, and the gene *c-2* has a significant effect on the total level of carotenoid accumulation in fruit. The *c-1* and *c-2* genes reduced the pigmentation of *y* and *y⁺* by the inhibition of beta-carotene. Popovskiy and Paran (2000) demonstrate the effect of the genetic background on fruit color segregation and provide additional evidence for two possible genotypes of the orange fruit color. In addition, the *im* gene was found to condition purple color at intermediate maturity in originally nonpurple immature fruit (Lippert et al., 1965).

The gene *Ccs*, coding for capsanthin-capsorubin synthase that synthesizes the red carotenoid pigments, corresponds to the morphological locus *y* (Lefebvre et al., 1998; Popovskiy and Paran, 2000). *Ccs*, a single-copy gene in pepper, was assigned to pepper chromosome 6, 1 cM away from CT109. A QTL affecting the intensity of mature red color was also detected in this region (Thorup

et al., 2000). A 500-bp fragment amplified by primer OPN-7 is linked with *Ccs/Y* at a distance of 7 cM (Thorup et al., 2000). In addition, one QTL affecting red chroma and another affecting red lightness were identified on chromosome 3 in an intraspecific *C. annuum* population (Thorup et al., 2000).

The locus *C2* cosegregated with phytoene synthase, *Psy* (Thorup et al., 2000), which is the locus responsible for the development of fruit color. *Psy/C2* may be a major gene acting as a rate-limiting factor in carotenoid production. *Psy* is the candidate for *C2* (Huh et al., 2001). A 700-bp fragment amplified by the primer OPO-12 and a 900-bp fragment amplified by the primer UBC-183 were mapped to chromosome 4, and were found to be 1 cM apart from each other and 36 cM away from *Psy/C2* (Thorup et al., 2000). A QTL affecting the red hue of fruit was also mapped to this region (Ben Chaim et al., 2001), implicating *Psy* as a source of both qualitative and quantitative variability in carotenoid biosynthesis.

Transition of fruit colors

Votava and associates (2000) noticed that the jalapeño cultivar, NuMex Piñata, had a unique transition of colors as the fruit matures, from light green in immature fruits, maturing to yellow, then orange, and finally to red. It was determined that the inheritance of luteous foliage color and fruit color transition phenotype of 'NuMex Piñata' is the result of a single homozygous recessive gene: *tra* (transition).

Genes Determining Physiological Traits

Pungency

Pungency, or the sensation of heat when eating pepper fruit, comes from the presence of the capsaicinoid alkaloids in the fruit. Early genetic studies reported that a single dominant gene *C* controlled the expression of heat (Deshpande 1935, Greenleaf, 1952), which can be modified by other genetic and environmental factors. This gene was later redesignated *Pun* (Daskalov and Poulos, 1994), and probably functions as an acyl-transferase to complete the capsaicinoid synthesis (Stewart et al., 2005). Loaiza-Figueroa and Tanksley (1988) reported a second nonpungency locus, *pun2*, in a wild, nonpungent pepper accession BG 3547; however, further studies cannot support the existence of this locus—most likely the nonpungent accession was expressing the *lov* gene (Votava and Bosland, 2002). Votava and Bosland (2002) described two novel nonpungent *C. chinense* accessions 'NMCA 30036' and 'PI 543190', in which loss of the vesicles (*lov*) on the placental walls is responsible for nonpungency. The *lov* gene is epistatic to *pun1* and results in pungent progenies. Blum and associates (2002) mapped the *Pun* locus to chromosome 2 in a hybridization between a pungent *C. frutescens* accession and a no-heat *C. annuum* bell pepper, and developed a polymerase chain reaction-based cleaved amplified polymorphic sequence (CAPS)

marker linked to *Pun* using the sequence of the *Capsicum* fibrillin gene located 0.4 cM from *Pun*. Recently, the *Pun-1* gene was cloned and characterized based on the candidate gene approach (Stewart et al., 2005). The full-length genomic sequence of *Pun-1* is 1897 bp, containing two exons of 738 bp and 585 bp respectively, and one intron of 348 bp. The *pun-1* allele results from a large deletion at this locus.

Beta-carotene contents

Three genes—*B*, *t*, and *bc*—have been identified that confer high beta-carotene contents of ripe fruits. Chalukova and colleagues (1993) and Daskalov and coworkers (1995) described the mutant variety Orangeva Kapia obtained from 'Pasardzhishka Kapia'. This mutant variety produces immature green fruits and mature orange fruits containing 2 to 2.5-fold higher contents of beta-carotene than their red counterparts. High beta-carotene content in this mutant variety is conferred by a recessive gene, *bc*, which prevents hydroxylation of beta-carotene to beta-cryptoxanthin.

Soft flesh and deciduous fruits

Smith (1951) found the deciduous ripe fruit character to be controlled by a single dominant gene, *S*. Later, Jeswani and associates (1956) obtained similar findings for this trait (cited by Greenleaf, 1986). Kormos and Kormos (1957) reported that the soft-fruited trait was controlled by the dominant gene *Ps* (cited by Greenleaf, 1986). The genetic reports of these two traits were independent, so the two traits were considered as distinct from each other (Daskalov and Poulos, 1994; Greenleaf, 1986). In the gene lists of Daskalov and Poulos (1994), and Greenleaf (1986), the gene symbol *S* given by Smith (1951) to the deciduous fruit trait was assigned to the soft flesh trait, and the gene symbol *Ps* was reassigned to the pod separation trait and is considered distinct from *S*. However, the fruits of the wild *C. frutescens* accession BG2816 were both deciduous and had soft flesh, and these two traits cosegregated in the F₂ progenies of 'BG2816' and the cultivar Maor (*C. annuum*). Therefore, it is likely that both characteristics in *C. frutescens* BG2816 are controlled by the same gene with pleiotropic effects (Rao and Paran, 2003). *S* is mapped to chromosome 10, and the polygalacturonase (PG) gene PG is a candidate gene for *S* (Rao and Paran, 2003).

Genes Determining Sterility Traits

Genic male sterility

Nearly 20 genes for genic male sterility have been reported. Shifriss and Frankel (1969) named the first male sterile gene *ms-1* in a spontaneous stable male sterile mutant from the *C. annuum* cv. All Big. A second male sterile gene, *ms-2*, was identified in a spontaneous stable male sterile mutant from 'California Wonder' (Shifriss and Rylski, 1972). Daskalov (1973b) identified five genes (*ms-3*, *ms-4*, *ms-6*, *ms-7*, and *ms-8*)

conferring male sterility in the irradiation-induced mutants. These seven nonallelic genes are mainly expressed as pollen sterility. Pochard found three genes (*ms-9*, *ms-10*, and *ms-11*) in three male sterile mutants obtained after treatment of monoploid materials with ethyl methansulphonate (EMS) (cited in Daskalov and Poulos, 1994). Shifriss (1973) reported a recessive gene, *ms-12*, governing the male sterility in a spontaneous mutant from *C. annuum* cv. Gambo. Meshram and Narkhede (1982) identified the *ms-13* gene that conditions male sterility in a mutant from *C. annuum* cv. Ca452-1. Pathak et al., (1983) isolated a male sterile mutant from cv. 'Kalyanpur Selection', and proved that male sterility was governed by the single recessive gene *ms-14*. In India, Deshpande and coworkers (1983) presented more than 20 male sterile mutants in India, whereas in China two genic male sterile genes (*msc-1* and *msc-2*) have been used to produce F₁ sweet pepper hybrids (Yang, 1981; Yang et al., 1994). Daskalov (1987) also reported a dominant genetic male sterility gene: *Dms* (cited in Daskalov and Poulos, 1994).

According to morphological changes exhibited in androecium, the male sterile mutants can be grouped into six categories (Deshpande et al., 1983): 1) androecium transformed into petaloid structure (*ms-13*); 2) shriveled anthers devoid of pollen grains, including *ms-1*, *ms-3*, *ms-6*, and *ms-8* (Daskalov, 1974); 3) anthers that are not reduced severely and contain a small amount of fertile and sterile pollen grains in some flowers (*ms-4* and *ms-7*) (Daskalov, 1974); 4) shrunken anthers that release numerous aborted pollen grains (*ms-2*) (Shifriss and Rylski, 1972); 5) anthers that appear to be normal, but pollen grains are sterile; and 6) yellow anther lobes that are flattened laterally to give an appearance of a fan blade and are devoid of pollen grains (Deshpande et al., 1983).

Cytoplasmic male sterility (CMS)

The inheritance of CMS in *C. annuum* was first studied by Peterson (1958), who showed that sterility was controlled by a major gene, *ms*, interacting with a specific *S* plasma type to generate (S) *msms* CMS plants. He also suggested that the second allelic pair was probably in another linkage group. Novac and colleagues (1971) worked with Peterson's male sterile material and found that the male sterility was conditioned on two pairs of nonallelic nuclear genes. Both the nuclear genes *ms-1* and *ms-2* have complementary genic interaction. The presence of at least one dominant allele at both loci is necessary to restore the pollen fertility in the plants with the S cytoplasm. Daskalov (1974) identified a CMS mutant from the variety 'Kalinkov 800/7' that is not identical with Peterson's (1958) CMS line, and found that this male sterility was probably conferred by more nuclear genes, including the gene originally designated *ms-5*, and the S factor in the cytoplasm. In China and Korea, some CMS lines have been used to produce commercial F₁ hybrids (Wang et al., 2003), but the

relationship between these CMS lines and Peterson's (1958) CMS line has not been evaluated.

Shifriss (1997) suggested the nuclear gene conferring CMS be redesignated *rf* and the restorer of fertility allele as *Rf* to differentiate between the *ms* genes in genic male sterility lines and the male sterility genes interacting with N and S cytoplasm that were originally designated as *ms* genes (Daskalov, 1974; Peterson, 1958). The *ms* genes are nonallelic to the *rf* ones. Two RAPD markers tightly linked to a major fertility restorer gene were detected (Zhang et al., 2000): OP13₁₄₀₀ with a genetic distance of 0.37 cM, and OW19₈₀₀ on the opposite side with a distance of 8.12 cM. Recently, Kim and Kim (2005) developed two CMS-specific sequence-characterized amplified region (SCAR) markers for early identification of CMS genotype based on the restriction-length polymorphisms between male fertile and CMS cytoplasm at the *coxII* and *atp6* loci of the mitochondrial DNA of *C. annuum*.

Functional male sterility

Yuan and Li (2000) reported a spontaneous stable functional male sterile mutant from the cultivar Fudijian (*C. annuum*) and determined that this functional male sterility was controlled by a recessive gene: *fms*.

Female sterility

Six types of female sterile mutants have been reported: 1) the female sterility mutant conferred by the recessive *fs* gene (Bergh and Lippert, 1964); 2) two female and male sterility mutants conferred by recessive *fems* and *fl* genes respectively (Aniel Kumar et al., 2001; Martin and Crawford, 1951); 3) a female sterile mutant with 27% to 55% pollen fertility conditioned by the recessive *fcf* gene (Pahlen, 1967; cited by Daskalov and Poulos, 1994); 4) two styleless mutants controlled by recessive genes *sl-1* and *sl-2* (Bergh and Lippert, 1965; Pathak et al., 1983b); 5) two seedless mutants conditioned by recessive genes *sel-1* and *sel-2* (Prolaram et al., 1990); and 6) 'complex' mutants. The genes *sp*, *bl*, *fi-1*, *prp*, and *pec* have marked effects on both vegetative organs and female fertility (Bergh and Lippert, 1964; Csillery, 1983). Allelisms between *sl-1* and *sl-2* are unknown. A conditional female sterility gene, *cfs*, was identified by Daskalov and Mihailov (1988).

Genes Determining Resistance to Diseases, Nematodes, and Herbicides

Resistance to tobacco mosaic virus (TMV)

Holmes (1937) found that resistance to TMV was controlled by a series of multiple alleles: *L* (localization of TMV), *L'* (imperfect localization of TMV), and *L⁺* (mottling), with $L > L' > L^+$. Boukema et al. (1980a) determined that the resistance of 10 *C. chinense* accessions (PI 152225, PI 159236, PI 315008, PI 315023, PI 315024, PI 159223, PI 213917, PI 257117, PI 257284, and PI 224424) was inherited monogenically

and was partially dominant, and that the resistant genes in these accessions appeared to be allelic and were allelic with the alleles *L'* and *L*. She designated the symbol *L³* for the new allele, and redesignated Holmes's allelic series $L > L' > L^+$ as $L^3 > L^2 > L^1 > L^+$. Later, Boukema (1984) reported that the *L⁴* allele originated from *C. chacoense* PI 260429 and SA185. Recently, Salamon and associates (2001) revealed the resistant allele *L^{2g}* in 'Greygo', which behaved like the allele *L²* with characteristics of *C. frutescens* cv. Tabasco. The identity of the allele *L^{2g}* relative to *L²* is not known.

However, the conferred resistance of *L* locus lessens when the air temperature surpasses 30 °C (Palloix, 1992). Daubeze and colleagues (1990) revealed the presence of secondary genes that stabilize the expression of *L'* under high temperature (32 °C). Such modifier genes were found in Chinese accessions ('Zao Feng' and 'Ben Xi') with *L'*, but also in tropical varieties susceptible to TMV ('Perennial' and 'PI 322719'). The Mexican variety Criollo de Morelos 334 (CM 334) also bears a particular allele at the *L* locus that confers resistance to TMV (0) at high temperatures, and secondary genes that control the rapid production of smaller local lesions in the inoculated organs (Palloix, 1992).

Zatyko and Moor (1998) confirmed a close linkage between the *al* and *L³* genes in the pepper line 'TL 791'. SCAR marker WA31–1500S was linked to the *L⁴* gene within a distance of 1.5 cM (Matsunaga et al., 2003).

Resistance to cucumber mosaic virus (CMV)

Resistance to CMV has showed the characteristics of genetic diversity (for a review see Wang et al., 1996). Some accessions have the recessive resistance gene (Cook, 1982; Herison et al., 2004; Singh and Thakur, 1977), some have oligogenes (Herison et al., 2004; Saito et al., 2004), and others carry polygenic resistance (Greenleaf, 1986; Pochard et al., 1983). Singh and Thakur (1977) confirmed a recessive gene with resistance to CMV in the line 'Perennial', and designated the gene symbol *cm*. Resistance in 'Perennial' was under polygenic control (Gil–Ortega and Arteaga, 1988), and four QTLs were significantly associated with resistance to CMV in this line, among which the QTL-controlling percentage (16%–33%) of the observed phenotypic variation was linked to the *L* locus that confers resistance to TMV (Ben Chaim et al., 2001). Pochard (1982) designated three resistant components of partial resistance to CMV, (i.e., tendency to escape infection, restriction of viral multiplication, and slowing of viral migration in the resistant reaction to CMV in different cultivars). Later, researchers added four more resistance components—namely, the ability to recover from systemic infection (Pochard and Daubeze, 1991), restriction of virus installation in host cells (Caranta et al., 1997b), restriction of virus multiplication in the whole plant (Nono–Wondim et al., 1993), and restriction of long-distance virus movement (Caranta

et al., 2002). Three QTLs significantly affecting restriction of CMV installation in host cells were detected, and each QTL from 'Perennial' was associated with an increased resistance (Caranta et al., 1997a). Partial restriction of CMV long-distance movement in 'Vania' is inherited as a dominant trait, and seven QTLs, including one major-effect and several minor-effect QTLs, were associated with this resistance (Caranta et al., 2002). The genes for resistance to CMV are not linked with those genes conferring fruit weight and size (Shifriss and Cohen, 1987).

Resistance to potyvirus

Pepper may be infected by six major potyviruses: potato virus Y (PVY), tobacco etch virus (TEV), pepper mottle virus (PepMoV), pepper vein mottle virus (PVMV), chile vein mottle virus (CVMV), and potyvirus E (PVE) (Green and Kim, 1991). PVY isolates have been traditionally classified into three pathotypes (-0, -1, and -1.2) (Cook, 1963; Gebre Selassie et al., 1983). Recently, a new pathotype has been described and provisionally named as PVY-PRW (Luis Arteaga et al., 1997). The gene designations of resistance in *Capsicum* to three potyviruses (PVY, TEV, and PepMoV) have not followed regular convention, so confusion has occurred. Kyle and Palloix (1997) proposed a nomenclature that clarifies the genetic and biological relationships among potyvirus resistance genes in *Capsicum*. They proposed the symbol *pvr* for the potyvirus resistance locus. Until now, eight major resistance genes (*pvr* genes) and several QTLs showing phenotypically distinct types of responses to potyvirus. The *pvr-1* gene is the locus with alleles for recessive resistance to TEV and PepMoV in 'PI 152225' (Greenleaf, 1956) (originally *et^f* and *et^g*) and 'PI 169236' (Greenleaf, 1986) (originally *et^{cl}* and *et^{c2}*). These PI accessions are allelic for PepMoV resistance and for TEV resistance (Murphy et al., 1998). An allelic series at the *pvr-2* locus controls the recessive resistance to PVY (Kyle and Palloix, 1997). For resistance to PVY (0), the resistance allele *pvr-2¹* replaces *y^a* and *vy¹* from 'Yolo RP10' and 'Yolo Y' respectively, (Cook, 1960, 1961a; Gebre Selassie et al., 1983). For resistance to PVY (1) and TEV derived from 'SC46252' and introduced to 'Florida VR2', *pvr-2²* replaces *et^f*, *ey^a*, and *vy²* (Cook and Anderson, 1959; Gebre Selassie et al., 1983).

In addition, a polygenic resistance to PVY from 'Perennial' was dissected into a combination of QTLs, including a major-effect gene that was mapped to the *pvr-2* locus (Caranta et al., 1997a). Ayme and colleagues (2004) proposed the name *pvr-2³* for this major-effect gene at the *pvr-2* locus. Both *pvr-2¹* and *pvr-2²* alleles are shown to correspond to the eukaryotic translation initiation factor 4E (eIF4E) (Ruffel et al., 2002). Recently, genetic complementation analysis demonstrated allelism of *pvr-1*, *pvr-2¹*, *pvr-2²*, and *pvr-2³* (Kang et al., 2005; Ruffel et al., 2004). Hence, *pvr-2¹* and *pvr-2²* have been redesigned *pvr-1¹* and *pvr-1²* respectively

(Kang et al., 2005). The third locus, *pvr-3*, was proposed for an allele for monogenic recessive potyvirus resistance to PepMoV in *C. annuum* 'Avelar' (Zitter and Cook, 1973).

Several resistance genes against potyviruses have been described in CM 334; the *Pvr-4* locus was named for a gene that gives resistance to all known pathotypes of PVY and to PeMV in *C. annuum* CM 334 (Boiteux et al., 1996; Dogimont et al., 1996; Palloix, 1992; Pasko et al., 1992). Pasko and coworkers (1992) described several levels of resistance in CM 334 against different PVY pathotypes. CM 334-derived materials show different responses, indicating that, besides the *Pvr-4* allele, other genes conferring resistance at different levels are also present (Arnedo-Andres et al., 1998). The gene conferring only the resistance to PVY (0) in CM 334 was designated *pvr-5* (Dogimont et al., 1996).

The gene *Pn-1* confers the necrotic response to PVY (0, 1, 2) isolates in 'Vat'. The genetic control for the appearance of systemic necrotic symptoms in 'CM 334(11)' after inoculation of PVY (1–2) isolate P-22–88 is the result of a codominant gene expressed only when *Pvr-4* is not present and with a maximum expression that is observed in the homozygous condition (Arnedo-Andres et al., 2004).

A recessive gene for resistance to PVMV from 'Perennial' is designated *pvr-6* (Caranta et al., 1996). The gene *pvr-6* is complementary to the *pvr-1* locus for resistance to PVMV. The dominant gene, *Pvr-7*, from *C. chinense* Jacq. 'PI 159236', confers resistance to PepMoV Florida (V1182) strain (Grube et al., 2000). This gene is tightly linked to the dominant potyvirus resistance gene, *Pvr-4*, with observed recombination frequencies of 0.012 to 0.016. Resistance to PVY in the A97011 line, derived by intraselection from CM 334, is controlled by a recessive and independent gene: *pvr-8* (Arnedo-Andres et al., 2004).

Caranta and Palloix (1996) found the polygenic resistance of 'Perennial' (*C. annuum*) to PVY (0), PVE, and CVMV, and a partial resistance to PVY (1, 2) was due both to genetic factors that apparently interact with several viruses, and strain-specific genetic factors. Later Caranta and colleagues (1997a) proved that the polygenic resistance in 'Perennial' to PVY and PVE consists of a combination of isolate-specific and broad-spectrum QTLs. In their studies, 11 chromosomal regions were determined to be associated with quantitative resistance in 'Perennial' to PVY and PVE. QTLs for potyvirus resistance, in some cases, coincide with positions for *pvr* loci. QTLs for PVY and PVE resistance are detected in the vicinity of the *pvr-2* and *pvr-6* loci. These results suggest a possible allelism between major genes and QTLs.

The modes of action of these major resistant genes have been determined. *pvr-1* and *pvr-2²* both control a complete inhibition of virus accumulation in infected cells (Deom et al., 1997); *pvr-2¹* impairs cell-to-cell

movement (Ponz et al., 1994; Arroyo et al., 1996) whereas *pvr-3* slows long-distance movement (Murphy and Kyle, 1995). Interaction between the potyvirus genome-linked protein (VPg) and eIF4E are important for PVY virus infectivity, suggesting that the *pvr-2* recessive resistance could be the result of incompatibility between the VPg and eIF4E in the resistant genotype (Ruffel et al., 2002). Moury and associates (2004) pointed out that 15 nucleotide changes corresponding to five putative amino acid differences in the same region of the VPg of PVY affected virulence toward the *pvr-2¹* and *pvr-2²* resistances. Both the *Pvr-4* and *pvr-5* control a complete inhibition of potyvirus replication or accumulation. This mechanism is pathotype specific when controlled by *pvr-5*, whereas it is effective against three different pathotypes and against PepMoV as well when controlled by *Pvr4* (Caranta et al., 1998).

The *pvr-1* locus, linked with tomato marker TG56, has been genetically mapped to a small linkage group with synteny to the short arm of tomato chromosome 3 (Murphy et al., 1998). Yeam and colleagues (2005) developed the allele-specific CAPS markers based on point mutations in resistance alleles at the *pvr-1* locus encoding eIF4E in *Capsicum*. Arnedo-Andres and associates (2002) identified one RAPD marker (UBC19₁₄₃₂) linked in repulsion phase to *Pvr-4* and converted it into a dominant SCAR marker (SCUBC19₁₄₂₃). Caranta and associates (1999) mapped eight amplified fragment length polymorphism (AFLP) markers in an interval from 2.1 ± 0.8 to 13.8 ± 2.9 cM around the *Pvr-4* locus, and converted the closest codominant AFLP marker into a codominant CAPS marker.

Resistance to tomato spotted wilt tospovirus (TSWV)

The hypersensitive resistance to TSWV was determined by a single gene, *Tsw*, in three *C. chinense* Jacq. accessions (PI 152225, PI 159236, and 7204). All three *C. chinense* lines have the same allele located at the *Tsw* locus (Moury et al., 1997), and showed the identical susceptibility response to tomato chlorotic spot virus and groundnut ringspot virus isolates after mechanical inoculation (Boiteux, 1995). The TSWV resistance controlled by the *Tsw* gene is completely stable at a lower temperature (22 °C) and is less stable at 32 °C continuous temperature (Moury et al., 1997). Luis Arteaga and Gil Ortega (1998) proved that the susceptibility of *C. chinense* could occur at low (22.5 °C) and high (30 °C) temperatures on both young and adult plants.

Genetic background was significantly less involved in the thermosensitivity of this resistant response. Heterozygosity at the *Tsw* locus enhanced the chance of inoculated seedlings to develop systemic necrotic symptoms (Moury et al., 1998). One codominant CAPS marker is tightly linked to *Tsw* (0.9 ± 0.6 cM) and is helpful for marker-assisted selection in a wide range of genetic

intercrosses (Moury et al., 2000). The *Tsw* gene is mapped to the distal portion of chromosome 10 (Jahn et al., 2000).

Resistance to bacterial leaf spot

Currently, nine pepper races (P0–P8) have been identified among *Xanthomonas campestris* *pv. vesicatoria* (*Xcv*) strains worldwide (Sahin and Miller, 1998). Four nonallelic dominant genes (*Bs-1*, *Bs-2*, *Bs-3*, and *Bs-4*) were reported to control hypersensitive reaction to *Xcv* according to the gene-for-gene hypothesis, and were found in PI 163192, PI 260435, PI 271322, and PI 235047 (Cook and Guevara, 1982, 1984; Cook and Stall, 1963; Hibberd et al., 1987; Kim and Hartmann, 1985; Sahin and Miller, 1997). The *Bs-2* gene from *C. chacoense* specifically recognizes and confers resistance to strains of *Xcv* that contain a virulence gene *avrBs2* (Minsavage et al., 1990). The *Bs-2* gene is a member of the nucleotide binding site leucine-rich repeat class of plant disease resistance genes (Tai et al., 1999a), and is predicted to reside in the plant cytoplasm.

Recently Jones and colleagues (2002) found a nonhypersensitive resistance to race 6 in the pepper genotype ECW-12346 that was developed with bacterial spot resistance derived from 'Pep13', PI 271322, and ECW123 (Early CalWonder containing *Bs-1*, *Bs-2*, and *Bs-3* genes), and identified that two recessive genes—*bs-5* and *bs-6* derived from PI 271322 and 'Pep13' respectively—determined this resistance. ECW12346 inhibits the population buildup of this *Xcv* strain without inducing the typical hypersensitive reaction. Hungarian scientists described another type of nonhypersensitive resistance against *Xcv* in *C. annuum* PI 163192, which used a general defense system of the host plant (Csillery et al., 2004; Szarka and Csillery, 1995). This resistance is regulated by a recessive gene: *gds* (*general defense system*). This gene localizes the pathogen with an entirely different strategy than the hypersensitive reaction. The resistance conditioned by *gds* promotes cell growth and cell wall thickening.

The instability of avirulence genes in *Xcv* has stimulated the interest for quantitative resistance. Accession CNPH703 was identified with a race nonspecific and nonhypersensitive resistance to *Xcv*, and low narrow-sense heritability for three components of resistance: lesion number, lesion diameter, and total lesion area (Poulos et al., 1991). Poulos and colleagues (1992) determined that dominance, additive, and interacting gene effects of at least two genes were involved in the inheritance of quantitative resistance to *Xcv* in 'CNPH703'.

Tai and associates (1999b) identified one AFLP marker, A2, cosegregated with the *Bs-2* locus, and two other markers, F1 and B3, flanking the *Bs-2* locus and being within 0.6 cM. Also, two RAPD markers, OPD05 and OPF10, were identified to link with the *Bs-2* gene (Kim et al., 2001). OPD05 was located 5.3 cM from *Bs-2* gene whereas OPF10 was located 4.9 cM from the *Bs-2* on the opposite

side to OPD05. SCAR marker SCF10, originating from marker OPF10, was successfully obtained. Based on the most tightly linked AFLP markers, a 2.1-cM genomic target interval encompassing the *Bs-3* locus was defined by Pierre and colleagues (2000). *Bs-3* is separated from the marker P23-70 and P22-3 by only 1 cM and 1.1 cM respectively.

Resistance to *Phytophthora*

Phytophthora capsici Leon. causes several disease syndromes (i.e., phytophthora root rot, stem rot, foliar rot, and fruit rot) (Sy et al., 2005; Walker and Bosland, 1999). Resistance to *Phytophthora* root rot exhibited the characteristics of genetic diversity (for a review see Wang et al., 1995). A single dominance gene was present in some accessions (Choi et al., 1990; Kim and Hur, 1992), oligogenes in some accessions (Cristinzio et al., 1992; Gil Ortega et al., 1991, 1992; Reifschneider et al., 1992), and quantitative genes in others (Thabuis et al., 2003). One dominant gene was necessary for resistance in CM 334 when the susceptible parent was 'Early Jalapeno' (Sy et al., 2005; Walker and Bosland, 1999).

A single dominant gene, *Psr*, conferred stem resistance in 'Criollo de Morelos-334' when choosing 'Early Jalapeno' as a susceptible parent (Sy et al., 2005). A dominant gene, *Pfo*, was required for foliar resistance in CM 334 when the susceptible parent was 'Early Jalapeno' (Sy et al., 2005; Walker and Bosland, 1999). Although when the susceptible parent was 'Keystone Resistant Giant no. 3', at least one dominant gene must be expressed for both root rot and foliar blight resistance besides a dominant gene required for foliar resistance and a different dominant gene required for root resistance (Walker and Bosland, 1999). However, the allelism tests were not determined. Resistance to *Phytophthora* fruit rot was controlled by the dominant gene *Pfr* in 'Waxy Globe' (Saini and Sharma, 1978).

Recently, six chromosomal regions (*Phyto4.1*, *Phyto5.1*, *Phyto5.2*, *Phyto6.1*, *Phyto11.1*, and *Phyto12.1*) were identified to be involved in one or more components of resistance to *P. capsici* (Thabuis et al., 2003). The *Phyto5.2* QTL may be widely distributed in highly resistant accessions. SCAR marker D04.717 located in chromosome 5 was tightly linked with *Phyto5.2* (Quirin et al., 2005).

Resistance to anthracnose

Resistance of *C. annuum* cv. Chungryong to *Colletotrichum dematium* was conferred by a dominant allele, *Anr1*, when the resistance was measured as a lesion with a diameter less than 18.1 mm (Park et al., 1992). The dominant genes were present for resistance to *C. gloeosporioides*: a single gene, *Anr-2*, in the accession BGH3077; and two genes, *Anr-3* and *Anr-4*, in 'BGH2850' and 'BGH5085' (Fernandes and Ribeiro, 1998). One dominant gene, *Anr-5*, was responsible for the resistance to anthracnose incited by

C. capsici in the line '83-168' at four days after inoculation (Lin et al., 2002). Allelism among *Anr* gene series is unknown.

Voorrips and colleagues (2004) scored three resistance-related traits for anthracnose in an F₂ population derived from the susceptible *C. annuum* cv. Jatilaba and the resistance *C. chinense* accession PRI95030. When fruits are inoculated with *C. gloeosporioides*, one main QTL, B1, was identified on all three traits, and three other QTLs were detected for overall lesion diameter and true lesion diameter, of which two also had an effect on infection frequency. When fruits are inoculated with *C. capsici*, the marker B1 was found for overall lesion diameter when marker G1 was used as cofactor in multiple QTL analysis. No significant QTLs were detected for two other traits.

Resistance to *ralstonia solanacearum*

The bacterial wilt resistance in the sweet pepper variety 'Mie-Midori' showed incomplete dominance, and at least two genes were involved in resistance (Matsunaga et al., 1998).

Resistance to powdery mildew

Leveillula taurica causes powdery mildew of pepper. The line H-V-12 immune to *L. taurica* races from Israel depends on three pairs of genes: *lmr-1*, *lmr-2*, and *lmr-3* (Shifriss et al., 1992). Daubeze and associates (1991) determined that at least three genes appeared to control resistance in the Ethiopian variety H3 to *L. taurica*. Later, Lefebvre and coworkers (2003) detected seven genomic regions, including additive QTLs and epistatic interactions contributing to the resistance of the variety H3.

Resistance to root knot nematodes (*Meloidogyne* spp.)

There are four economically important root-knot nematode species: *Meloidogyne incognita* (Kofoid and White) Chitwood, *M. arenaria* (Neal) Chitwood, *M. javanica* (Treb) Chitwood, and *M. hapla* Chitwood. As early as 1957, Hare (Fery and Harrison, 1990) identified a dominant gene, *N*, for resistance to *M. incognita acrita* in the *C. annuum* 'Santaka XS' line. Expression of the *N* gene in bell pepper is modified and decreased at temperatures more than 28 °C (Thies and Fery, 1998, 2002). Cytoplasmic factors are not involved in expression of *N*-type resistance. The resistance of 'Carolina Hot' to *M. incognita* is conditioned by two genes: one dominant allelic to the dominant resistance gene *N*, and one recessive (Fery and Dukes, 1996). The resistance to *M. incognita* in *C. chinense* 'PA-426' is conditioned by a single dominant gene that is allelic to the dominant gene *N* in the *C. annuum* 'Carolina Cayenne' (Fery and Thies, 1998). Resistance to *M. arenaria* race 1 in *C. chinense* lines PA-353 and PA-426 was conditioned by a single dominant gene that is allelic to a resistance gene in *C. annuum* 'Carolina Cayenne' (Fery and Thies, 2000). However, the allelism tests did not

demonstrate conclusively that the *M. arenaria* race 1 resistance gene in *C. chinense* is the *N* gene in *C. annuum*. Five main resistance dominant genes, *Me-1* to *Me-5*, in *C. annuum* line PM217 (PI 201234) and PM687 (PI 322719) were identified by Hendy et al. (1985) to confer resistance to *Meloidogyne* spp. (cited by Djian-Caporalino et al., 1999, and Souza-Sobrinho et al., 2002), all acting individually in a gene-for-gene interaction. The *Me-6* gene specifically controlled resistance to *M. arenaria* and *M. javanica* (French population) in 'Yolo Wonder' (Djian-Caporalino, personal communication). *Me-7* was found in CM 334, conferring a high level of resistance to *M. arenaria*, *M. incognita*, and *M. javanica* (Pegard et al., 2005). Two other loci, *Mech-1* (in 'PM217') and *Mech-2* (in 'CM334') were identified to control the resistance to *M. chitwoodi* (Djian-Caporalino et al., 2004). Among them, three dominant and thermostable loci with broad-spectrum resistance (*Me-3*, *Me-1*, and *Me-7*), *Mech-1*, and *Mech-2* suppressed nematode reproduction (Djian-Caporalino et al., 1998, 1999, 2004). It appears that the *N* gene and the *Me-3* gene both confer higher resistance than the *Me-1* gene (Thies, 2004).

Fine mapping with AFLP markers flanked the resistance genes in coupling, and the nearest marker was located less than 2 cM from *Mech-1*, 3 cM from *Me-1*, and 1 cM from *Mech-2* (Djian-Caporalino et al., 2004). The *Me-3* nearest AFLP marker was 10.1 cM from a RAPD marker Q04_0.3 and 2.7 cM from RFLP marker CT135. *Me-4* was linked 10 cM to *Me-3* (Djian-Caporalino et al., 2001). The genes *Me-3*, *Me-1*, *Me-7*, *Mech-1*, and *Mech-2* are effectively different, but linked, and were all assigned to chromosome P9 (Djian-Caporalino et al., 2004).

Bentazon herbicide tolerance

The dominant gene *Bzt* is responsible for a high level of tolerance to the herbicide, bentazon, in *C. annuum* (Fery and Harrison, 1990; Wolff et al., 1992). A possible cytoplasmic involvement was present in the expression of the *Bzt* gene in the Santaka cultivar, and modifying genes affected the major gene, *Bzt*, controlling tolerance in the Bohemian Chilli cultivar.

Conclusions and Perspectives

Capsicum genetics have been extensively studied for nearly a century, and *Capsicum* breeding has benefited greatly from this knowledge. Some characteristics/traits appearing in the *Capsicum* genetic literature are not included in this list because incomplete inheritance data were provided. Many gene mutants or lines are not available. Hence, a need to have genetic stocks deposited and maintained in a repository for further research is warranted. Unfortunately, resources for a *Capsicum* Gene Stock Center are not available. Nevertheless, the Chile Pepper Institute at New Mexico State University maintains some of the mutants and makes them available to bonified *Capsicum*

scientists. Future genetic exploration of *Capsicum* genes will include studying the allelic relationship among the similar genes, obtaining more gene mutants by the application of mutagens, developing a set of chromosome location lines using information from the tomato genome sequencing project, establishing linked molecular markers to genes, and characterizing gene function.

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