

Gene List 2005 for Cucumber

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This is the latest version of the gene list for cucumber (*Cucumis sativus* L.). In addition to morphological and resistance genes, this list includes genes that have been cloned from different plant tissues of cucumber. The genes in the list have been grouped into ten categories as follows: seedling markers, stem mutants, leaf mutants, flower mutants, fruit type mutants, fruit color mutants, resistance genes (mostly to diseases), protein (isozyme) variants, DNA (RFLPs and RAPDs) markers (Table 1), and cloned genes (Table 2). There is also a review of linkage of the morphological and resistance genes. Complete lists and updates of genes for have been published previously, as follows:

Previous Lists

- Robinson et al., 1976
- Robinson et al., 1982
- Pierce and Wehner, 1989
- Wehner, 1993
- Wehner and Staub, 1997
- Xie and Wehner, 2001

Revisions to the 2005 cucumber gene list include the addition of *Psm* for paternal sorting of mitochondria (Havey et al., 2004).

Researchers are encouraged to send reports of new genes, as well as seed samples to the cucumber gene curator (Nischit V. Shetty), or to the assistant curator (Todd C. Wehner). Please inform us of omissions or errors in the gene list. Scientists should consult the list as well as the rules of gene nomenclature for the Cucurbitaceae (Robinson et al., 1976; Robinson et al., 1982) before choosing a gene name and symbol. That will avoid duplication of gene names and symbols. The rules of gene nomenclature were adopted in order to provide guidelines for

naming and symbolizing genes. Scientists are urged to contact members of the gene list committee regarding rules and gene symbols.

Gene Mutants

Seedling Mutants

One of the advantages of using the cucumber in genetic research is the availability of seedling markers. To date, five non-lethal color mutants [virescent (*v*) (Poole, 1944; Tkachenko, 1935), variegated virescence (*vvi*) (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 4 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 which affect traits other than color include bitterfree (*bi*) (Andeweg, 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*) (Shanmugasundarum and Williams, 1971; Shanmugasundarum et al., 1972).

Stem Mutants

Seven genes have been identified which 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 confirmation, 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 which tightly clasp the corolla, 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 which affect color or anatomical features of the foliage are golden leaves (*g*) (Tkachenko, 1935), glabrous (*gl*) (Inggamer and de Ponti, 1980; Robinson and Mishanec, 1964), glabrate (*glb*) (Whelan, 1973), short petiole (*sp*) (den Nijs and Boukema, 1985) and tendriless (*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, 1969; Rosa, 1928; Shifriss, 1961; Tkachenko, 1935; Wall, 1967). Androecious plants are produced if *aa* and *ff* occur in combination, otherwise plants are hermaphroditic if *mm FF*, andromonoecious if *mm ff*, gynoeceous if *MM FF* and monoecious if *MM ff*. 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 gynoeceous (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 which may give the impression of eliciting daylength sensitivity by causing a delay in flowering is *Fba*. In reality, *Fba* triggers flower bud abortion prior to 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 which Fujieda et al. (1982) later labeled as *pf* for plural pistillate flowering. However, they indicated that 3 different alleles were responsible, with single pistillate being incompletely dominant over multiple pistillate: *pf*⁺ for single pistillate, *pf*^d for double pistillate and *pf*^m for multiple pistillate (more than 2 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 gynoecious 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 abortion before anthesis; *ms-1* plants are also partially female sterile (Robinson and Mishanec, 1965; Shanmugasundaram and Williams, 1971; Whelan, 1972a). Apetalous mutants (*ap*) on the other hand have infertile anthers which appear to have been transformed into sepal-like structures (Grimbly, 1980). Ginko (*gi*), mentioned earlier as a leaf mutant, also causes male sterility (John and Wilson, 1952).

One of 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*), negative geotropic peduncle response (*n*) (Odland and Groff (64). 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 which increases the prominence of the tubercles (Tkachenko, 1935).

There are 3 genes which affect internal fruit quality, each identified by viewing transections of fruits; Empty chambers-1 (*Es-1*), Empty chambers-2 (*Es-2*) and locule number (*l*) (Youngner, 1952).

Hutchins (1940) proposed that 2 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 2 separate genes involved, and named them *ss* and *ns* for small spines and numerous spines, respectively.

These may differ from those that led Carruth (1975) to conclude that 2 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 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 European 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 3 major isomeric genes with additive action.

A modifier of fruit length, *Fl*, was identified by its linkage with scab resistance (*Cca*) (Henry Munger, personal communication; Wilson, 1968). Expressed in an additive

fashion, fruit length decreases incrementally from heterozygote to homozygote (*fl fl*).

Fruit Color

Twelve mutants have been identified which 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 which are (*RR CC*), (*RR cc*), (*rr CC*) and (*rr cc*) 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*) (Andeweg, 1956; Strong, 1931).

Kooistra (1971) reported 2 genes that affect fruit mesocarp color. White flesh (*wf*) and yellow flesh (*yf*) gene loci interact to produce either white (*WfWf YfYf* or *wfwf YfYf*), yellow (*WfWf yfyf*), or orange (*wfwf yfyf*) flesh color.

Insect Resistance

Bitterfree, *bi*, is responsible for resistance to spotted and banded cucumber beetles (*Diabrotica* spp.) (Chambliss, 1978; Da Costa & Jones, 1971a; Da Costa & Jones, 1971b) and two-spotted spider mites (*Tetranychus urticae* Koch.) (Da Costa &

Jones, 1971a; Soans et al., 1973). However, this gene works inversely for the 2 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 the authors labeled the gene for resistance to *Diabrotica* spp. *di*, but wish to retract it in light of recent evidence.

Disease Resistance

Currently 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 (Provvidenti, 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; Andeweg, 1956; Bailey and Burgess, 1934) and *Bw* (Nuttall and Jasmin, 1958; Robinson and Whitaker, 1974), respectively. Other dominant genes providing resistance are: *Cca* for resistance to target leaf spot (*Corynespora cassiicola*) (Abul-Hayja et al., 1978), *Cm* for resistance to *Corynespora* blight (*Corynespora melonis*) (Shanmugasundarum 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 (Hujieda and Akiya, 1962; Kooistra, 1968; Shanmugasundarum et al., 1971b). The resistance genes *pm-1* and *pm-2* were first reported by Hujieda and Akiya (1962) in a cultivar which 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 PI200815 and PI200818. Shimizu et al. (1963) also supported 3 recessive genes which are responsible for resistance of 'Aojihai' over 'Sagamihan'.

Several genes with specific effects have been identified more recently (Shanmugasundarum 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 Shanmugasundarum 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*.

Currently, one gene, *dm*, has been identified which 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

Presently, only 2 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).

Other Traits

The dominant allele, *Psm*, induces paternal sorting of mitochondria, where *Psm* is from MSC 16 and *psm* is from PI 401734 (Havey et al., 2004).

Molecular and Protein Markers

Isozyme variant nomenclature for this gene list follows the form according to Staub et al. (Staub et al., 1985), such that loci coding for enzymes (e.g. glutamine dehydrogenase, G2DH) are designated as abbreviations, where the first letter is capitalized (e.g. G2dh). If an enzyme system is conditioned by multiple loci, then those are designated by hyphenated numbers, which are numbered from most cathodal to most anodal and enclosed in parentheses. The most common allele of any particular isozyme is designated 100, and all other alleles for that enzyme are assigned a value based on their mobility relative to that allele. For example, an allele at locus 1 of FDP (fructose diphosphatase) which has a mobility 4 mm less that of the most common allele would be assigned the designation *Fdp(1)*-96.

RFLP marker loci were identified as a result of digestion of cucumber DNA with *DraI*, *EcoRI*, *EcoRV*, or *HindIII* (Kennard et al., 1994). Partial-genomic libraries were constructed using either *PstI*-digested DNA from the cultivar Sable and from *EcoRV*-digested DNA from the inbred WI 2757. Derived clones were hybridized to genomic DNA and banding patterns were described for mapped and unlinked loci (CsC482/H3, CsP314/E1, and CsP344/E1, CsC477/H3, CsP300/E1).

Clones are designated herein as CsC = cDNA, CsP = *PstI*-genomic, and CsE = *EcoRI*-genomic. Lower-case a or b represent two independently-segregating loci detected with one probe. Lower-case s denotes the slowest fragment digested out of the vector. Restriction enzymes designated as DI, *DraI*; EI, *EcoRI*; E5, *EcoRV*; and H3, *HindIII*. Thus, a probe identified as CsC336b/E5 is derived from a cDNA library (from 'Sable') which was restricted using the enzyme *EcoRV* to produce a clone designated as 336 which displayed two independently segregating loci one of which is b. Clones are available in limited supply from Jack E. Staub.

RAPD marker loci were identified using primer sequences from Operon Technologies (OP; Alameda, California, U.S.A.) and the University of British Columbia (Vancouver, BC, Canada). Loci are identified by sequence origin (OP or BC), primer group letter (e.g., A), primer group array number (1-20), and locus (a, b, c, etc.) (Kennard et al., 1994). Information regarding unlinked loci can be obtained from Jack E. Staub.

Because of their abundance, common source (two mapping populations), and the accessibility of published information on their development (Kennard et al., 1994) DNA marker loci are not included in Table 1, but are listed below.

The 60 RFLP marker loci from mapping cross Gy 14 x PI 183967 (Kennard et al., 1994):

CsP129/E1,	CsC032a/E1,	
CsP064/E1,	CsP357/H3,	CsC386/E1,
CsC365/E1,	CsP046/E1,	CsP347/H3,
CsC694/E5,	CsC588/H3,	CsC230/E1,
CsC593/D1,	CsP193/H3,	CsP078s/H3,
CsC581/E5,	CsE084/E1,	CsC341/H3,
CsP024/E1,	CsP287/H3,	CsC629/H3,
CsP225s/E1,	CsP303/H3,	CsE051/H3,
CsC366a/E5,	CsC032b/E1,	CsP056/H3,
CsC378/E1,	CsP406/E1,	CsP460/E1,
CsE060/E1,	CsE103/E1,	CsP019/E1,
CsP168/D1,	CsC560/H3,	CsP005/E1,

CsP440s/E1, CsP221/H3, CsC625/E1,
 CsP475s/E1, CsP211/E1, CsP215/H3,
 CsC613/E1, CsC029/H3, CsP130/E1,
 CsC443/H3, CsE120/H3, CsE031/H3,
 CsC366b/E5, CsC082/H13, CsP094/H3,
 CsC362/E1, CsP441/E1, CsP280/H3,
 CsC137/H3, CsC558/H3, CsP037a/E1,
 CsP476/H3, CsP308/E1, CsP105/E1, and
 Csc166/E1.

The 31 RFLP marker loci from mapping cross Gy 14 x PI 432860 (Kennard et al., 1994): CsC560/D1, CsP024/E5, CsP287/H3, CsC384/E5, CsC366/E5, CsC611/D1, CsP055/D1, CsC482/H3, CsP019/E1, CsP059/D1, CsP471s/H13, CsC332/E5, CsP056/H3, CsC308/E5, CsP073/E5, CsP215/H3, CsC613/D1, CsP266/D1, CsC443/H3, CsE031/E1, CsE120/H3, CsE063/E1, CsP444/E1, CsC612/D1, Cs362/E1, CsP280/H3, CsC558/H3, CsP008/D1, CsP308/E1, CsC166/E1, and CsP303/H3.

The 20 RAPD marker loci from mapping cross Gy 14 x PI 432860 (Kennard et al., 1994): OPR04, OPW16, OPS17, OPE13a, OPN06, OPN12, OPP18b, BC211b, OPN04, OPA10, OPE09, OPT18, OPA14b, OPU20, BC460a, OPAB06, OPAB05, OPH12, OPA14a, and BC211a.

In addition to the isozymes, RFLPs and RAPDs, nearly 100 cloned genes are listed here (Table 2).

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 is the two-locus model (*R c*) for fruit color. We have been unable

to locate any plants with red or yellow colored mature fruits. All plants evaluated in other studies have color inherited as a single gene. Hutchins may have separated fruit with cream color into 2 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 like 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. Currently, 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*, *vvi*, *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* leafspot. Mary 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* leafspot (Henry Munger, personal communication).

Genetic Linkage

Since cucumber has just 7 chromosome pairs and over 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 2 gene loci, and this is the first review to 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 since common parents were not compared. This problem was discussed in the previous section. Secondly, 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 which has 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 A

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* ($rf=.215\pm.029$) and *de* ($rf=.335\pm.042$) 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* ($rf=.04$) (Kubicki, 1974), *bi* ($rf=.375$) and *df* ($rf=34.7$) (Fanourakis, 1984; Fanourakis 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 *Ccu*, *B*, *F* or *pm?* (Wang et al., 1987).

Two reports show that *dvl* is weakly linked with *gl* ($rf=.40$) 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 B

Group II is composed of 9 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 7, two pairs have been defined with

recombination values. Youngner (1952) determined that *m* and *l* were linked with a recombination frequency of $.326 \pm .014$ 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 ($rf=.011 \pm .003$). Iezzoni et al. (1982) 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 C

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, it is also felt that these characteristics may be the response of 2 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 $.163 \pm .065$. 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) which indicate that errors may be common when attempting to distinguish linkages with *F* since classification of *F* is difficult. This difficulty may also explain many conflicting reports.

Linkage Group D

Twelve genes (*ns*, *ss*, *Tu*, *Pc*, *D*, *U*, *te*, *cp*, *dm*, *Ar*, *coca* 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 approximately the same locus, was independent of *te*. He suggested that there were either 2 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 2 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 7-gene segment is not probable since there are few other supportive linkages between genes of this segment and linkage group I. A more likely explanation is the occurrence of 2 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 *coca* for susceptibility to target leaf spot but that linkage, though fairly tight, was breakable.

The last 4 genes in this group are *Tu*, *D*, *te* and *u* (Strong, 1931). Until recently it was believed that each in the recessive form were pleiotropic and consistent with European type cucumbers and each in the dominant form were 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 3 genes which 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 E

Group V is currently composed of 3 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 since it was difficult to distinguish *ul* under their growing conditions.

Linkage Group F

Group VI is comprised of 2 genes, *Fl* and *Ccu* which appear to be tightly associated. Wilson (1968) concluded that pleiotropy existed between scab resistance and fruit length because backcrossing scab resistance into commercial varieties consistently resulted in reduced fruit length. However, Munger and Wilkinson (1975) were able to break this linkage producing varieties with scab resistance and longer fruit (Tablegreen 65 and 66, Marketmore 70 and Poinsett 76). Now when these varieties 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*, *Tu*, 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* is 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* is independent of *lh* and *ccu* is 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 3 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*.

Like linkage data, independent assortment data may be very valuable in developing gene maps, but care must be taken when utilizing them. 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.

Table 1. The non-molecular genes of cucumber.

Gene	Synonym	Character	References ^z	Supplemental references ^z	Available ^y
<i>a</i>	-	<i>androecious</i> . Produces primarily staminate flowers if recessive for <i>F</i> . <i>A</i> from MSU 713-5 and Gy 14; <i>a</i> from An-11 and An-314, two selections from 'E-e-szan' of China.	Kubicki, 1969		P
<i>Ak-2</i>	-	<i>Adenylate kinase</i> (E.C.# 2.7.4.3). Isozyme variant found segregating in PI 339247, and 271754; 2 alleles observed.	Meglic and Staub, 1996		P
<i>Ak-3</i>	-	<i>Adenylate kinase</i> (E.C.# 2.7.4.3). Isozyme variant found segregating in PI 113334, 183967, and 285603; 2 alleles observed.	Meglic and Staub, 1996		P
<i>al</i>	-	<i>albino cotyledons</i> . White cotyledons and slightly light green hypocotyl; dying before first true leaf stage. Wild type Al from 'Nishiki-suyo'; <i>al</i> from M ₂ line from pollen irradiation.	Iida and Amano, 1990, 1991		?
<i>ap</i>	-	<i>apetalous</i> . Male-sterile. Anthers become sepal-like. <i>Ap</i> from 'Butcher's Disease Resisting'; <i>ap</i> from 'Butcher's Disease Resisting Mutant'.	Grimbly, 1980		L
<i>Ar</i>	-	<i>Anthracnose 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 with <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	Andeweg and	Cantliffe, 1972;	W

		cucurbitacins. Plants with <i>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.	DeBruyn, 1959	Da Costa and Jones, 1971a, 1971b; Soans et al., 1973	
<i>bi-2</i>		<i>bitterfree-2</i> . Leaves lacking cucurbitacins; <i>bi-2</i> from NCG-093 (short petiole mutant).	Wehner et al., 1998a		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</i> leaf. 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>by</i>	<i>bu</i>	<i>bushy</i> . Short internodes; normal seed viability. Wild type <i>By</i> from 'Borszczagowski'; <i>by</i> from induced mutation of 'Borszczagowski'. Linked with <i>F</i> and <i>gy</i> , not with <i>B</i> or <i>bi</i> .	Kubicki et al., 1986a		?
<i>c</i>	-	<i>cream mature fruit color</i> . Interaction with <i>R</i> is evident in the F ₂ ratio of 9 red (<i>RC</i>) : 3 orange (<i>Rc</i>) : 3 yellow (<i>rC</i>) : 1 cream (<i>rc</i>).	Hutchins, 1940		L
<i>Cca</i>	-	<i>Corynespora cassiicola</i> resistance. Resistance to target leaf spot; dominant to susceptibility. <i>Cca</i> from Royal Sluis Hybrid 72502; <i>cca</i> from Gy 3.	Abul-Hayja et al., 1975		W
<i>Ccu</i>	-	<i>Cladosporium cucumerinum</i> resistance. 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 a light green; lethal unless grafted. <i>cd</i> from a mutant selection of backcross of MSU 713-5 x 'Midget' F1 to 'Midget'.	Burnham, et al., 1966		L
<i>chp</i>	-	<i>choripetalous</i> . Small first true leaf; choripetalous flowers; glossy ovary; small fruits; few seeds. Wild type <i>Chp</i> from 'Borszczagowski'; <i>chp</i> from chemically induced mutation.	Kubicki and Korzeniewska, 1984		?
<i>cl</i>	-	<i>closed flower</i> . Staminate and pistillate flowers do not open; male-sterile (nonfertile pollen).	Groff and Odland, 1963		W
<i>cla</i>	-	<i>Colletotrichum lagenarium</i> resistance. Resistance to race 1 of anthracnose; recessive to susceptibility. <i>Cla</i> from Wis. SMR 18; <i>cla</i> from SC 19B.	Abul-Hayja et al., 1978		W
<i>Cm</i>	-	<i>Corynespora melonis</i> resistance. Resistance to <i>C. melonis</i> dominant to susceptibility. <i>Cm</i> from 'Spotvrie'; <i>cm</i> from 'Esvier'.	van Es, 1958		?
<i>Cmv</i>	-	<i>Cucumber mosaic virus</i> resistance. 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. SR 6'.	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
<i>cp-2</i>	-	<i>compact-2</i> . Short internodes; small seeds; similar to <i>cp</i> , but allelism not checked. Wild type <i>Cp-2</i> from 'Borszczagowski'; <i>cp-2</i> from induced mutation of 'Borszczagowski' called W97. Not linked with <i>B</i> or <i>F</i> ; interacts with <i>by</i> to produce super dwarf.	Kubicki et al., 1986b		?
<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.	Caruth, 1975; Pike and Caruth, 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; Tkachenko, 1935		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 ₂ -1 (and inbred selection from Line 541)**.	Denna, 1971*; George, 1970**; Hutchins, 1940	Nuttall and Jasmin, 1958	W
<i>de-2</i>	-	<i>determinate-2</i> . Main stem growth ceases after 3 to 10 nodes, producing flowers at the apex; smooth, fragile, dark-green leaves; similar to <i>de</i> , but not checked for allelism. Wild type <i>De-2</i> from 'Borszczagowski'; <i>de-2</i> from W-sk mutant induced by ethylene-imine from 'Borszczagowski'.	Soltysiak et al., 1986		?
<i>df</i>	-	<i>delayed flowering</i> . Flowering delayed by long photoperiod; associated with dormancy. <i>df</i> from 'Baroda' (PI 212896)* and PI 215589 (<i>hardwickii</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>dm-1</i>	<i>dm</i>	<i>downy mildew resistance-1</i> . One of three genes for resistance to downy mildew caused by <i>Pseudoperonospora cubensis</i> (Berk &	Doruchowski and Lakowska-Ryk, 1992		?

		Curt). Wild type <i>Dm-1</i> from Wisconsin SMR 18; <i>dm-1</i> from WI 4783. Not checked for allelism with <i>dm</i> .			
<i>dm-2</i>	-	<i>downy mildew resistance-2</i> . One of three genes for resistance to downy mildew caused by <i>Pseudoperonospora cubensis</i> (Berk & Curt). Wild type <i>Dm-2</i> from Wisconsin SMR 18; <i>dm-2</i> from WI 4783. Not checked for allelism with <i>dm</i> .	Doruchowski and Lakowska-Ryk, 1992		?
<i>dm-3</i>	-	<i>downy mildew resistance-3</i> . One of three genes for resistance to downy mildew caused by <i>Pseudoperonospora cubensis</i> (Berk & Curt). Wild type <i>Dm-3</i> from Wisconsin SMR 18; <i>dm-3</i> from WI 4783. Not checked for allelism with <i>dm</i> .	Doruchowski and Lakowska-Ryk, 1992		?
<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>dvl-2</i>	<i>dl-2</i>	<i>divided leaf-2</i> . Divided leaves after the 2nd true leaf; flower petals free; similar to <i>dvl</i> , but allelism not checked. Wild type <i>Dvl-2</i> from 'Borszczagowski'; <i>dvl-2</i> from mutant induced by ethylene-imine from 'Borszczagowski'.	Rucinska et al., 1992b		?
<i>dw</i>	-	<i>dwarf</i> . Short internodes. <i>dw</i> from an induced mutant of 'Lemon'.	Robinson and Mishanec, 1965		?
<i>dwc-1</i>	-	<i>dwarf cotyledons-1</i> . Small cotyledons; late germination; small first true leaf; died after 3rd true leaf. Wild type <i>Dwc-1</i> from 'Nishiki Suyo'; <i>dwc-1</i> from M ₂ line from pollen irradiation.	Iida and Amano, 1990, 1991		?
<i>dwc-2</i>	-	<i>dwarf cotyledons-2</i> . Small cotyledons; late germination; small first true leaf. Wild type <i>Dwc-2</i> from 'Nishiki Suyo'; <i>dwc-2</i> from M ₂ line from pollen irradiation.	Iida and Amano, 1990, 1991		?
<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^F</i> , <i>D</i> , <i>st</i>	<i>Female</i> . High degree of pistillate 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, 1987b*; 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>Fdp-1</i>	-	<i>Fructose diphosphatase</i> (E.C.# 3.1.3.11). Isozyme variant found segregating in PI 192940, 169383 and 169398; 2 alleles observed.	Meglic and Staub, 1996		P
<i>Fdp-2</i>	-	<i>Fructose diphosphatase</i> (E.C.# 3.1.3.11). Isozyme variant found segregating in PI 137851, 164952, 113334 and 192940; 2 alleles	Meglic and Staub, 1996		P

		observed.			
<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>Fcu-1</i>	<i>Fusarium oxysporum f. sp. cucumerinum resistance</i> . Resistance to fusarium wilt races 1 and 2; dominant to susceptibility. <i>Foc</i> from WIS 248; <i>foc</i> from 'Shimshon'.	Netzer et al., 1977; Vakalounakis, 1993, 1995, 1996		W
<i>G2dh</i>	-	<i>Glutamine dehydrogenase</i> (E.C.# 1.1.1.29). Isozyme variant found segregating in PI 285606; 5 alleles observed.	Knerr and Staub, 1992		P
<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		?
<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>ginkgo</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 backcrosses involving 'National Pickling', 'Chinese Long', 'Tokyo Long Green', 'Vickery', 'Early Russian', 'Ohio 31' and an unnamed white spine slicer.	John and Wilson, 1952		L
<i>gi-2</i>	-	<i>ginkgo-2</i> . Spatulate leaf blade with reduced lobing and altered veins; recognizable at the 2nd true leaf stage; similar to <i>gi</i> , fertile instead of sterile. Wild type <i>Gi-2</i> from 'Borszczagowski'; <i>gi-2</i> from mutant in the Kubicki collection.	Rucinska et al., 1992b		?
<i>gig</i>	-	<i>gigantism</i> . First leaf larger than normal. Wild type <i>Gig</i> from 'Borszczagowski'; <i>gig</i> from chemically induced mutation.	Kubicki et al., 1984		?
<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>gn</i>	-	<i>green mature fruit</i> . Green mature fruits when <i>rr gngn</i> ; cream colored when <i>rr GnGn</i> ; orange when <i>R_ _</i> . Wild type <i>Gn</i> from 'Chipper', SMR 58 and PI 165509; <i>gn</i> from TAMU 830397.	Peterson and Pike, 1992		W
<i>Gpi-1</i>	-	<i>Glucose phosphate isomerase</i> (E.C.# 5.3.1.9). Isozyme variant found segregating (1 and 2) in PI 176524, 200815, 249561, 422192, 432854, 436608; 3 alleles observed.	Knerr and Staub, 1992		P
<i>Gr-1</i>	-	<i>Glutathione reductase-1</i> (E.C.# 1.6.4.2). Isozyme variant found segregating in PI 109275; 5 alleles observed.	Knerr and Staub, 1992		P
<i>gy</i>	-	<i>gynoecious</i> . Recessive gene for high degree of pistillate sex expression.	Kubicki, 1974		W
<i>H</i>	-	<i>Heavy netting of fruit</i> . Dominant to no netting and completely linked or pleiotropic with	Hutchins, 1940; Tkachenko, 1935		W

<i>hl</i>	-	black spines (<i>B</i>) and red mature fruit color (<i>R</i>). <i>heart leaf</i> . Heart shaped leaves. Wild type <i>Hl</i> from Wisconsin SMR 18; <i>hl</i> from WI 2757. Linked with <i>ns</i> and <i>ss</i> in the linkage group with <i>Tu-u-D-pm</i> .	Vakalounakis, 1992	W	
<i>hn</i>	-	<i>horn like cotyledons</i> . Cotyledons shaped like bull horns; true leaves with round shape rather than normal lobes; circular rather than ribbed stem cross section; divided petals; spineless fruits; pollen fertile, but seed sterile. Wild type <i>Hn</i> from 'Nishiki-suyo'; <i>hn</i> from M ₂ line from pollen irradiation.	Iida and Amano, 1990, 1991	?	
<i>hsl</i>	-	<i>heart shaped leaves</i> . Leaves heart shaped rather than lobed; tendrils branched. Wild type <i>Hsl</i> from 'Nishiki-suyo'; <i>hsl</i> from M ₂ line from pollen irradiation.	Iida and Amano, 1990, 1991	?	
<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>Idh</i>	-	<i>Isocitrate dehydrogenase</i> (E.C.# 1.1.1.42). Isozyme variant found segregating in PI 183967, 215589; 2 alleles observed.	Knerr and Staub, 1992	P	
<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 (S ₅ -1 and S ₅ -6, respectively) from a determinant inbred S ₂ -1, 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 pistillate 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>lg-1</i>	-	<i>light green cotyledons-1</i> . Light green cotyledons, turning dark green; light green true leaves, turning dark green; poorly developed stamens. Wild type <i>Lg-1</i> from 'Nishiki-suyo'; <i>lg-1</i> from M ₂ line from pollen irradiation.	Iida and Amano, 1990, 1991	?	
<i>lg-2</i>	-	<i>light green cotyledons-2</i> . Light green cotyledons, turning dark green (faster than <i>lg-1</i>); light green true leaves, turning dark green; normal stamens. Wild type <i>Lg-2</i> from 'Nishiki-suyo'; <i>lg-2</i> from M ₂ line from pollen irradiation.	Iida and Amano, 1990, 1991	?	
<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 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>ls</i>	<i>gc</i>	<i>light sensitive</i> . Yellow cotyledons, lethal in high light. Abstract gave <i>gc</i> as symbol; article that followed gave <i>ls</i> as symbol. Mutant <i>ls</i> from a selection of 'Burpless Hybrid'.	Whelan, 1971, 1972	?	
<i>m</i>	<i>a, g</i>	<i>andromonoecious</i> . Plants are andromonoecious if (<i>mf</i>); monoecious if (<i>Mf</i>); gynoeceous if (<i>MF</i>) and hermaphroditic if (<i>mF</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>Mdh-1</i>	-	<i>Malate dehydrogenase-1</i> (E.C.# 1.1.1.37). Isozyme variant found segregating in PI 171613, 209064, 326594; 3 alleles observed.	Knerr and Staub, 1992		P
<i>Mdh-2</i>	-	<i>Malate dehydrogenase-2</i> (E.C.# 1.1.1.37). Isozyme variant found segregating in PI 174164, 185690, 357835, 419214; 2 alleles observed.	Knerr and Staub, 1992		P
<i>Mdh-3</i>	-	<i>Malate dehydrogenase-3</i> (E.C.# 1.1.1.37).	Knerr et al., 1995		P
<i>Mdh-4</i>	<i>Mdh-3</i>	<i>Malate dehydrogenase-4</i> (E.C.# 1.1.1.37). Isozyme variant found segregating in PI 255236, 267942, 432854, 432887; 2 alleles observed.	Knerr and Staub, 1992		P
<i>mj</i>		A single recessive gene for resistance to the root-knot nematode (<i>Meloidogyne javanica</i>) from <i>Cucumis sativus</i> var. <i>hardwickii</i> ; <i>mj</i> from NC-42 (LJ 90430).	Walters et al., 1996; 1997	Walters and Wehner, 1998	W
<i>mp</i>	<i>pf</i> ⁺ , <i>pf</i> ^{dt} , <i>pf</i> ^p	<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.	Nandgaonkar 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>Mpi-1</i>	-	<i>Mannose phosphate isomerase</i> (E.C.# 5.3.1.8). Isozyme variant found segregating in PI 176954, and 249562; 2 alleles observed.	Meglic and Staub, 1996		P
<i>Mpi-2</i>	-	<i>Mannose phosphate isomerase</i> (E.C.# 5.3.1.8). Isozyme variant found segregating in PI 109275, 175692, 200815, 209064, 263049, 354952; 2 alleles observed.	Knerr and Staub, 1992		P
<i>mpy</i>	<i>mpi</i>	<i>male pygmy</i> . Dwarf plant with only staminate flowers. Wild type <i>Mpy</i> from Wisconsin SMR 12; <i>mpy</i> from Gnome 1, a selection of 'Rochford's Improved'.	Pyzhenkov and Kosareva, 1981		?
<i>ms-1</i>	-	<i>male sterile-1</i> . Staminate flowers abort before anthesis; partially female-sterile. <i>ms-1</i> from selections of '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>ms-2</i> ^(PS)	-	<i>male sterile-2 pollen sterile</i> . Male-sterile; allelic to <i>ms-2</i> , but not to <i>ap</i> . <i>ms-2</i> ^(PS) from a mutant of Sunseeds 23B-X26.	Zhang et al., 1994		?
<i>mwm</i>	-	Moroccan watermelon mosaic virus resistance single recessive gene from Chinese cucumber cultivar 'TMG-1'	Kabelka and Grumet, 1997		W
<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	Robinson, 1987e		W

<i>P</i>	-	incomplete penetrance. <i>opp</i> from 'Lemon'. <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>Parthenocarp</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; Whelan, 1973	de Ponti and Garretsen, 1976	?
<i>Pe</i>	-	<i>Palisade epidermis</i> . Epidermal cells arranged perpendicular to the fruit surface. Wild type <i>Pe</i> from 'Wisconsin SMR 18', 'Spartan Salad' and Gy 2 compact; <i>pe</i> from WI 2757.	Fanourakis and Simon, 1987		W
<i>Pep-gl-1</i>	-	<i>Peptidase with glycyl-leucine</i> (E.C.# 3.4.13.11). Isozyme variant found segregating in PI 113334, 212896; 2 alleles observed.	Meglic and Staub, 1996		P
<i>Pep-gl-2</i>	-	<i>Peptidase with glycyl-leucine</i> (E.C.# 3.4.13.11). Isozyme variant found segregating in PI 137851, 212896; 2 alleles observed.	Meglic and Staub, 1996		P
<i>Pep-la</i>	-	<i>Peptidase with leucyl-leucine</i> (E.C.# 3.4.13.11). Isozyme variant found segregating in PI 169380, 175692, 263049, 289698, 354952; 5 alleles observed.	Knerr and Staub, 1992		P
<i>Pep-pap</i>	-	<i>Peptidase with phenylalanyl-L-proline</i> (E.C.# 3.4.13.11). Isozyme variant found segregating in PI 163213, 188749, 432861; 2 alleles observed.	Knerr and Staub, 1992		P
<i>Per-4</i>	-	<i>Peroxidase</i> (E.C.# 1.11.1.7). Isozyme variant found segregating in PI 215589; 2 alleles observed.	Knerr and Staub, 1992		P
<i>Pgd-1</i>	-	<i>Phosphogluconate dehydrogenase-1</i> (E.C.# 1.1.1.43). Isozyme variant found segregating in PI 169380, 175692, 222782; 2 alleles observed.	Knerr and Staub, 1992		P
<i>Pgd-2</i>	-	<i>Phosphogluconate dehydrogenase-2</i> (E.C.# 1.1.1.43). Isozyme variant found segregating in PI 171613, 177364, 188749, 263049, 285606, 289698, 354952, 419214, 432858; 2 alleles observed.	Knerr and Staub, 1992		P
<i>Pgm-1</i>	-	<i>Phosphoglucomutase</i> (E.C.# 5.4.2.2). Isozyme variant found segregating in PI 171613, 177364, 188749, 263049, 264229, 285606, 289698, 354952; 2 alleles observed.	Knerr and Staub, 1992		P
<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	Shanmugasundarum 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	Shanmugasundarum 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	Shanmugasundarum 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	Fanourakis, 1984; Shanmugasundarum et al., 1971b		W

		susceptibility. <i>Pm-h</i> from 'Wis. SMR 18'; <i>pm-h</i> from 'Gy 2 cp cp', 'Spartan Salad', and Wis. 2757.			
<i>pr</i>	-	<i>protruding ovary</i> . Exerted carpels. <i>pr</i> from 'Lemon'.	Youngner, 1952.		W
<i>prsv</i>	<i>wmv-1-1</i>	<i>watermelon mosaic virus 1 resistance</i> . Resistance to papaya ringspot virus (formerly watermelon mosaic virus 1). Wild type <i>Prsv</i> from WI 2757; <i>prsv</i> from 'Surinam'.	Wang et al., 1984		
<i>Prsv-2</i>		Resistance to papaya ringspot virus; <i>Prsv-2</i> from TMG-1.	Wai and Grumet, 1995	Wai et al., 1997	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 14.	Dessert et al., 1982		W
<i>Psm</i>	-	<i>Paternal sorting of mitochondria</i> . Mitochondria sorting induced by dominant gene <i>Psm</i> , found in MSC 16; <i>psm</i> from PI 401734.	Havey et al., 2004.		W
<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 are short, narrow, and cupped downwards; enlarged perianth. <i>rc</i> from 'Burpless Hybrid' mutant.	Whelan et al., 1975		L
<i>rc-2</i>		recessive gene for revolute cotyledons; <i>rc-2</i> from NCG-0093 (short petiole mutant)	Wehner et al., 1998b		W
<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	Caruth, 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.	Caruth, 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.	Caruth, 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 177362; <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>sh</i>	-	<i>short hypocotyl</i> . Hypocotyl of seedlings 2/3 the length of normal. Wild type <i>Sh</i> from 'Borszczagowski'; <i>sh</i> from khp, an induced mutant from 'Borszczagowski'.	Soltysiak and Kubicki 1988		?

<i>shl</i>	-	<i>shrunk leaves</i> . First and 2nd true leaves smaller than normal; later leaves becoming normal; slow growth; often dying before fruit set. Wild type <i>Shl</i> from 'Nishiki-suyo'; <i>shl</i> from M ₂ line from pollen irradiation.	Iida and Amano, 1990, 1991		?
<i>Skdh</i>	-	<i>Shikimate dehydrogenase</i> (E.C.# 1.1.1.25). Isozyme variant found segregating in PI 302443, 390952, 487424; 2 alleles observed.	Meglic and Staub, 1996		P
<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>sp-2</i>	-	<i>short petiole-2</i> . Leaf petioles shorter, darker green than normal at 2-leaf stage; crinkled leaves with slow development; short hypocotyl and stem; little branching. Not tested for allelism with <i>sp</i> . Wild type <i>Sp-2</i> from 'Borszczagowski'; <i>sp-2</i> from chemically induced mutation.	Rucinska et al., 1992a		?
<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 <i>cp</i> <i>cp</i> '; <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 'Southern Pickler'; <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 staminate, perfect, and pistillate 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 ₂ of 12 white (<i>WfWf YfYf</i> or <i>wfwf YfYf</i>) : 3 yellow (<i>WfWf yfyf</i>) : 1 orange (<i>wfwf yfyf</i>). <i>Wf</i> from EG and G6, each being dingy	Kooistra, 1971		?

<i>wi</i>	-	white (<i>WfWf YfYf</i>): <i>wf</i> from 'NPI' which is orange (<i>wfwf yfyf</i>). <i>wilty leaves</i> . Leaves wilting in the field, but not in shaded greenhouse; weak growth; no fruiting. Wild type <i>Wi</i> from 'Nishiki-suyo'; <i>wi</i> from M ₂ line from pollen irradiation.	Iida and Amano, 1990, 1991		?
<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 'Beit Alpha'.	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	Provvidenti, 1985	?
<i>wmv-2</i>	-	<i>watermelon mosaic virus resistance</i> . Expressed in the cotyledon and throughout the plant; <i>wmv-2</i> from TMG-1.	Wai et al., 1997		W
<i>wmv-3</i>	-	<i>watermelon mosaic virus resistance</i> . Expressed only in true leaves; <i>wmv-3</i> from TMG-1.	Wai et al., 1997		W
<i>wmv-4</i>	-	<i>watermelon mosaic virus resistance</i> . Expressed only in true leaves; <i>wmv-4</i> from TMG-1.	Wai et al., 1997		W
<i>wy</i>	-	<i>wavy rimed cotyledons</i> . Wavy rimed cotyledons, with white centers; true leaves normal. Wild type <i>Wy</i> from 'Nishiki-suyo'; <i>wy</i> from M ₂ line from pollen irradiation.	Iida and Amano, 1990, 1991		?
<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 MR 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 ₂ of 12 white (<i>Wf Yf</i> and <i>wf Yf</i>) : 3 yellow (<i>Wf yf</i>) : 1 orange (<i>wf 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>	<i>gr</i>	<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>ys</i>	-	<i>yellow stem</i> . Yellow cotyledons, becoming cream-colored; cream-colored stem, petiole and leaf veins; short petiole; short internode. Wild type <i>Ys</i> from 'Borszczagowski'; <i>ys</i> from chemically induced mutation.	Rucinska et al., 1991		?
<i>zym-Dina</i>	-	<i>zucchini yellow mosaic virus resistance</i> ; <i>zym-Dina</i> from Dina-1.	Kabelka et al., 1997	Wai et al., 1997	P
<i>zym-TMG1</i>	<i>zymv</i>	<i>zucchini yellow mosaic virus resistance</i> . Inheritance is incomplete, but usually inherited in a recessive fashion; source of resistance is 'TMG-1'.	Provvidenti, 1987; Kabelka et al., 1997	Wai et al., 1997	W

^Z Asterisks on cultigens and associated references indicate the source of information for each.

Y W = Mutant available through T.C. 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.

* Isozyme nomenclature follows a modified form of Staub et al. (1985) previously described by Richmond (1972) and Gottlieb (1977).

Table 2. The cloned genes of cucumber and their function.^Z

Gene accession	Tissue source	Function	Clone type	Reference
Genes involved in seed germination or seedling development				
X85013	Cotyledon cDNA library	Encoding a T-complex protein	cDNA	Ahnert et al., 1996
AJ13371	Cotyledon cDNA library	Encoding a matrix metalloproteinases	cDNA	Delorme et al., 2000
X15425	Cotyledon cDNA library	Glyoxysomal enzyme malate synthase	Genomic DNA fragment	Graham et al., 1989; 1990
X92890	Cotyledon cDNA library	Encoding a lipid body lipoxxygenase	cDNA	Höhne et al., 1996
L31899	Senescing cucumber cotyledon cDNA library	Encoding an ATP-dependent phosphoenolpyruvate carboxykinase (an enzyme of the gluconeogenic pathway)	cDNA	Kim and Smith, 1994a
L31900	Cotyledon cDNA library	Encoding microbody NAD(+)-dependent malate dehydrogenase (MDH)	cDNA	Kim and Smith, 1994b
L44134	Senescing cucumber cDNA library	Encoding a putative SPF1-type DNA binding protein	cDNA	Kim et al., 1997
U25058	Cotyledons	Encoding a lipoxxygenase-1 enzyme	cDNA	Matsui et al., 1995; 1999
Y12793	Cotyledon cDNA library	Encoding a patatin like protein	cDNA	May et al., 1998
X67696	Cotyledon cDNA library	Encoding the 48539 Da precursor of thiolase	cDNA	Preisig-Muller and Kindl, 1993a
X67695	Cotyledon cDNA library	Encoding homologous to the bacterial dnaJ protein	cDNA	Preisig-Muller and Kindl, 1993b
X79365	Seedling cDNA library	Encoding glyoxysomal tetrafunctional protein	cDNA	Preisig-Muller et al., 1994
X79366	Seedling cDNA library	Encoding glyoxysomal tetrafunctional protein	cDNA	Preisig-Muller et al., 1994
Z35499	Genomic library	Encoding the glyoxylate cycle enzyme isocitrate lyase	Genomic gene	Reynolds and Smith, 1995
M59858	Cotyledon cDNA library	Encoding a stearyl-acyl-carrier-protein (ACP) desaturase	cDNA	Shanklin and Somerville, 1991
M16219	Cotyledon cDNA library	Encoding glyoxysomal malate synthase	cDNA	Smith and Leaver, 1986
Genes involved in photosynthesis and photorespiration activities				
M16056	Cotyledon cDNA library	Encoding ribulose biphosphate carboxylase/oxygenase	cDNA	Greenland et al., 1987
M16057	Cotyledon cDNA library	Encoding chlorophyll a/b-binding protein	cDNA	Greenland et al., 1987
M16058	Cotyledon cDNA library	Encoding chlorophyll a/b-binding protein	cDNA	Greenland et al., 1987
X14609	cotyledon cDNA library	Encoding a NADH-dependent hydroxypyruvate reductase (HPR)	cDNA	Greenler et al., 1989
Y09444	Chloroplast genomic	tRNA gene	Chloroplast	Hande and

	library		DNA fragment	Jayabaskaran, 1997
X75799	Chloroplast genomic library	Chloroplast tRNA (Leu) (cAA) gene	Genomic DNA fragment	Hande et al., 1996
D50456	Cotyledon cDNA library	Encoding 17.5-kDa polypeptide of cucumber photosystem I	cDNA	Iwasaki et al., 1995
S69988	Hypocotyls	Cytoplasmic tRNA (Phe)	cytoplasmic DNA fragment	Jayabaskaran and Puttaraju, 1993
S78381	Cotyledon cDNA library	Encoding NADPH-protochlorophyllide oxidoreductase	cDNA	Kuroda et al., 1995
D26106	Cotyledon cDNA library	Encoding ferrochelatase	cDNA	Miyamoto et al., 1994
U65511	Green peelings cDNA library	Encoding the 182 amino acid long precursor stellacyanin	cDNA	Nersissian et al., 1996
AF099501	Petal cDNA library	Encoding the carotenoid-associated protein	cDNA	Ovadis et al., 1998
X67674	Cotyledon cDNA library	Encoding ribulosebisphosphate carboxylase/oxygenase activase	cDNA	Preisig-Muller and Kindl, 1992
X58542	Cucumber genomic library	Encoding NADH-dependent hydroxypyruvate reductase	Genomic DNA fragment	Schwartz et al., 1991
U62622	Seedling cDNA library	Encoding monogalactosyldiacylglycerol synthase	cDNA	Shimajima et al., 1997
D50407	Cotyledon cDNA library	Encoding glutamyl-tRNA reductase proteins	cDNA	Tanaka et al., 1996
D67088	Cotyledon cDNA library	Encoding glutamyl-tRNA reductase proteins	cDNA	Tanaka et al., 1996
D83007	Cotyledon cDNA library	Encoding a subunit XI (psi-L) of photosystem I	cDNA	Toyama et al., 1996
Genes expressed mainly in roots.				
AB025717	Root RNA	Lectin-like xylem sap protein	cDNA	Masuda et al., 1999
U36339	Root cDNA library	Encoding root lipoxygenase	cDNA	Matsui et al., 1998
AB015173	Root cDNA library	Encoding glycine-rich protein-1	cDNA	Sakuta et al., 1998
AB015174	Root cDNA library	Encoding glycine-rich protein-1	cDNA	Sakuta et al., 1998
Flower genes				
AF035438	Female flower cDNA library	MADS box protein CUM1	cDNA	Kater et al., 1998
AF035439	Female flower cDNA library	MADS box protein CUM10	cDNA	Kater et al., 1998
D89732	Seedlings	Encoding 1-aminocyclo-propane-1-carboxylate synthase	cDNA	Kamachi et al., 1997
AB003683	Seedlings	Encoding 1-aminocyclo-propane-1-carboxylate synthase	cDNA	Kamachi et al., 1997
AB003684	Seedlings	Encoding 1-aminocyclo-propane-1-carboxylate synthase	cDNA	Kamachi et al., 1997
AB035890	Fruit RNA	Encoding polygalacturonase	cDNA	Kubo et al., 2000
AF022377	Floral buds	Encoding agamous-like putative transcription factor (CAG1) mRNA	cDNA	Perl-Treves et al., 1998
AF022378	Floral buds	Encoding agamous like putative transcription factor (CAG2) mRNA	cDNA	Perl-Treves et al., 1998
AF022379	Floral buds	Encoding agamous-like putative transcription factor (CAG3) mRNA	cDNA	Perl-Treves et al., 1998

U59813	Genomic DNA	Encoding 1-aminocyclo-propane-1-carboxylate synthase	Genomic DNA fragment	Trebitsh et al., 1997
X95593	Corolla cDNA library	Encoding carotenoid-associated protein	cDNA	Vishnevetsky et al., 1996
AB026498	Shoot apex RNA	Ethylene-receptor-related gene	cDNA	Yamasaki et al., 2000
Genes involved in fruit development and maturation				
AB010922	Fruit cDNA library	Encoding the ACC synthase	cDNA	Mathooko et al., 1999
J04494	Fruit cDNA library	Encoding an ascorbate oxidase	cDNA	Ohkawa et al., 1989; 1990
AB006803	Fruit cDNA library	Encoding ACC synthase	cDNA	Shiomi et al., 1998
AB006804	Fruit cDNA library	Encoding ACC synthase	cDNA	Shiomi et al., 1998
AB006805	Fruit cDNA library	Encoding ACC synthase	cDNA	Shiomi et al., 1998
AB006806	Fruit cDNA library	Encoding ACC oxidase	cDNA	Shiomi et al., 1998
AB006807	Fruit cDNA library	Encoding ACC oxidase	cDNA	Shiomi et al., 1998
AB008846	Pollinated fruit cDNA library	Corresponding genes preferentially expressed in the pollinated fruit	cDNA	Suyama et al., 1999
AB008847	Pollinated fruit cDNA library	Corresponding genes preferentially expressed in the pollinated fruit	cDNA	Suyama et al., 1999
AB008848	Pollinated fruit cDNA library	Corresponding genes preferentially expressed in the pollinated fruit	cDNA	Suyama et al., 1999
Genes involved in cell wall loosening and cell enlargement				
AB001586	Hypocotyl RNA	Encoding homologous to serine/threonine protein kinases (for CsPK1.1)	cDNA	Chono et al., 1999
AB001587	Hypocotyl RNA	Encoding homologous to serine/threonine protein kinases (for CsPK1.2)	cDNA	Chono et al., 1999
AB001588	Hypocotyl RNA	Encoding homologous to serine/threonine protein kinases (for CsPK2.1)	cDNA	Chono et al., 1999
AB001589	Hypocotyl RNA	Encoding homologous to serine/threonine protein kinases (for CsPK2.2)	cDNA	Chono et al., 1999
AB001590	Hypocotyl RNA	Encoding homologous to serine/threonine protein kinases (for CsPK3)	cDNA	Chono et al., 1999
AB001591	Hypocotyl RNA	Encoding homologous to serine/threonine protein kinases (for CsPK4.1)	cDNA	Chono et al., 1999
AB001592	Hypocotyl RNA	Encoding homologous to serine/threonine protein kinases (for CsPK4.2)	cDNA	Chono et al., 1999
AB001593	Hypocotyl RNA	Encoding homologous to serine/threonine protein kinases (for CsPK5)	cDNA	Chono et al., 1999
U30382	Hypocotyl cDNA library	Encoding expansins	cDNA	Shcherban et al., 1995
U30460	Hypocotyl cDNA library	Encoding expansins	cDNA	Shcherban et al., 1995
Genes induced or repressed by plant hormones				
D49413	Hypocotyl cDNA library	Corresponding to a gibberellin-responsive gene encoding an extremely hydrophobic protein	cDNA	Chono et al., 1996

AB026821	Seedling RNA	Encoding IAA induced nuclear proteins	cDNA	Fujii et al., 2000
AB026822	Seedling RNA	Encoding IAA induced nuclear proteins	cDNA	Fujii et al., 2000
AB026823	Seedling RNA	Encoding IAA induced nuclear proteins	cDNA	Fujii et al., 2000
M32742	Cotyledon cDNA library	Encoding ethylene-induced putative peroxidases	cDNA	Morgens et al., 1990
D29684	Cotyledon cDNA library	Cytokinin-repressed gene	cDNA	Teramoto et al., 1994
D79217	Genomic library	Cytokinin-repressed gene	Genomic DNA fragment	Teramoto et al., 1996
D63451	Cotyledon cDNA library	Homologous to Arabidopsis cDNA clone 3003	cDNA	Toyama et al., 1995
D63384	Cotyledon cDNA library	Encoding catalase	cDNA	Toyama et al., 1995
D63385	Cotyledon cDNA library	Encoding catalase	cDNA	Toyama et al., 1995
D63386	Cotyledon cDNA library	Encoding catalase	cDNA	Toyama et al., 1995
D63387	Cotyledon cDNA library	Encoding lectin	cDNA	Toyama et al., 1995
D63388	Cotyledon cDNA library	Encoding 3-hydroxy-3-methylglutaryl CoA reductase	cDNA	Toyama et al., 1995
D63389	Cotyledon cDNA library	Encoding 3-hydroxy-3-methylglutaryl CoA reductase	cDNA	Toyama et al., 1995
D63388	Cotyledon cDNA library	Encoding a basic region/helix-loop-helix protein	cDNA	Toyama et al., 1999
Resistance genes				
M84214	Genomic library	Encoding the acidic class III chitinase	cDNA	Lawton et al., 1994
M24365	Leave cDNA library	Encoding a chitinase	cDNA	Metraux et al., 1989
D26392	Seedling cDNA library	Encoding FAD-Enzyme monodehydroascorbate (MDA) reductase	cDNA	Sano and Asada, 1994
Somatic embryo gene.				
X97801	Embryogenic callus cDNA library	MADS-box gene	cDNA	Filipecki et al., 1997
Repeated DNA sequences				
X03768	Genomic DNA	Satellite type I	Genomic DNA fragment	Ganal et al., 1986
X03769	Genomic DNA	Satellite type II	Genomic DNA fragment	Ganal et al., 1986
X03770	Genomic DNA	Satellite type III	Genomic DNA fragment	Ganal et al., 1986
X69163	Genomic DNA	Satellite type IV	Genomic DNA fragment	Ganal et al., 1988a
X07991	rDNA	Ribosomal DNA intergenic spacer	Genomic DNA fragment	Ganal et al., 1988b
X51542	Cotyledons	Ribosomal DNA intergenic spacer	Genomic DNA fragment	Zentgraf et al., 1990

^Z Only the sequences published in both journals and the genebank database are listed.

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