

## FEATURE

# Review of Genes and Linkage Groups in Cucumber

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The Cucurbitaceae family is composed of several species in which the genetics have been extensively studied. This knowledge, together with the ease in growing cucurbits, make them excellent candidates for use in genetic studies as well as biotechnology research. For example, cucumber (*Cucumis sativus* L.) is easily propagated vegetatively by cuttings or adventitious bud culture. It is graft-compatible with closely related species, and sex expression can be altered from gynoeceous to monoecious (and vice versa) using growth regulators (Atsmon and Tabak, 1979; Cantliffe, 1972; Cantliffe et al., 1972; Tolla and Peterson, 1979). Cucumber also possesses a short reproductive cycle, bears fruit prolifically, has potential for interspecific hybridization, and may be seed-propagated as a polyploid. As a naturally outcrossing species, the cucumber is also unusual in demonstrating little inbreeding depression, although hybrid vigor is documented in several studies (Aleksandrov, 1952; Lower et al., 1982; Winnik and Vetuskjek, 1952). Gene maps might be relatively uncomplicated and easy to develop using the known markers because of the low chromosome number ( $n = 7$ ) in cucumber.

Investigators have identified numerous genes in cucumber since the 1930s. Recently (1978), the Cucurbit Genetics Cooperative (CGC) began to facilitate the exchange of knowledge and to lay the groundwork for organized data collection and coordinated research in the cucurbitaceae. The purpose of this review was to 1) summarize all of the cucumber genes in one place, 2) provide information on the lines that carry the published alleles for future checks of allelism, 3) point out possible duplications, and 4) summarize the gene linkages reported so far.

Table 1 lists the 105 known genes that are

updated from four previous reviews (Pierce and Wehner 1987; Robinson, 1979; Robinson et al., 1976, 1982). Gene nomenclature rules adopted by the Cucurbit Genetics Cooperative were used in developing this list of genes (Robinson et al., 1982). In many instances, we have identified the lines that carry the mutant forms of the genes and have attempted to identify their availability. Following is a discussion of the known genes grouped according to their effect on the phenotype.

### GENE MUTANTS

#### Seedling mutants

One of the advantages of using the cucumber in genetic research is the availability of seedling markers. To date, five nonlethal color mutants [virescent (*v*) (Poole, 1944; Tkachenko, 1935), variegated virescence (*vv*) (Abul-Hayja and Williams, 1976), yellow cotyledons-1 (*yc-1*) (Aalders, 1959), yellow cotyledons-2 (*yc-2*) (Whelan and Chubey, 1973; Whelan et al., 1975), yellow plant (*yp*) (Abul-Hayja and Williams, 1976)], and four lethal, color mutants [chlorophyll deficient (*cd*) (Burnham et al., 1966), golden cotyledon (*gc*) (Whelan, 1971), light sensitive (*ls*) (Whelan, 1972b), pale lethal (*pl*) (Whelan, 1973)], have been identified.

Six seedling traits that affect traits other than color include bitterfree (*bf*) (Andrews, 1959), blind (*bl*) (Carlsson, 1961), delayed growth (*dl*) (Miller and George, 1979), long hypocotyl (*lh*) (Robinson et al., 1982), revolute cotyledons (*rc*) (Whelan et al., 1975), and stunted cotyledons (*sc*) (Shanmugasundaram and Williams, 1971; Shanmugasundaram et al., 1972).

#### Stem mutants

Seven genes have been identified that affect stem length: bush (*bu*) (Pyzenkov and Kosareva, 1981), compact (*cp*) (Kauffman and Lower, 1976), determinate (*de*) (Denna, 1971; Kooistra, 1971; Odland and Groff, 1963b), dwarf (*dw*) (Robinson and Mishanec, 1965), tall height (*T*) (Hutchins, 1940), and *In-de*, which behaves as an intensifier for *de* (George, 1970). Rosette (*ro*), which also affects height, is characterized by muskmelon-like leaves (de Ruiter et al., 1980).

Unlike these genes, fasciated (*fa*) (Robinson, 1978b; Shifriss, 1950) affects stem conformation, not length.

#### Leaf mutants

Several genes have been shown to control leaf or foliage characteristics. Eight in particular are responsible for leaf shape: blunt leaf apex (*bla*) (Robinson, 1987a), cordate leaves-1 (*cor-1*) (Gornitskaya, 1967), cordate leaves-2 (*cor-2*) (Robinson, 1987c), crinkled leaf (*cr*) (Odland and Groff, 1963a), divided leaf (*dvl*) (den Nijs and Mackiewicz, 1980), ginko leaf (*gi*) (John and Wilson, 1952), little leaf (*ll*) (Goode et al., 1980; Wehner et al., 1987), and umbrella leaf (*ul*) (den Nijs and de Ponti 1983). Note that ginko leaf is a misspelling of the genus *Ginkgo*.

The original cordate leaf gene identified by Gornitskaya (1967) differs from *cor* proposed by Robinson (1987c), which also had calyx segments tightly clasping the corolla, thus hindering flower opening and insect pollination. Therefore, we propose that the first gene identified by Gornitskaya be labeled *cor-1* and the second identified by Robinson be labeled *cor-2*.

It should be noted that plants with stunted cotyledon may look similar to those with ginko at the younger stages, but the cotyledons of *sc* mutants are irregular and *gi* mutants are sterile.

Opposite leaf arrangement (*opp*) is inherited as a single recessive gene with linkages to *m* and *l*. Unfortunately, incomplete penetrance makes the opposite leaf arrangement difficult to distinguish from normal plants with alternate leaf arrangement (Robinson, 1987e).

Five mutants that affect color or anatomical features of the foliage are golden leaves (*g*) (Tkachenko, 1935), glabrous (*gl*) (Ingamier and de Ponti, 1980; Robinson and Mishanec, 1964), glabrate (*glb*) (Whelan, 1973), short petiole (*sp*) (den Nijs and Boukema, 1985), and tendrillless (*td*) (Rowe and Bowers, 1965).

#### Flower mutants

Sex expression in cucumber is affected by several single-gene mutants. The *F* locus affects gynoecey (femaleness), but is modified by other genes and the environment, and interacts with *a* and *m* (androecious and andromonoecious, respectively) (Galun, 1961; Kubicki, 1969a, 1969c; Rosa, 1928; Shifriss, 1961; Tkachenko, 1935; Wall, 1967). Androecious plants are produced if *aa* and *ff* occur in combination, otherwise plants are hermaphroditic if *mF*, andromonoecious if *m+*, gynoeceous if *+F*, and monoecious if

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Table 1. The 105 genes of cucumber.

Gene symbol		Character	References*	Supplemental references*	Availability*
Preferred	Synonym				
<i>a</i>	---	<i>androecious</i> . Produces primarily staminate flowers if recessive for <i>F</i> . <i>A</i> from MSU 713-5 and <i>Gy</i> 14A; <i>a</i> from An-11 and An-314, two selections from 'E-c-szan' of China.	Kubicki, 1969	---	P
<i>ap</i>	---	<i>apetalous</i> . Male-sterile. Anthers become sepal-like. <i>Ap</i> from 'Butchers Disease Resisting'; <i>ap</i> from 'Butchers Disease Resisting Mutant'.	Grimbly, 1980	---	L
<i>Ar</i>	---	<i>Anthraxnose resistance</i> . One of several genes for resistance to <i>Colletotrichum lagenarium</i> . <i>Ar</i> from PI 175111, PI 175120, PI 179676, PI 183308, PI 183445; <i>ar</i> from 'Palmetto' and 'Santee'.	Barnes and Epps, 1952	---	P
<i>B</i>	---	<i>Black or brown spines</i> . Dominant to white spines on fruit.	Strong, 1931; Tkachenko, 1935; Wellington, 1913	Cochran, 1938; Fujieda and Akiya, 1962; Hutchins, 1940; Jenkins, 1946; Youngner, 1952	W
<i>B-2</i>	---	<i>Black spine-2</i> . Interacts with <i>B</i> to produce $F_2$ of 15 black: 1 white spine. <i>B-2</i> from Wis. 9362; <i>b-2</i> from PI 212233 and 'Pixie'.	Shanmugasundaram et al., 1971a	---	?
<i>B-3</i>	---	<i>Black spine-3</i> . Interacts with <i>B-4</i> to produce an $F_2$ of nine black : 7 white spine. <i>B-3</i> from LJ90430; <i>b-3</i> from MSU 41.	Cowen and Helsel, 1983	---	W
<i>B-4</i>	---	<i>Black spine-4</i> . Interacts conversely of <i>B-3</i> . <i>B-4</i> from LJ90430; <i>b-4</i> from MSU 41.	Cowen and Helsel, 1983	---	W
<i>bi</i>	---	<i>bitterfree</i> . All plant parts lacking cucurbitacins. Plants with <i>bi bi</i> less preferred by cucumber beetles. Plants with <i>Bi</i> resistant to spider mites in most American cultivars; <i>bi</i> in most Dutch cultivars.	Andeweg and DeBruyn, 1959	Cantliffe, 1972; Da Costa and Jones, 1971a, 1971b; Soans et al., 1973	W
<i>bl</i>	<i>t</i>	<i>blind</i> . Terminal bud lacking after temperature shock. <i>bl</i> from 'Hunderup' and inbred HP3.	Carlsson, 1961	---	L
<i>bla</i>	---	<i>blunt leaf</i> . Leaves have obtuse apices and reduced lobing and serration. <i>bla</i> from a mutant of 'Wis. SMR-18'.	Robinson, 1987a	---	W
<i>Bt</i>	---	<i>Bitter fruit</i> . Fruit with extreme bitter flavor. <i>Bt</i> from PI 173889 (Wild Hanzil Medicinal Cucumber).	Barham, 1953	---	W
<i>bu</i>	---	<i>bush</i> . Shortened internodes. <i>bu</i> from 'KapAhk 1'.	Pyzenkov and Kosareva, 1981	---	L
<i>Bw</i>	---	<i>Bacterial wilt resistance</i> . Resistance to <i>Erwinia tracheiphila</i> . <i>Bw</i> from PI 200818; <i>bw</i> from 'Marketer'.	Nuttall and Jasmin, 1958	Robinson and Whitaker, 1974	W
<i>c</i>	---	<i>cream mature fruit color</i> . Interaction with <i>R</i> is evident in the $F_2$ ratio of 9 red ( $R +$ ) : 3 orange ( $R c$ ) : 3 yellow ( $++$ ) : 1 cream ( $++ c$ ).	Hutchins, 1940	---	L
<i>Cca</i>	---	<i>Corynespora cassiicola resistance</i> . Resistance to target leaf spot; dominant to susceptibility. <i>Cca</i> from Royal Sluis Hybrid 72502; <i>cca</i> from <i>Gy</i> 3.	Abul-Hayja et al., 1975	---	W
<i>Ccu</i>	---	<i>Cladosporium cucumerinum resistance</i> . Resistance to scab. <i>Ccu</i> from line 127.31, a selfed progeny of 'Longfellow'; <i>ccu</i> from 'Davis Perfect'.	Bailey and Burgess, 1934*	Abul-Hayja and Williams, 1976; Abul-Hayja et al., 1975; Andeweg, 1956	W
<i>cd</i>	---	<i>chlorophyll deficient</i> . Seedling normal at first, later becoming light green; lethal unless grafted. <i>cd</i> from a mutant selection of backcross of MSU 713-5 x 'Midget' to 'Midget'.	Burnham et al., 1966	---	L
<i>cl</i>	---	<i>closed flower</i> . Male and female flowers do not open; male-sterile (nonfertile pollen).	Groff and Odland, 1963	---	W
<i>cla</i>	---	<i>Colletotrichum lagenarium resistance</i> . Resistance to race 1 of anthracnose; recessive to susceptibility. <i>Cl</i> from 'Wis. SMR 18'; <i>cla</i> from SC 19B.	Abul-Hayja et al., 1978	---	W
<i>Cm</i>	---	<i>Corynespora melonis resistance</i> . Resistance to <i>C. melonis</i> dominant to susceptibility. <i>Cm</i> from 'Spot-vrie'; <i>cm</i> from 'Esvier'.	van Es, 1958	---	?
<i>Cmv</i>	---	<i>Cucumber mosaic virus resistance</i> . One of several genes for resistance to CMV. <i>Cmv</i> from 'Wis. SMR 12', 'Wis. SMR 15', and 'Wis. SMR 18'; <i>cmv</i> from 'National Pickling' and Wis. SR6.	Wasuwat and Walker, 1961	Shifriss et al., 1942	W
<i>co</i>	---	<i>green corolla</i> . Green petals that turn white with age and enlarged reproductive organs; female-sterile. <i>co</i> from a selection of 'Extra Early Prolific'.	Hutchins, 1935	Currence, 1954	L
<i>cor-1</i>	---	<i>cordate leaves-1</i> . Leaves are cordate. <i>cor-1</i> from 'Nezhinskii'.	Gornitskaya, 1967	---	L
<i>cor-2</i>	<i>cor</i>	<i>cordate leaves-2</i> . Leaves are nearly round with revolute margins and no serration. Insect pollination is hindered by short calyx segments that tightly clasp the corolla, preventing full opening. <i>cor-2</i> from an induced mutant of 'Lemon'.	Robinson, 1987c	---	?
<i>cp</i>	---	<i>compact</i> . Reduced internode length, poorly developed tendrils, small flowers. <i>cp</i> from PI 308916.	Kauffman and Lower, 1976	---	W

continued

Table 1. continued

Gene symbol		Character	References <sup>a</sup>	Supplemental references <sup>a</sup>	Availability <sup>a</sup>
Preferred	Synonym				
<i>cr</i>	---	<i>crinkled leaf</i> . Leaves and seed are crinkled.	Odland and Groff, 1963a	---	?
<i>cs</i>	---	<i>carpel splitting</i> . Fruits develop deep longitudinal splits. <i>cs</i> from TAMU 1043 and TAMU 72210, which are second and fifth generation selections of MSU 3249 x SC 25.	Carruth, 1975; Pike and Carruth, 1977	---	?
<i>D</i>	<i>g</i>	<i>Dull fruit skin</i> . Dull skin of American cultivars, dominant to glossy skin of most European cultivars.	Poole, 1944; Strong, 1931; ---	---	W
<i>de</i>	<i>I</i>	<i>determinate habit</i> . Short vine with stem terminating in flowers; modified by <i>In-de</i> and other genes; degree of dominance depends on gene background. <i>de</i> from Penn 76.60G*, Minn 158.60*, 'Hardin's PG57'*, 'Hardin's Tree Cucumber'*, and S <sub>2</sub> -1 (and inbred selection from Line 541)**.	Denna, 1971*; George, 1970**; Nuttall and Jasmin, 1958	Hutchins, 1940	W
<i>df</i>	---	<i>delayed flowering</i> . Flowering delayed by long photoperiod; associated with seed dormancy. <i>df</i> from 'Baroda' (PI 212896)* and PI 215589 ( <i>hard-wickii</i> )**.	Della Vecchia et al., 1982*; ---	Shifriss and George, 1965**	W
<i>dl</i>	---	<i>delayed growth</i> . Reduced growth rate; shortening of hypocotyl and first internodes. <i>dl</i> from 'Dwarf Marketmore' and 'Dwarf Tablegreen', both deriving dwarfness from 'Hardin's PG-57'.	Miller and George, 1979	---	W
<i>dm</i>	<i>P</i>	<i>downy mildew resistance</i> . One of several genes for resistance to <i>Pseudoperonospora cubensis</i> . <i>Dm</i> from Sluis & Groot Line 4285; <i>dm</i> from 'Poinsett'.	van Vliet and Meysing, 1977	Jenkins, 1946; Shimizu, 1963	W
<i>dvl</i>	<i>dl</i>	<i>divided leaf</i> . True leaves are partly or fully divided, often resulting in compound leaves with two to five leaflets and having incised corollas.	den Nijs and Mackiewicz, 1980	---	W
<i>dw</i>	---	<i>dwarf</i> . Short internodes. <i>dw</i> from an induced mutant of 'Lemon'.	Robinson and Mishanec, 1965	---	?
<i>Es-1</i>	---	<i>Empty chambers-1</i> . Carpels of fruits separated from each other, leaving a small to large cavity in the seed cell. <i>Es-1</i> from PP-2-75; <i>es-1</i> from Gy-30-75.	Kubicki and Korzeniewska, 1983	---	?
<i>Es-2</i>	---	<i>Empty chambers-2</i> . Carpels of fruits separated from each other, leaving a small to large cavity in the seed cell. <i>Es-2</i> from PP-2-75; <i>es-2</i> from Gy-30-75.	Kubicki and Korzeniewska, 1983	---	?
<i>F</i>	<i>Acr</i> , <i>acr<sup>f</sup></i> , <i>D</i> , <i>st</i>	<i>Female</i> . High degree of female sex expression: interacts with <i>a</i> and <i>M</i> ; strongly modified by environment and gene background. <i>F</i> and <i>f</i> are from 'Japanese'.	Galun, 1961; Tkachenko, 1935	Kubicki, 1965, 1969a; Poole, 1944; Shifriss, 1961	W
<i>fa</i>	---	<i>fasciated</i> . Plants have flat stems, short internodes, and rugose leaves. <i>fa</i> was from a selection of 'White Lemon'.	Robinson, 1978b*; Shifriss, 1950	---	?
<i>Fba</i>	---	<i>Flower bud abortion</i> . Preanthesis abortion of floral buds, ranging from 10% to 100%. <i>fba</i> from MSU 0612.	Miller and Quisenberry, 1978	---	?
<i>Fl</i>	---	<i>Fruit length</i> . Expressed in an additive fashion, fruit length decreases incrementally with each copy of <i>fl</i> (H. Munger, personal communication).	Wilson, 1968	---	W
<i>Foc</i>	---	<i>Fusarium oxysporum f. sp. cucumerinum resistance</i> . Resistance to fusarium wilt; dominant to susceptibility. <i>Foc</i> from Wis. 248; <i>foc</i> from 'Shimshon'.	Netzer et al., 1977	---	W
<i>g</i>	---	<i>golden leaves</i> . Golden color of lower leaves. <i>G</i> and <i>g</i> are both from different selections of 'Nezhin'.	Tkachenko, 1935	---	L
<i>gb</i>	<i>n</i>	<i>gooseberry fruit</i> . Small, oval-shaped fruit. <i>gb</i> from the 'Klin mutant'.	Tkachenko, 1935	---	?
<i>gc</i>	---	<i>golden cotyledon</i> . Butter-colored cotyledons; seedlings die after 6 to 7 days. <i>gc</i> from a mutant of 'Burpless Hybrid'.	Whelan, 1971	---	W
<i>gi</i>	---	<i>ginko</i> . Leaves reduced and distorted, resembling leaves of Ginkgo; male- and female-sterile. Complicated background: It was in a segregating population whose immediate ancestors were offspring of crosses and BC's involving 'National', 'Chinese Long', 'Tokyo Long Green', 'Vickery', 'Early Russian', 'Ohio 31', and an unnamed white spine slicer.	John and Wilson, 1952	---	L
<i>gl</i>	---	<i>glabrous</i> . Foliage lacking trichomes; fruit without spines. Iron-deficiency symptoms (chlorosis) induced by high temperature. <i>gl</i> from NCSU 75* and M834-6**.	Robinson and Mishanec, 1964*	Inggamer and de Ponti, 1980**; Robinson, 1987b	W
<i>glb</i>	---	<i>glabrate</i> . Stem and petioles glabrous, laminae slightly pubescent. <i>glb</i> from 'Burpless Hybrid'.	Whelan, 1973	---	W
<i>gy</i>	---	<i>gynoecious</i> . Recessive gene for high degree of female sex expression.	Kubicki, 1974	---	W
<i>H</i>	---	<i>Heavy netting of fruit</i> . Dominant to no netting and completely linked or pleiotropic with black spines ( <i>B</i> ) and red mature fruit color ( <i>R</i> ).	Hutchins, 1940; Tkachenko, 1935	---	W

continued

Table 1. continued

Gene symbol		Character	References*	Supplemental references*	Availability*
Preferred	Synonym				
<i>I</i>	---	<i>Intensifier of P</i> . Modifies effect of <i>P</i> on fruit warts in <i>Cucumis sativus</i> var. <i>tuberculatus</i> .	Tkachenko, 1935	---	?
<i>In-de</i>	<i>In(de)</i>	<i>Intensifier of de</i> . Reduces internode length and branching of <i>de</i> plants. <i>In-de</i> and <i>in-de</i> are from different selections ( <i>S<sub>2</sub>-1</i> and <i>S<sub>2</sub>-6</i> , respectively) from a determinant inbred <i>S<sub>2</sub>-1</i> , which is a selection of line 541.	George, 1970	---	?
<i>In-F</i>	<i>F</i>	<i>Intensifier of female sex expression</i> . Increases degree of female sex expression of <i>F</i> plants. <i>In-F</i> from monoecious line 18-1; <i>in-F</i> from MSU 713-5.	Kubicki, 1969b	---	?
<i>l</i>	---	<i>locule number</i> . Many fruit locules and pentamerous androecium; five locules recessive to the normal number of three.	Youngner, 1952	---	W
<i>lh</i>	---	<i>long hypocotyl</i> . As much as a 3-fold increase in hypocotyl length. <i>lh</i> from a 'Lemon' mutant.	Robinson and Shail, 1981	---	W
<i>ll</i>	---	<i>little leaf</i> . Normal-sized fruits on plants with miniature leaves and smaller stems. <i>ll</i> from 'Little John' (Ark. 79-75).	Goode et al., 1980; Wehner et al., 1987	---	W
<i>ls</i>	---	<i>light sensitive</i> . Pale and smaller cotyledons, lethal at high light intensity. <i>ls</i> from a mutant of 'Burpless Hybrid'.	Whelan, 1972b	---	L
<i>m</i>	<i>a, g</i>	<i>andromonoecious</i> . Plants are andromonoecious if ( <i>m</i> +); monoecious if (+ +); gynoeceous if (+ <i>F</i> ) and hermaphroditic if ( <i>m F</i> ). <i>m</i> from 'Lemon'.	Rosa, 1928*; Tkachenko, 1935	Shifriss, 1961; Wall, 1967; Youngner, 1952	W
<i>m-2</i>	<i>h</i>	<i>andromonoecious-2</i> . Bisexual flowers with normal ovaries.	Iezzoni; 1982; Kubicki, 1974	---	?
<i>mp</i>	<i>pf*</i> , <i>pf<sup>st</sup></i> <i>pf<sup>b</sup></i>	<i>multi-pistillate</i> . Several pistillate flowers per node, recessive to single pistillate flower per node. <i>mp</i> from MSU 604G and MSU 598G.	Nandgaonker and Baker, 1981	Fujieda et al., 1982	W
<i>Mp-2</i>	---	<i>Multi-pistillate-2</i> . Several pistillate flowers per node. Single dominant gene with several minor modifiers. <i>Mp-2</i> from MSU 3091-1.	Thaxton, 1974	---	?
<i>ms-1</i>	---	<i>male sterile-1</i> . Male flowers abort before anthesis; partially female-sterile. <i>ms-1</i> from 'Black Diamond' and 'A & C'.	Shifriss, 1950	Robinson and Mishanec, 1967	L
<i>ms-2</i>	---	<i>male sterile-2</i> . Male-sterile; pollen abortion occurs after first mitotic division of the pollen grain nucleus. <i>ms-2</i> from a mutant of 'Burpless Hybrid'.	Whelan, 1973	---	?
<i>n</i>	---	<i>negative geotropic peduncle response</i> . Pistillate flowers grow upright; <i>n</i> from 'Lemon'; <i>N</i> produces the pendant flower position of most cultivars.	Odland, 1963b	---	W
<i>ns</i>	---	<i>numerous spines</i> . Few spines on the fruit is dominant to many. <i>ns</i> from Wis. 2757.	Fanourakis, 1984; Fanourakis and Simon, 1987	---	W
<i>O</i>	<i>y</i>	<i>Orange-yellow corolla</i> . Orange-yellow dominant to light yellow. <i>O</i> and <i>o</i> are both from 'Nezhin'.	Tkachenko, 1935	---	?
<i>opp</i>	---	<i>opposite leaf arrangement</i> . Opposite leaf arrangement is recessive to alternate and has incomplete penetrance. <i>opp</i> from 'Lemon'.	Robinson, 1987e	---	W
<i>P</i>	---	<i>Prominent tubercles</i> . Prominent on yellow rind of <i>Cucumis sativus</i> var. <i>tuberculatus</i> , incompletely dominant to brown rind without tubercles. <i>P</i> from 'Klin'; <i>p</i> from 'Nezhin'.	Tkachenko, 1935	---	W
<i>Pc</i>	<i>P</i>	<i>Parthenocarpy</i> . Sets fruit without pollination. <i>Pc</i> from 'Spotvrie'; <i>pc</i> from MSU 713-205*.	Pike and Peterson, 1969*; Wellington and Hawthorn, 1928	de Ponti and Garretsen, 1976	?
<i>pl</i>	---	<i>pale lethal</i> . Slightly smaller pale-green cotyledons; lethal after 6 to 7 days. <i>Pl</i> from 'Burpless Hybrid'; <i>pl</i> from a mutant of 'Burpless Hybrid'.	Whelan, 1973	---	L
<i>pm-1</i>	---	<i>powdery mildew resistance-1</i> . Resistance to <i>Sphaerotheca fuliginia</i> . <i>pm-1</i> from 'Natsufushinari'.	Fujieda and Akiya, 1962; Kooistra, 1971	Shanmugasundaram et al., 1972	?
<i>pm-2</i>	---	<i>powdery mildew resistance-2</i> . Resistance to <i>Sphaerotheca fuliginia</i> . <i>pm-2</i> from 'Natsufushinari'.	Fujieda and Akiya, 1962; Kooistra, 1971	Shanmugasundaram et al., 1972	?
<i>pm-3</i>	---	<i>powdery mildew resistance-3</i> . Resistance to <i>Sphaerotheca fuliginia</i> . <i>pm-3</i> found in PI 200815 and PI 200818.	Kooistra, 1971	Shanmugasundaram et al., 1972	W
<i>pm-h</i>	<i>s, pm</i>	<i>powdery mildew resistance expressed by the hypocotyl</i> . Resistance to powdery mildew as noted by no fungal symptoms appearing on seedling cotyledons is recessive to susceptibility. <i>Pm-h</i> from 'Wis. SMR-18'; <i>pm-h</i> from 'Gy 2 cp cp', 'Spartan Salad', and Wis. 2757.	Fanourakis, 1984; Shanmugasundaram et al., 1971b	---	W
<i>pr</i>	---	<i>protruding ovary</i> . Exserted carpels. <i>pr</i> from 'Lemon'.	Youngner, 1952	---	W
<i>psl</i>	<i>pl</i>	<i>Pseudomonas lachrymans resistance</i> . Resistance to <i>Pseudomonas lachrymans</i> is recessive. <i>psl</i> from 'National Pickling' and 'Wis. SMR 18'; <i>psl</i> from MSU 9402 and Gy 14A.	Dessert et al., 1982	---	W

continued



Table 1. continued

Gene symbol		Character	References <sup>a</sup>	Supplemental references <sup>a</sup>	Availability <sup>a</sup>
Preferred	Synonym				
<i>R</i>	---	<i>Red mature fruit</i> . Interacts with <i>c</i> ; linked or pleiotropic with <i>B</i> and <i>H</i> .	Hutchins, 1940	---	W
<i>rc</i>	---	<i>revolute cotyledon</i> . Cotyledons short, narrow, and cupped downwards; enlarged perianth. <i>rc</i> from 'Burple Hybrid' mutant.	Whelan et al., 1975	---	L
<i>ro</i>	---	<i>rosette</i> . Short internodes, muskmelon-like leaves. <i>ro</i> from 'Megurk', the result of a cross involving a mix of cucumber and muskmelon pollen.	de Ruiter et al., 1980	---	W
<i>s</i>	<i>f, a</i>	<i>spine size and frequency</i> . Many small fruit spines, characteristic of European cultivars is recessive to the few large spines of most American cultivars.	Strong, 1931; Tkachenko, 1935	Carruth, 1975; Poole, 1944	W
<i>s-2</i>	---	<i>spine-2</i> . Acts in duplicate recessive epistatic fashion with <i>s-3</i> to produce many small spines on the fruit. <i>s-2</i> from Gy 14; <i>s-2</i> from TAMU 72210.	Carruth, 1975	---	?
<i>s-3</i>	---	<i>spine-3</i> . Acts in duplicate recessive epistatic fashion with <i>s-2</i> to produce many small spines on the fruit. <i>s-3</i> from Gy 14; <i>s-3</i> from TAMU 72210.	Carruth, 1975	---	?
<i>sa</i>	---	<i>salt tolerance</i> . Tolerance to high salt levels is attributable to a major gene in the homozygous recessive state and may be modified by several minor genes. <i>Sa</i> from PI 177361; <i>sa</i> from PI 192940.	Jones, 1984	---	P
<i>sc</i>	<i>cm</i>	<i>stunted cotyledons</i> . Small, concavely curved cotyledons; stunted plants with cupped leaves; abnormal flowers. <i>Sc sc</i> from Wis. 9594 and 9597.	Shanmugasundaram and Williams, 1971; Shanmugasundaram et al., 1972	---	W
<i>Sd</i>	---	<i>Sulfur dioxide resistance</i> . Less than 20% leaf damage in growth chamber. <i>Sd</i> from 'National Pickling'; <i>sd</i> from 'Chipper'.	Bressan et al., 1981	---	W
<i>sp</i>	---	<i>short petiole</i> . Leaf petioles of first nodes 20% the length of normal. <i>sp</i> from Russian mutant line 1753.	den Nijs and de Ponti, 1983	---	W
<i>ss</i>	---	<i>small spines</i> . Large, coarse fruit spines is dominant to small, fine fruit spines. <i>Ss</i> from 'Spartan Salad', 'Wis. SMR-18' and 'Gy 2 cp cp'; <i>ss</i> from Wis. 2757.	Fanourakis, 1984; Fanourakis and Simon, 1987	---	W
<i>T</i>	---	<i>Tall plant</i> . Tall incompletely dominant to short.	Hutchins, 1940	---	?
<i>td</i>	---	<i>tendriless</i> . Tendrils lacking; associated with misshapen ovaries and brittle leaves. <i>Td</i> from <i>td</i> from a mutant of 'Southern Pickler'.	Rowe and Bowers, 1965	---	W
<i>te</i>	---	<i>tender skin of fruit</i> . Thin, tender skin of some European cultivars; recessive to thick tough skin of most American cultivars.	Poole, 1944; Strong, 1931	---	W
<i>Tr</i>	---	<i>Trimonoecious</i> . Producing male, bisexual, and female flowers in this sequence during plant development. <i>Tr</i> from Tr-12, a selection of a Japanese cultivar belonging to the Fushinari group; <i>tr</i> from H-7-25, MOA-309, MOA-303, and AH-311-3.	Kubicki, 1969d	---	P
<i>Tu</i>	---	<i>Tuberculate fruit</i> . Warty fruit characteristic of American cultivars is dominant to smooth, non-warty fruits characteristic of European cultivars.	Strong, 1931; Wellington, 1913	Andeweg, 1956; Poole, 1944	W
<i>u</i>	<i>M</i>	<i>uniform immature fruit color</i> . Uniform color of European cultivars recessive to mottled or stippled color of most American cultivars.	Strong, 1931	Andeweg, 1956	W
<i>ul</i>	---	<i>umbrella leaf</i> . Leaf margins turn down at low relative humidity making leaves look cupped. <i>ul</i> source unknown.	den Nijs and de Ponti, 1983	---	W
<i>v</i>	---	<i>virescent</i> . Yellow leaves becoming green.	Strong, 1931; Tkachenko, 1935	---	L
<i>vvi</i>	---	<i>variegated virescent</i> . Yellow cotyledons, becoming green; variegated leaves.	Abul-Hayja and Williams, 1976	---	L
<i>w</i>	---	<i>white immature fruit color</i> . White is recessive to green. <i>W</i> from 'Vaughan', 'Clark's Special', 'Florida Pickle', and 'National Pickling'; <i>w</i> from 'Bangalore'.	Cochran, 1938	---	W
<i>wf</i>	---	<i>White flesh</i> . Intense white flesh color is recessive to dingy white; acts with <i>yf</i> to produce F <sub>2</sub> of 12 white (+ + and + wf) : 3 yellow (yf +) : 1 orange (yf wf). <i>Wf</i> from EG and G6, each being dingy white (+ +); <i>wf</i> from 'NPI', which is orange (yf wf).	Kooistra, 1971	---	?
<i>Wmv</i>	---	<i>Watermelon mosaic virus resistance</i> . Resistance to strain 2 of watermelon mosaic virus. <i>Wmv</i> from 'Kyoto 3 Feet'; <i>wmv</i> from 'Bet-Alfa'.	Cohen et al., 1971	---	P
<i>wmv-1-1</i>	---	<i>watermelon mosaic virus-1 resistance</i> . Resistance to strain 1 of watermelon mosaic virus by limited systemic translocation; lower leaves may show severe symptoms. <i>Wmv-1-1</i> from Wis. 2757; <i>wmv-1-1</i> from 'Surinam'.	Wang et al., 1984	---	?

continued

Table 1. continued

Gene symbol	Preferred	Synonym	Character	References <sup>a</sup>	Supplemental references <sup>a</sup>	Availability <sup>a</sup>
<i>yc-1</i>	---	---	<i>yellow cotyledons-1</i> . Cotyledons yellow at first, later turning green. <i>yc-1</i> from a mutant of Ohio M.R. No. 25.	Aalders, 1959	---	W
<i>yc-2</i>	---	---	<i>yellow cotyledons-2</i> . Virescent cotyledons. <i>yc-2</i> from a mutant of 'Burpless Hybrid'.	Whelan and Chubey, 1973; Whelan et al., 1975	---	W
<i>yf</i>	v	---	<i>yellow flesh</i> . Interacts with <i>wf</i> to produce F <sub>2</sub> of 12 white (+ + and + <i>wf</i> ) : 3 yellow ( <i>yf</i> +) : 1 orange ( <i>yf yf</i> ). <i>Yf</i> from 'Natsufushinari', which has an intense white flesh ( <i>Yf wf</i> ); <i>yf</i> from PI 200815, which has a yellow flesh ( <i>yf wf</i> ).	Kooistra, 1971	---	P
<i>yg</i>	gr	---	<i>yellow-green immature fruit color</i> . Recessive to dark green and epistatic to light green. <i>yg</i> from 'Lemon'.	Youngner, 1952	---	W
<i>yp</i>	---	---	<i>yellow plant</i> . Light yellow-green foliage; slow growth.	Abul-Hayja and Williams, 1976	---	?
<i>zymv</i>	---	---	<i>zucchini yellow mosaic virus</i> . Inheritance is incomplete. Believed to be inherited in a recessive fashion with the source of resistance being 'TMG-1'.	Provvidenti, 1985	---	W

<sup>a</sup>Asterisks on cultigens and associated references indicate the source of information for each.

<sup>b</sup>W = Mutants available through T. Wehner, cucumber gene curator for the Cucurbit Genetics Cooperative; P = mutants are available as standard cultivars or accessions from the Plant Introduction Collection; ? = availability not known; L = mutant has been lost.

+ +. The gene *F* may also be modified by an intensifier gene *In-F*, which increases the femaleness (Kubicki, 1969b). Other genes that affect sex expression are *gy* for gynoeceious (Kubicki, 1974), *m-2* for andromonoecious (Kubicki, 1974), and *Tr* for trimonoecious expression (Kubicki, 1969d).

Cucumbers, typically considered day-neutral plants, have occasionally been shown to express sensitivity to long days. Della Vecchia et al. (1982) and Shifriss and George (1965) demonstrated that a single gene for delayed flowering (*df*) is responsible for this short-day response.

Another gene that may give the impression of eliciting daylength sensitivity by causing a delay in flowering is *Fba*. In reality, *Fba* triggers flower bud abortion before anthesis in 10% to 100% of the buds (Miller and Quisenberry, 1978).

Three separate groups have reported single genes for multiple pistillate flowers per node. Nandgaonkar and Baker (1981) found that a single recessive gene (*mp*) was responsible for multiple pistillate flowering. This may be the same gene that Fujieda et al. (1982) later labeled as *pf* for plural pistillate flowering. However, they indicated that three different alleles were responsible, with single pistillate being incompletely dominant over multiple pistillate: *pf*<sup>+</sup> for single pistillate, *pf*<sup>h</sup> for double pistillate, and *pf*<sup>m</sup> for multiple pistillate (more than two flowers per node).

Thaxton (1974) reported that clustering of pistillate flowers is conditioned by a single dominant gene (we propose the symbol *Mp-2*), and that modifier genes influence the amount of clustering. Thaxton (1974) also determined that clustering of perfect flowers is controlled by genes different from clustering of gynoeceious flowers.

Several genes for male sterility have been reported for cucumber, but because of the ease of changing sex expression with growth regulators, little commercial use has been made of them. Five genes—*ms-1*, *ms-2*, *ap*, *cl*, and *gi*—have been identified. The genes *ms-1* and *ms-2* cause sterility by pollen abor-

tion before anthesis; *ms-1* plants are also partially female-sterile (Robinson and Mishanec, 1965; Shanmugasundaram and Williams, 1971; Whelan, 1972a). Apetalous mutants (*ap*), however, have infertile anthers that appear to have been transformed into sepal-like structures (Grimby, 1980). Ginko (*gi*), mentioned earlier as a leaf mutant, also causes male sterility (John and Wilson, 1952).

These male-steriles may be of little use except as a genetic marker. Closed flower (*cl*) mutants are both male- and female-sterile, so seed production must be through the heterozygotes only (Groff and Odland, 1963). With this mutant, the pollen is inaccessible to bees because the buds remain closed.

Three genes alter floral characteristics: green corolla (*co*) (Currence, 1954; Hutchins, 1935), orange-yellow corolla (*O*), and negative geotropic peduncle response (*n*) (Odland and Groff, 1963a). Green corolla (*co*), named because of its green petals, has enlarged but sterile pistils (Currence, 1954; Hutchins, 1935), and has potential for use as a female-sterile in hybrid production.

### Fruit mutants

Because the fruit is the most important part of the cucumber economically, considerable attention has been given to genes affecting it. One such gene is Bitter fruit, *Bt*, (Barham, 1953), which alters fruit flavor by controlling cucurbitacin levels. The gene *Bt* is different from *bi* because it consistently alters only the fruit cucurbitacin levels compared to *bi*, which affects the whole plant.

Five genes conditioning skin texture are *Tu*, *te*, *P*, *I*, and *H*. Smooth (*tu*) and tender (*te*) skin are usually associated with European types, while American types are generally warty and thick-skinned (Poole, 1944; Strong, 1931). Heavy netting (*H*), which occurs when fruit reach maturity, may be tightly linked or pleiotropic with *R* and *B* (discussed later).

In *Cucumis sativus* var. *tuberculatus*, Tkachenko (1935) found that gene *P*, causing fruit with yellow rind and tubercles, was

modified by gene *I*, an intensifier that increases the prominence of the tubercles (Tkachenko, 1935).

There are three genes affecting internal fruit quality, each identified by viewing transections of fruits—Empty chambers-1 (*Es-1*), Empty chambers-2 (*Es-2*) (Kubicki and Korzeniewska, 1983), and locule number (*l*) (Youngner, 1952).

Hutchins (1940) proposed that two genes controlled spine characteristics, with *f* producing many spines and being tightly linked with *s*, which produced small spines. Poole (1944) used the data of Hutchins (1940) to suggest that *s* and *f* were the same gene and proposed the joint symbol *s* for a high density of small spines. Tkachenko (1935), who used the same symbol for control of less-dense spines, did not look at spine size, and the same gene might have been involved. However, Fanourakis (1984) and Fanourakis and Simon (1987) reported two separate genes involved, and named them *ss* and *ns* for small spines and numerous spines, respectively. These genes may differ from those that led Carruth (1975) to conclude that two genes act in a double recessive epistatic fashion to produce the dense, small spine habit. We propose that these genes be labeled *s-2* and *s-3*, and *s-1* be used instead of *s* proposed by Poole (1944).

Carruth (1975) and Pike and Carruth (1977) also suggested that carpel rupture along the sutures was inherited as a single recessive gene that was tightly linked with round, fine-spined fruits. This trait may be similar to what Tkachenko (1935) noted in the "Klin mutant" as occasional deep-splitting flesh. We suggest the symbol *cs* for carpel splitting, but note that, because penetrance of the trait may be lower under certain environmental conditions (Carruth, 1975), this trait may be related to the gooseberry (*gb*) fruit reported by Tkachenko (1935). Another character not found in commercial cultivars was protruding ovary (*pr*) reported by Youngner (1952).

There is dispute over the inheritance of parthenocarpy, a trait found in many Euro-

pean cucumbers (Wellington and Hawthorn, 1928). Pike and Peterson (1969) suggested an incompletely dominant gene (*Pc*), affected by numerous modifiers, was responsible. In contrast, de Ponti and Garretsen (1976) explained the inheritance by three major isomeric genes with additive action.

A modifier of fruit length (*Fl*) was identified by its linkage with scab resistance (*Cca*) (H. Munger, personal communication; Wilson, 1968). Expressed in an additive fashion, fruit length decreases incrementally from dominant to heterozygote to recessive (*fl fl*).

## Fruit color

Twelve mutants have been identified that affect fruit color either in the spines, skin, or flesh, and a few of these appear to act pleiotropically. For example, *R* for red mature fruit color is very closely linked or pleiotropic to *B* for black or brown spines and *H* for heavy netting (Hutchins, 1935; Tkachenko, 1935; Wellington, 1913). It also interacts with *c* for cream-colored mature fruit in such a way that plants that are (*R* +), (*Rc*), (+ +), and (+ *c*) have red, orange, yellow, and cream-colored fruits, respectively (Hutchins, 1940).

The *B* gene produces black or brown spines and is pleiotropic to or linked with *R* and *H* (Wellington, 1913). The homozygous recessive plant is white-spined with cream-colored mature fruit and lacks netting. Other spine color genes are *B-2*, *B-3*, and *B-4* (Cowen and Helsel, 1983; Shanmugasundaram et al., 1971a).

White immature skin color (*w*) is recessive to the normal green (Cochran, 1938), and yellow green (*yg*) is recessive to dark green and epistatic with light green (Youngner, 1952). Skin color may also be dull or glossy (*D*) (Strong, 1931; Tkachenko, 1935) and uniform or mottled (*u*) (Andrews, 1956; Strong, 1931).

Kooistra (1971) reported two genes that affect fruit mesocarp color. Yellow flesh (*yf*) and white flesh (*wf*) interact to produce either white (+ + or + *wf*), yellow (*yf* +), or orange (*yf wf*) flesh.

## Insect resistance

Bitterfree (*bf*) is responsible for resistance to spotted and banded cucumber beetles (*Diabrotica* spp.) (Chambliss, 1978; Da Costa and Jones, 1971a, 1971b) and two-spotted spider mites (*Tetranychus urticae* Koch.) (Da Costa and Jones, 1971a, Soans et al., 1973). However, this gene works inversely for the two species. The dominant allele, which conditions higher foliage cucurbitacin levels, incites resistance to spider mites by an antibiotic affect of the cucurbitacin. The homozygous recessive results in resistance to cucumber beetles because cucurbitacins are attractants.

In the 1989 Cucurbit Genetics Cooperative Report, we labeled the gene for resistance to *Diabrotica* spp. *di*, but wish to retract it in light of recent evidence.

## Disease resistance

At present there are 15 genes known to control disease resistance in *C. sativus*. Three of these condition virus resistance. Wasuwat and Walker (1961) found a single dominant gene (*Cmv*) for resistance to cucumber mosaic virus. However, others have reported more complex inheritance (Shifriss et al., 1942). Two genes condition resistance to watermelon mosaic virus—*Wmv* (Cohen et al., 1971) and *wmv-1-1* (Wang et al., 1984). Most recently, resistance to zucchini yellow mosaic virus (*zymv*) has been identified (Providenti, 1985).

Both resistance to scab, caused by *Cladosporium cucumerinum* Ell. & Arth., and resistance to bacterial wilt, caused by *Erwinia tracheiphila* (E. F. Smith) Holland, are dominant and controlled by *Ccu* (Abul-Hayja et al., 1978; Andrews, 1956; Bailey and Burgess, 1934) and *Bw* (Nuttall and Jamin, 1958; Robinson and Whitaker, 1974), respectively. Other dominant genes providing resistance are: *Cca* for resistance to target leaf spot (*Corynespora cassicola*) (Abul-Hayja et al., 1978), *Cm* for resistance to *Corynespora* blight (*Corynespora melonis*) (Shanmugasundaram et al., 1971b), *Foc* for resistance to fusarium wilt (*Fusarium oxysporum* f. sp. *cucumerinum*) (Netzer et al., 1977), and *Ar* for resistance to anthracnose [*Colletotrichum lagenarium* (Pars.) Ellis & Halst.] (Barnes and Epps, 1952). In contrast, resistance to *Colletotrichum lagenarium* race 1 (Abul-Hayja et al., 1978) and angular leaf spot (*Pseudomonas lachrymans*) (Dessert et al., 1982) are conditioned by the recessive genes *cla* and *psl*, respectively.

Several reports have indicated that more than one gene controls resistance to powdery mildew [*Sphaerotheca fuliginea* (Schlecht) Poll.], with interactions occurring among loci (Fujieda and Akiya, 1962; Kooistra, 1968; Shanmugasundaram et al., 1971b). The resistance genes *pm-1* and *pm-2* were first reported by Fujieda and Akiya (1962) in a cultivar they developed and named 'Natsufushinari'. Kooistra (1968), using this same cultivar, later confirmed their findings and identified one additional gene (*pm-3*) from USDA accessions PI 200815 and PI 200818. Shimizu et al. (1963) also supported three recessive genes that are responsible for resistance of 'Aojihai' over 'Sagamihan'.

Several genes with specific effects have been identified more recently (Shanmugasundaram et al., 1971b), but, unfortunately, direct comparisons were not made to see if the genes were identical with *pm-1*, *pm-2*, and *pm-3*. Fanourakis (1984) considered a powdery mildew resistance gene in an extensive linkage study and proposed that it was the same gene used by Shanmugasundaram et al. (1971b), which also produces resistance on the seedling hypocotyl. Because expression is identified easily and since it is frequently labeled in the literature as "*pm*", we believe that this gene should be added to the list as *pm-h*, with the understanding that this may be the same as *pm-1*, *pm-2*, or *pm-3*.

At present, one gene, *dm*, has been identified that confers resistance to downy mildew [*Pseudoperonospora cubensis* (Berk. & Curt.) Rostow] (van Vliet and Meysing, 1974). Inherited as a single recessive gene, it also appeared to be linked with *pm* (van Vliet, 1977). There are, however, indications that more than one gene may be involved (Jenkins, 1946).

## Environmental stress resistance

At present, only two genes have been identified in this category: resistance to sulfur dioxide air pollution conditioned by *Sd* (Bressan et al., 1981) and increased tolerance to high salt levels conditioned by major gene, *sa*, Jones (1984).

## POSSIBLE ALLELIC OR IDENTICAL GENES

Several of the genes listed may be either pleiotropic, closely linked, or allelic. Additional research is needed to compare the sources of the various similar genes to ensure that they are not duplicates. In some instances, this may be difficult because many of the earlier publications did not list the source of the genes or the methods used to measure the traits, and many of these authors are deceased.

An example of this problem is the two-locus model (*R c*) for fruit color. We have been unable to locate any plants with red or yellow mature fruits. All plants evaluated in other studies have color inherited as a single gene. Hutchins may have separated fruit with cream color into two groups, yellow and cream, and fruits with orange color into two groups, orange and red. However, those distinctions are difficult to make using available germplasm. Situations such as these may be impossible to resolve.

In the future, researchers should use the marker lines listed here, or describe and release the marker lines used so that allelism can be checked by others. At present, groups of similar genes that need to be checked to determine how they are related include the following: the chlorophyll deficiency mutants (*cd*, *g*, *ls*, *pl*, *v*, *vv*, *yc-1*, *yc-2*, and *yp*), the stem mutants (*bu*, *de*, *dw*, *In-de*, and *T*), the leaf shape mutants (*rc* and *ul*), the sex expression mutants (*a*, *F*, *gy*, *In-F*, *m*, *m-2*, and *Tr*), the male sterility genes (*ap*, *cl*, *ms-1*, and *ms-2*), the flowering stage mutants (*df* and *Fba*), the flower color mutants (*co* and *O*), the powdery mildew resistance mutants (*pm-1*, *pm-2*, *pm-3*, and *pm-h*), the fruit spine color mutants (*B*, *B-2*, *B-3*, and *B-4*), the fruit skin color mutants (*c*, *R*, and *w*), the spine size and density mutants (*s*, *s-2*, and *s-3*), and the seed cell mutants (*cs* and *gb*).

Two groups of associated traits, one from 'Lemon' cucumber (*m*, *pr*, and *s*) and the other involving fruit skin color, surface texture, and spine type (*R*, *H*, and *B*), need to be checked using large populations to determine whether they are linked or pleiotropic. Recent gains have been made in this area by



Robinson (1978a), who demonstrated that the *m* gene is pleiotropic for fruit shape and flower type, producing both perfect flowers and round fruits, and Abul-Hayja et al. (1975) and Whelan (1973), who determined that *gl* and *glb* are independent genes.

New information indicates that comparisons also need to be made between resistance to scab (*Ccu*) and fusarium wilt (*Foc*) and between resistance to target leaf spot (*Cca*) and *Ulocladium cucurbitae* leaf spot. M. Palmer (personal communication) found a fairly consistent association between resistances to scab and fusarium wilt, which suggests that they might be linked or using the same mechanism for defense against the pathogen.

Similar defense mechanisms might also be responsible for similarities in resistance to target leaf spot (*Cca*) and *Ulocladium cucurbitae* leaf spot (H. Munger, personal communication).

## GENETIC LINKAGE

Since cucumber has just seven chromosome pairs and >100 known genes, it would seem that linkage maps would be fairly complete by now. Unfortunately, we know of few references reporting linkages of more than two gene loci, and we know of no other reviews that summarize the literature for linkages and attempt to describe different linkage groups.

Many difficulties were encountered and should be considered when reading this review. First, a portion of the nomenclature is still unclear, and some of the genes may be duplicates of others because common parents were not compared. This problem was discussed in the previous section. Second, some of the linkage relationships analyzed in previous studies did not involve specific genes. Linkages in several reports were discussed for plant traits that might have been inherited in multigenic fashion, or, if a single gene were involved, it was not specifically identified.

Therefore, in this review linkages for traits without genes will be omitted and a "?" will follow each gene with a questionable origin. Six linkage groups could be determined from the current literature (Fig. 1). The order in which the genes were expressed in each group does not necessarily represent the order in which they may be found on the chromosome.

### Linkage group I

The largest linkage group in cucumber has 12 genes, composed of *wmv-1-1*, *gy*, *gl*, *dl*, *dvl*, *de*, *F*, *ms-2*, *glb*, *bi*, *df*, and *B-3* or *B-4*. In contributing to this grouping, Whelan (1974) noted that *ms-2* is linked with *glb* ( $rf = 0.215 \pm 0.029$ ) and *de* ( $rf = 0.335 \pm 0.042$ ) while being independent of *bi*, *gl*, *yc-1*, *yc-2*, and *cr*. Gene *de* is linked with *F* (Odland and Groff, 1963b; Owens and Peterson, 1982), which, in turn, is linked with *B-3* or *B-4* (Cowen and Helsel, 1983), *gy* ( $rf = 0.04$ ) (Kubicki, 1974), *bi* ( $rf = 0.375$ ), and *df* ( $rf = 34.7$ ) (Fanourakis, 1984; Fan-

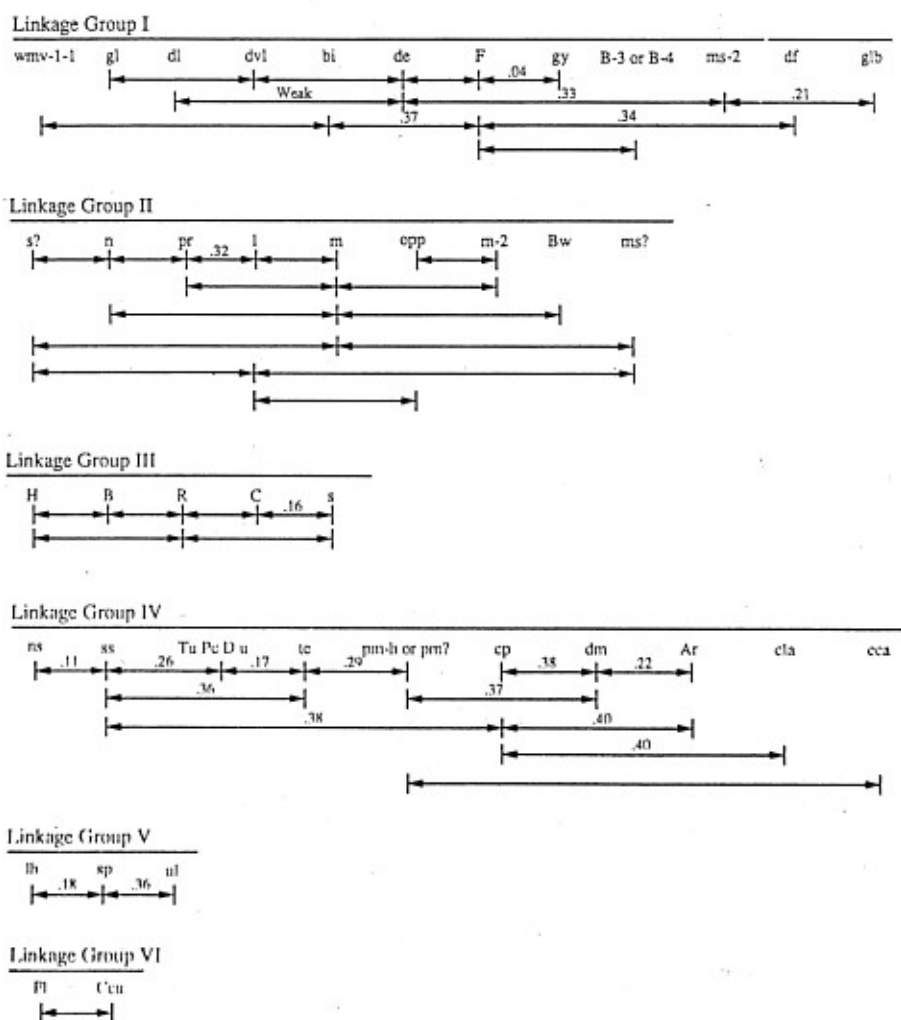


Fig. 1. The six linkage groups of cucumber assembled from published information (not necessarily on different chromosomes). Arrows indicate that linkage was reported between the associated gene loci. Recombination frequencies are given where known.

ourakis and Simon, 1987). Gene *de* is also weakly linked with *dl* (Miller and George, 1979), strongly linked with *dvl* (Netherlands, 1982), and independent of *cp* (Kauffman and Lower, 1976). Gene *wmv-1-1* is linked with bitterfree (*bi*), but independent of *Ccy*, *B*, *F*, or *pm?* (Wang et al., 1987).

Two reports show that *dvl* is weakly linked with *gl* ( $rf = 0.40$ ), and independent of *bi* and *Ccu* (Netherlands, 1982; den Nijs and Boukema, 1983), while Robinson (1978f) originally indicated that *gl* was linked with *yc* and independent of *B*, *m*, *l*, and *yg*, as well as *bi* (Netherlands, 1982) and *sp* (den Nijs and Boukema, 1985), but, more recently, he indicated that *gl* was independent of *yc* (Robinson, 1987d).

Completing linkage group I, Cowen and Helsel (1983) demonstrated that the spine color genes (*B-3* and *B-4*) were independent of the genes for bitterness, and Whelan (1973) found that *pl* was independent of *glb* and *bi*, while *glb* was independent of *gl*, *bi*, *ls*, *yc*, and *cr*. The last clarifies that *gl* and *glb* must indeed be separate loci.

### Linkage group II

Group II is composed of nine genes (*n*, *pr*, *l*, *m*, *opp*, *m-2*, *Bw*, *s?*, and *ms?*) unless

*s?* (Robinson, 1978) is the same as *s* from Hutchins (1940) and Poole (1944). If these are the same, then linkage groups II and III will be joined for a total of 12 genes. Of the first seven, two pairs have been defined with recombination values. Youngner (1952) determined that *m* and *l* were linked with a recombination frequency of  $0.326 \pm .014$ , and Robinson determined that *opp* was linked to both (Robinson, 1987e). Iezzoni and Peterson (1979, 1980) found that *m* and *Bw* were separated by only one map unit ( $rf = 0.011 \pm 0.003$ ). Iezzoni et al. (1932) also determined that *m-2* was closely linked with both *m* and *Bw*, and that *Bw* was independent of *F* from linkage group I (Iezzoni and Peterson, 1980).

Robinson (1978c, 1978d) and Youngner (1952) found that linkages existed between *m*, *l*, *n*, *pr*, and spine number (*s?*), with the possibility of pleiotropy being responsible for the *m/pr* relationship. They also demonstrated that *B*, *yg*, and *pm?* were independent of the same genes (Robinson, 1978c; Youngner, 1952).

Rounding out the linkage group is one of the male sterility genes (*ms?*). Robinson (1978d) found that it was linked with both *m* and *l*, but did not identify which male-sterile gene it was.



### Linkage group III

Group III is the oldest and most mystifying linkage group. It is currently composed of *R* for red or orange mature fruit color, *H* for heavy netting, *B* for black or brown spine color, *c* for cream mature fruit color, and *s* for spine frequency and size (Hutchins, 1940; Poole, 1944; Strong, 1931; Tkachenko, 1935). However, there is speculation on the nature of this linkage group. Since very few recombinants of the *R*, *H*, *B*, and *c*, *h*, *b* linkage groups have been reported, we also believe that these characteristics may be the response of two alleles at a single pleiotropic gene. There is also speculation that *R* and *c* are different alleles located at the same locus (see earlier discussion).

Hutchins (1940) found that *s* was independent of *B* and *H*, while *s* was linked with *R* and *c*. If he was correct, then pleiotropy of *H* and *B* with *R* and *c* is ruled out. His report also indicated that *B* and *s* were independent of *de*, as was *de* of *R*, *c*, and *H*.

A possibility exists that this linkage group may be a continuation of group II through the *s* gene. Poole (1944) used the data of Hutchins (1940) to determine that *c* and *s* are linked with a recombination frequency of  $0.163 \pm 0.065$ . The question that remains is whether *s* (Hutchins, 1940; Poole, 1944) is the same as the gene for spine number in the findings of Robinson (1978c). If Cowen and Helsel (1983) are correct in their finding that a linkage exists between *F* and *B*, then groups I and III may be on the same chromosome. However, in this text they will remain separated based on conclusions of Fanourakis (1984), who indicated that errors may be common when attempting to distinguish linkages with *F* because classification of *F* is difficult. This difficulty may also explain many conflicting reports.

### Linkage group IV

Twelve genes (*ns*, *ss*, *Tu*, *Pc*, *D*, *U*, *te*, *cp*, *dm*, *Ar*, *cca*, and *pm?* or *pm-h*) are in group IV, but the identity of the specific gene for powdery mildew resistance is elusive. Van Vliet and Meysing (1947, 1977) demonstrated that the gene for resistance to downy mildew (*dm*) was either linked or identical with a gene for resistance to powdery mildew (*pm?*), but because the linkage between *pm?* and *D* was broken while that of *dm* and *D* was not, *pm?* and *dm* must be separate genes. The problem lies in the lack of identity of *pm?*, because Kooistra (1971) also found that a gene for powdery mildew resistance (*pm?*) was linked to *D*.

Further complicating the identity of *pm*, Fanourakis (1984) found that *pm-h* was linked to *te* and *dm*, yet *cp*, which must be located at about the same locus, was independent of *te*. He suggested that there were either two linkage groups, *ns*, *ss*, *Tu*, *Pc*, *D*, *U*, *te* and *cp*, *dm*, *Ar*, located at distal ends of the same chromosome with *pm-h* at the center, or the two groups are located on different chromosomes with a translocation being responsible for apparent cross-linkages. However, evidence for the latter, which suggested that

*F* was associated with the seven-gene segment, is not probable because there are few other supportive linkages between genes of this segment and linkage group I. A more likely explanation is the occurrence of two or more genes conditioning resistance to powdery mildew being found on this chromosome.

More recently, Lane and Munger (1985) and Munger and Lane (1987) determined that a gene for resistance to powdery mildew (*pm?*) was also linked with *cca* for susceptibility to target leaf spot, but that linkage, although fairly tight, was breakable.

The last four genes in this group are *Tu*, *D*, *te*, and *u* (Strong, 1931). Until recently, it was believed that each in the recessive form was pleiotropic and consistent with European-type cucumbers and each in the dominant form was pleiotropic and consistent with American-type cucumbers. Fanourakis (1984) and Fanourakis and Simon (1987) reported that crossing over ( $R = 23.7$ ) occurred between *te* and the other three genes that still appeared to be associated. However, using triple backcrosses, they demonstrated that there is a definite order for *Tu*, *D*, and *u* within their chromosome segment and that the *Tu* end is associated with the *ns* and *ss* end.

### Linkage group V

Group V is currently composed of three genes—*lh*, *sp*, and *ul*. The gene *sp* was strongly linked with *lh* and weakly linked with *ul* (Zijlstra and den Nijs, 1986). However, Zijlstra and den Nijs (1986) expressed concern for the accuracy of the *sp* and *ul* linkage data because it was difficult to distinguish *ul* under their growing conditions.

### Linkage group VI

Group VI is comprised of two genes (*Fl* and *Ccu*) that appear to be tightly associated. Wilson (1968) concluded that pleiotropy existed between scab resistance and fruit length because backcrossing scab resistance into commercial cultivars consistently resulted in reduced fruit length. However, Munger and Wilkinson (1975) were able to break this linkage, producing cultivars with scab resistance and longer fruit ('Tablegreen 65', 'Tablegreen 66', 'Marketmore 70', and 'Poinsett 76'). Now, when these cultivars are used to introduce scab resistance, long fruit length is consistently associated.

### Unaffiliated genes

Independent assortment data are as important in developing linkage maps as direct linkage data and several researchers have made additional contributions in this area. One of the most extensive studies, based on the number of genes involved, is by Fanourakis (1984). He indicated that *Ar* was independent of *df*, *F*, *ns*, *B*, *u*, *mc*, *pm*, *Tu*, and *D*; *dm* was independent of *bi*, *df*, *F*, *ns*, *ss*, *B*, *te*, *u*, *mc*, *Tu*, and *D*; *bi* was independent of *cp*, *df*, *B*, *pm-h*, *te*, *u*, *mc*, and *Tu*; *cp* was independent of *df*, *F*, *ns*, *ss*, *te*, *u*, and *D*; *F* was independent of *sf*, *b*, *pm-h*, *te*, *u*, *mc*, *Tu*, and *D*; *df* was independent of *te*, *u*, *Tu*, and *D*; *ns* was independent of *B*, *pm-h*, and *mc*; *ss* was independent of *B* and *mc*; and *B* was independent of *pm-h*, *te*, *u*, *Tu*, and *D*.

Two other extensive studies indicated that *yc-2* was not linked with *rc*, *yc-1*, *de*, *bi*, *cr*, *glb*, *gl*, and *m* (Whelan et al., 1975), and both *Ccu* and *Bw* were independent of *bi*, *gl*, *glb*, *ls*, *rc*, *sc*, *cr*, *mc*, *gy-1*, and *gy-2* (Abul-Hayja et al., 1975). Meanwhile, white immature fruit color (*w*) was inherited independently of black spines (*B*) and locule number (*l*) (Cochran, 1938; Youngner, 1952).

Whelan (1973) found that light-sensitive (*ls*) was not linked with nonbitter (*bi?*), but did not indicate which bitter gene he used. Zijlstra (1987) also determined that *bi* was independent of *cp*, *gl* was independent of *lh*, and *ccu* was independent of *lh*, *ro*, and *cp*.

Powdery mildew has been the subject of several linkage studies. Robinson (1978e) indicated that resistance in 'Ashley', which contains three recessive factors, was independent of *B*, *l*, *pr*, *yg*, *fa*, *s*, and *H*. Kooistra (1971) found that powdery mildew resistance was not linked with *yf* or *wf*, and Barham (1953) determined that the resistance genes in USDA PI 173889 were independent of *Bt*.

Similar to linkage data, independent assortment data may be very valuable in developing gene maps, but care must be taken when using the data. For example, resistance to powdery mildew was demonstrated in the previous paragraph, but none of the researchers were able to identify the particular gene involved.

### CONCLUSIONS

The goal of this review was to show specific areas where research could provide a clearer understanding of the cucumber linkage map as well as to encourage the collection of linkage data. The potential for attracting additional research efforts in the areas of biotechnology and genetic engineering for work with cucumber will be increased once a linkage map has been developed.

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