Cucurbit Genetics Cooperative

2016 & 2017

39 & 40

Cucurbit Genetics Cooperative

39-40

2016-2017

ISSN 1064-5594

USDA, ARS, U.S. Vegetable Laboratory
2700 Savannah Highway
Charleston, SC 29414

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http://cuke.hort.ncsu.edu/cgc/

On the front cover: *Cucurbita pepo* L. From L. van Houtte, *Flore des serres et des jardins de l'Europe*, 1845 – 1888.

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ISSN 1064-5594

Contents

Generation and Potential Use of Interspecific *Cucumis* Hybrids

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Introduction.

Grafting is a traditional method used to avoid soil stresses. It is commonly used today in vegetable production as an alternative to conventional agrochemical control. *Cucurbita* hybrids are widely used as rootstocks for cucurbits, such as watermelon (*Citrullus lanatus* (Thunb.) Mansf.) and melon (*Cucumis melo* L.), but they sometimes have negative effects on fruit quality (5) or lack resistance against nematodes (3)(14). The *Cucumis* genus represents an important source of germplasm to obtain new potential rootstocks useful for melons. Interspecific hybrids between *Cucumis* species can provide resistances against important pathogens without altering fruit quality due to a closer genetic relationship between the rootstock and the scion. Some attempts have been conducted to cross cultivated *Cucumis* species (melon and cucumber) with wild ones, but with limited success (2)(10)(12)(15). However, hybridization among wild *Cucumis* species is successful for some cross combinations (2). We have performed several interspecific crosses and found promising results with the hybrid between *C. ficifolius* A.Rich x *C. myriocarpus* Naudin.

Materials & Methods

Interspecific hybridization

The experiments were conducted in the greenhouses at COMAV-UPV (Universitat Politècnica de València, Spain) during the spring-summer seasons of 2015 and 2016. The crossing ability among some wild *Cucumis* was evaluated and one of the most successful crosses was *C. ficifolius* x *C. myriocarpus* (F x My). Seeds of both species (from accessions maintained at the COMAV´s Gene bank) were germinated in Petri dishes. Seedlings were transplanted into plastic pots (6 x 6 cm) with fertirrigated substrate and vermiculite (2:1) and grown in the greenhouse for three months. At anthesis, self-pollinations and reciprocal crosses were performed between both species. Two to three month old mature fruits were harvested and seeds were extracted for further characterization of F1 progeny.

Characterization of parental lines and F1 hybrids

Germination rate was estimated for both parental and hybrid seeds. Morphological traits such as hypocotyl length and diameter, vine length and number of true leaves were measured on plantlets. Botanical identification keys were used to confirm the hybrid nature of the characterized plants (7)(11). Distinct taxonomic characters between parents were used to verify the hybrid nature of the F1.

Resistance to pathogens

An F x My hybrid and two parents were tested for resistance to *Fusarium* wilt (using a culture of *F. oxysporum* Schltdl. f. sp. *melonis* race 1, 2y for artificial inoculation). The resistance to the two fungal strains was evaluated at 10, 20 and 30 days after inoculation (DAI) using a visual scale.

Grafting assay

Charentais melon (*Cucumis melo* L. var. *cantalupensis* Naud.) was grafted onto the F x My hybrid. Grafting was carried out at two developmental stages for both the scions and rootstocks. Grafting was carried out at two growth stages: early and mature. For the early growth stage technique, young rootstock seedlings with developed cotyledons and scion seedlings just after germination were used. For the mature growth stage technique, grafting was conducted with five-true-leaf rootstock plants and scion seedlings with fully developed cotyledons. The cleft method was used in both cases.

Results & Discussion

Successful interspecific crosses using C. ficifolius as female parent

The success rate of interspecific hybridization was low (0 and 4.6% in 2014 and 2015, respectively) when *C. myriocarpus* was used as the female parent and *C. ficifolius* as the pollen source. However, the reciprocal cross with *C. ficifolious* as female parent showed a considerable cross-compatibility with 68.3 and 83.8% effective pollinations in 2105 and 2016, respectively. Hybrid fruits with viable seeds were obtained. The average number of viable seeds per fruit in the cross F x My was significantly higher (ANOVA $p<0.01$) than that obtained in the self-pollinations of *C. myriocarpus*, and similar to that of *C. ficiolifus* (201.7 seeds *versus* 89.6 and 201.7, respectively). At 5d after germination, the germination rate of the F x My hybrid was higher than that of the corresponding parents (1). This effect is likely due to genotypic interactions and hybrid vigor.

These results were consistent with those of Singh and Yadava (13) in which *C. ficifolius* and *C. myriocarpus* were classified into the same compatibility group, whereas other important wild species were classified in a different group, less compatible with the others. Furthermore, the crossability polygon of the African wild *Cucumis* species (4) also described the presence of unilateral incompatibility between *C. ficifolius* and some other species. Kho et al. (6) obtained seeded fruits from *C. ficifolius* x *C. anguria,* but failed to obtain fruit set in *C. ficifolius* x *C. myriocarpus*, although this could be explained by the variability of the different accessions.

Taxonomic characterization of the F x My hybrid

Leaf size and shape were not evaluated as they appeared to be polymorphic, as was also indicated in the identification keys (7). The F x My hybrid was morphologically intermediate in most discriminatory characters between the parents. Hybrids appeared to have aculei in stems and leaf petioles, as *C. ficifolius* did, and showed an intermediate ratio between the hyaline part and the opaque part of the aculei from the ovaries, and the size and shape of the mature fruits were also intermediate between those from two parental lines. Figure 1 shows plant length from 15 until 60 days after transplanting. Interspecific hybrid F x My showed an intermediate vine length between their parents, *C. ficioflius* and *C. myriocarpus*.

Grafting melon onto F x My hybrid

The development of vigorous seedlings is a necessary characteristic for a rootstock. Success of rootstock/scion union depends on hypocotyl diameter; a sufficient length of hypocotyl can avoid contamination and penetration of soil and pathogens in the bound tissue. Table 1 shows hypocotyl length and diameter of parental genotypes and hybrids measured at 7, 14 and 21 days after sowing. Significant differences were found between the F1 hybrid and both parents in hypocotyl characteristics. F x My hybrid showed wider hypocotyls than either parent at 21 days after sowing and longer hypocotyl than one or both parents from 7 days after sowing.

Good rootstock/scion union was obtained at both developmental stages (early and mature) with an average grafting success of 70%. However, only plants grafted at the mature stage developed properly. In contrast, in the first procedure (early stage), the development of the scion (melon) was faster than that of the rootstock, resulting in collapse of the grafted plants (Figure 2A). Plants grafted at the mature stage were transplanted to a greenhouse to study their agronomical behavior, which were compared to ungrafted and self-grafted plants (Figure 2B and C).

Resistance to pathogens

Fusarium wilt is a severe disease worldwide in melon and resistance to *Fusarium oxysporum* f. *sp*. *melonis* race 1,2y is an important trait in the development of melon rootstocks. We evaluated the response of the interspecific hybrid F x My and its parents to infection of this pathogen, using the cantaloupe scion as susceptible control. Plants from *C. ficifolius*, *C. myriocarpus,* and F x My F1 hybrids did not show symptoms of *Fusarium* wilt at 10 days post inoculation (DPI), whereas the first symptoms, yellowing and mild spot in stem, were observed in Cantaloupe plants at this time. At 30 DPI, all genotypes showed 100% survival and most cantaloupe plants collapsed with only 15% of plants alive. The long-term response of these genotypes confirmed the resistance to *Fusarium oxysporum* f. *sp*. *melonis* race 1, 2y. Resistance to *Fusarium* in field trails or artificial inoculation has been already described in *C. myriocarpus* and *C. ficifolius* (8)(9), but not in their hybrids F x My, which are experimentally tested here for the first time with positive and promising results.

We have obtained hybrids between *C. ficifolius* x *C. myriocarpus* that could be useful as rootstocks of melon, with good grafting compatibility, good emergence behavior (germination, hypocotyl diameter and length) and resistance to *Fusarium*. These hybrids could also be useful in breeding programs.

Acknowledgements

This work was supported by a project funded by the Ministerio de Economía y Competitividad AGL2014-53398-C2-2-R (jointly funded by FEDER), and project PHBP14/00021 funded by the Dirección de Política

Universitaria del Ministerio de Educación, Cultura y Deporte of Spain.

Literature cited

1. Cáceres, A., B. Picó, C. Gisbert. 2016. Germination of wild *Cucumis* species and interspecific hybrids. Proc. CUCURBITACEAE. Eucarpia. 11: 227-230.
2. Chen, J.F., J. Adelberg. 2000. Interspecific hybridization in *Cucumis*: Progress, problems, and perspectives. HortScience 35(1): 11-15.
3. Cohen, R., J. Tyutyunik, E. Fallik, Y. Oka, Y. Tadmor, and M. Edelstein M. 2014. Phytopatological evaluation of exotic watermelon germplasm as a basis for rootstock breeding. Scientia Hort. 165: 203-210.
4. Den Nijs, A.P.M., and D.L. Visser. 1985. Relationships between African species of the genus *Cucumis* L. estimated by the production, vigour and fertility of F1 hybrids. Euphytica 34(2):279-290.
5. Fredes, A., S. Roselló, J. Beltrán, J. Cebolla-Cornejo, A. Pérez-de-Castro, C. Gisbert, and M.B. Picó. 2016. Fruit quality assessment of watermelons grafted onto citron melon rootstock. J. Sci. Food and Agr. doi:10.1002/jsfa.7915
6. Kho, Y.O., A.P.M. Den Nijs, and J. Franken. 1980. Interspecific hybridization in *Cucumis* L. II.: The crossability of species, an investigation of *in vivo* pollen tube growth and seed set. Euphytica 29(3):661–672.
7. Kirkbride, J.H. 1993. Biosystematic monograph of the genus *Cucumis* (Cucurbitaceae): Botanical identification of cucumbers and melons. 1st ed. Parkway Publishers. Boone, N.C.
8. Liu, B., J. Ren, Y. Zhang, J. An, M. Chen, H. Chen, Ch. Xu, and H. Ren. 2015. A new grafted rootstock against root-knot nematode for cucumber, melon, and watermelon. Agron. Sustain. Dev. 35(1):251-259.
9. Matsumoto, Y., T. Ogawara, M. Miyagi, N. Watanabe, and T. Kuboyama. 2011. Response of wild *Cucumis* to inoculation with *Fusarium oxysporum* f.sp. *melonis* race 1, 2y. J. Japan. Soc. Hort. Sci. 80(4):414-419.
10. Matsumoto, Y., M. Miyagi, N. Watanabe, T. Kuboyama. 2012. Temperature-dependent enhancement of pollen tube growth observed in interspecific crosses between wild *Cucumis* spp. and melon (*C. melo* L.). Scientia Hort. 138:144-150.
11. Schaefer, H. 2007. *Cucumis* (Cucurbitaceae) must include *Cucumella, Dicoelospermum, Mukia, Myrmecosicyos*, and *Oreosyce*: a recircumscription based on nuclear and plastid DNA data. Blumea 52: 165-177.
12. Sebastian, P. M., H. Schaefer, I. R. H. Telford, and S. S. Renner. 2010. Cucumber and melon have their wild progenitors in India, and the sister species of *Cucumis melo* is from Australia. Proc. Natl. Acad. Sci. U.S.A. 107(32):14269–14273.
13. Singh, A.K., and K.S. Yadava. 1984. An analysis of interspecific hybrids and phylogenetic implications in *Cucumis* (Cucurbitaceae). Pl. Syst. Evol. 147(3-4):237-252.
14. Soteriou, G.A., M.C. Kyriacou, A.S. Siomos, and D. Gerasopoulos. 2014. Evolution of watermelon fruit physicochemical and phytochemical composition during ripening as affected by grafting. Food Chem. 165:282-289.
15. Walters, S.A., and T.C. Wehner. 2002. Incompatibility in diploid and tetraploid crosses of *Cucumis sativus* and *Cucumis metuliferus*. Euphytica. 128(3):371-374.

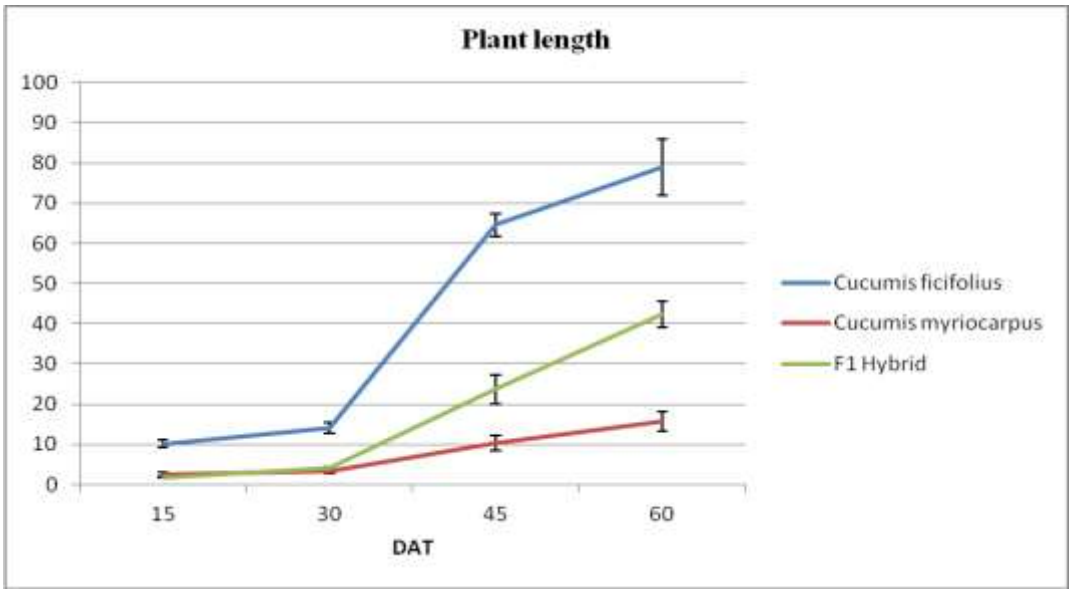

Figure 1. Plant Length measured in *C. ficifolius, C. myriocarpus* and F_1 hybrid (F x My) from 15 to 60 days after transplanting.

Table 1. Hypocotyl diameter (mm) and length (cm) of two wild *Cucumis* species and their F_1 hybrid measured at different days

Genotypes	Hypocotyl diameter (mm)[y]			Hypocotyl length (cm)		
	7d	14d	21d	7d	14d	21d
C. ficifolius	1.21 a[z y]	1.50 a	2.17 a	1.41 a	1.70 a	1.74 a
C. myriocarpus	1.32 a	1.54 a	2.25 ab	1.83 b	1.76 a	1.89 ab
Interspecific F1	1.21 a	1.48 a	2.53 b	1.78 b	2.24 b	2.15 b

[z] Different letters in the same column indicate significant differences according to the LSD multiple range test ($P < 0.05$).
[y] Average of ten plants per genotype.

Figure 2. Plants of *C. melo* var. *cantalupensis* grafted onto F x My at 10 days of grafting by the cleft procedure using an early grafting (A) or mature grafting (B) procedure. The plant seen in (B) was transplanted for evaluation under greenhouse conditions (C).

New Charentais Lines with Delayed Climacteric Ripening Derived from an Introgression Lines Collection.

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Introduction

Melon (*Cucumis melo* L., 2n = 2x = 24) is one of the most variable species within the Cucurbitaceae family, with a current total world production of over 29 million tons (5). The *cantalupensis* horticultural group includes some of the most important melon varieties cultivated worldwide. 'Vedrantais' is a reference variety for the Charentais-type market class Cantaloupe. It produces medium-size, oval-to-round, sutured and orange-fleshed fruits, with a typical climacteric ripening behavior, that are aromatic and have a medium sugar content (9). One of the main problems of Charentais melons is the short posthaverst life associated to a reduction of flesh firmness and sugar content throughout the postharvest process.

The recent availability of new markers derived from massive sequencing melon projects (1, 2, 3) may be integrated in more efficient breeding programs. New mapping and pre-breeding populations are developed using these genomic tools. Introgression lines (IL) are an excellent breeding tool to incorporate exotic natural variation into recurrent genetic backgrounds. We have recently developed a new melon IL collection by introgressing the exotic genetic background of a Japanese cultivar 'Ginsen makuwa' (MAK) melon (*Cucumis melo* var. *makuwa*) into a French 'Vedrantais' (VED) cultivar (8). This collection includes some interesting ILs showing favorable traits that can be used to develop new cultivars. In this paper, we characterize one of these ILs containing a major introgression of the MAK genome in the chromosome 10 (MAK_10). This line shows a delay in the climacteric ripening behavior, providing a longer postharvest life associated with firmer fruits.

Materials and Methods

The assay was conducted in Paiporta (Valencia, Spain) (Latitude 39º 25' 2.208'' N, Longitude 0º 25' 3, 01'' W and Altitude 17 m), in the spring-summer season 2016 (from March to July), in a greenhouse with automatic control of temperature with cooler and window aperture. Plants were grown in substrate bags of 29 kg (70 % coconut fiber and 30 % coconut chips). Nutrients were provided through the irrigation system and pruning was done manually when necessary to regulate vegetative growth and flowering. Fifty plants of the VED cultivar and thirty of MAK_10 were cultivated. These plants were self-pollinated and the pollination day was recorded with the aim to harvest the fruits at different days after pollination (DAP), from 30 to 39, from 40 to 49 and >50 DAP. All the fruits were phenotyped for flesh firmness (measured as kg/cm^2 with a fruit pressure tester, FT 327, with a plunger diameter of 8 mm, Alfonsine, Italy) and for the presence of abscission layer (an external signal of climacteric ripening in melon, scored visually as 0, absent and 1, present). Also fruits of the two genotypes collected at 40-49 DAP were stored in a chamber at room temperature and phenotyped at 5 and 10 days after harvesting (DAH), with the aim to study the postharvest behavior.

The fruits collected at 40-49 DAP were additionally phenotyped for fruit weight (FW in grams, with digital scale), fruit length and diameter (FL and FD in millimeters, with graduated rule), cavity width (CW, as the ratio of the width of the seminal cavity to the fruit diameter), flesh and rind thickness (Fth and Rth in mm, with electronic digital caliper, I.C.T, S.L., La Rioja, España), occurrence of external aroma of the whole fruit and netting (AR and NET, scored visually as 0, absent and 1, present), flesh color measured with a CR-400 colorimeter (Konica Minolta, Inc., Tokyo, Japan) with Hunter Lab coordinates where L* expresses luminosity (L=0 black and L=100 white), a* expresses the color direction between red (positive) and green (negative) and b* expresses the color direction between yellow (positive) and blue (negative)) (FCHl, FCa, FCb), and soluble solids content (SSC, measured as ºBrix from drops of juice (with a hand-held "Pocket" refractometer (PAL-α), Atago CO., LTD, Tokyo, Japan).

A t-test was used to identify significant differences between the fruits of the recurrent parent and those of the IL MAK_10.

Results

Differences in the formation of the abscission layer between VED and MAK_10 were observed clearly. The abscission layer started to appear in VED fruits collected at 40-49 DAP and was fully formed in all fruits collected at >50 DAP. No fruits of MAK_10 formed the abscission layer at any of the harvesting times (Figure 1).

Apart from the abscission layer, the climacteric ripening process is associated with a loss of flesh firmness. VED fruits, as expected, suffered a progressive decrease of flesh firmness during ripening, dropping from 6.18 ± 0.46 kg/cm^2 in immature fruits (collected at 30-39 DAP) (Figure 2) to 1.38 ± 0.32 kg/cm^2 in overripe fruits (collected at >50 days DAP). MAK_10 fruits had a clearly different behavior maintaining a more constant flesh firmness throughout all the ripening process (ranging from 4.00 ± 0.49 kg/cm^2 to 3.71 ± 0.39 kg/cm^2). T-test results indicated that these differences in fruit firmness between MAK_10 and the recurrent parent VED were significant during all the ripening period (Figure 2 and Table 1). Flesh firmness differences between MAK_10 and VED are important in fruits collected at commercial maturity (40-49 DAP), the fruits of MAK 10 being firmer (4.35 ± 0.3 *versus* 3.19 ± 0.2 kg/cm^2 in MAK_10.1 and VED respectively). At this ripening time the fruits of both genotypes only differed in the external aroma (VED fruits were more aromatic than MAK_10), VED and MAK_10 were similar in fruit weight, length, diameter, cavity width, rind thickness, soluble solids content and flesh color (Table 2).

The differences in flesh firmness found between the two genotypes in fruits collected at 40-49 days were maintained at 5 and 10 days after harvesting (DAH) and conservation at room temperature. Fruits of the ILs MAK_10 conserved a higher flesh firmness (2.5 ± 1 kg/cm^2 and 2.1 ± 0.05 kg/cm^2 at 5 and 10 DAH) than VED fruits that were too soft to be marketable at this postharvest time (0.6 ± 0.05 kg/cm^2 and 1.06 ± 0.14 kg/cm^2) (Table 3).

Discussion

Fruit ripening is a complex process regulated by multiple genetic pathways. Ethylene plays a major role in the regulation of some ripening-associated processes, such as the formation of the abscission layer and the synthesis of aroma volatiles. Other processes related to ripening seem to be ethylene-independent, like sugar accumulation (7). The flesh softening process that is correlated to cell wall degrading is an ethylene-dependent and independent process (4). The suppression of ethylene maintains the flesh firmness and inhibits the development of the abscission layer (4, 6, 7).

In this study, we characterized a new line, MAK_10, derived from the introgression lines collection described by Perpiñá et al. (8), generated by introgressing the MAK genome into a VED background. Unlike VED fruits, MAK_10 fruits do not form an abscission layer during the growing cycle and the postharvest period. Likewise, MAK_10 presents a constant flesh firmness until harvested, unlike fruits of VED that lose flesh firmness throughout the ripening process. Also MAK_10 has an extended shelf-life during the post-harvest process retaining a marketable flesh firmness. This line has a major introgression of 0.9 Mb in LGX of the MAK genome not shared with any other IL of the collection, being IL lacking abscission layer at maturity. In the specific genomic region of LGX several ripening-related genes are located, annotated as NAC transcription factor (belonging to the same TF family as the ripening regulator NOR, non ripening), ERF (ethylene responsive transcription factor), and PEI (pectin esterase inhibitor).

The occurrence of MAK alleles in NAC TFs, ethylene signaling components and genes involved in cell wall metabolism of the MAK_10 introgression might alter the climacteric ripening process causing the absence of abscission layer formation, the low aroma production and the delay in flesh softening.

In conclusion, this line provides fruits with a slower ripening process and a longer postharvest life. A deeper study of the candidate genes involved in the ripening behavior of this line will serve to understand the ripening process in melon.

Acknowledgments

This work has been carried out in the framework of the Programa de Valorización y Recursos Conjuntos de I+D+i de VLC/CAMPUS and has been funded by the Ministerio de Educación, Cultura y Deporte as part of the Programa Campus de Excelencia Internacional. IL generation, genotyping and phenotyping was supported by SAFQIM project, AGL2012-40130-C02-02 of the Spanish Ministry of Economy and Competitivity (MINECO). The authors also wish to thank the MINECO project AGL2014-53398-C2-2-R, co-funded with FEDER funds.

Literature Cited

1. Blanca J., J. Cañizares, P. Ziarsolo, C. Esteras, G. Mir, F. Nuez, J. Garcia-Mas, B. Picó. 2011. Melon transcriptome characterization: Simple Sequence

Repeats and Single Nucleotide Polymorphisms discovery for high throughput genotyping across the species. The Plant Genome 4(2):118-131.
2. Blanca J., C. Esteras, P. Ziarsolo, D. Pérez, V. Fernandez-Pedrosa, C. Collado, R. Rodríguez de Pablos, A. Ballester, C. Roig, J. Cañizares, B. Picó. 2012. Transcriptome sequencing for SNP discovery across Cucumis melo. BMC Genomics 13:280.
3. Esteras C., G. Formisano, C. Roig, A. Díaz, J. Blanca, J. Garcia-Mas, M.L.Gómez, M.L.Gómez-Guillamón, A.I. López-Sesé, A. Lázaro, A.J. Monforte, B. Picó. 2013. SNP genotyping in melons: genetic variation, population structure, and linkage disequilibrium. Theoretical Applied Genetics 126:1285–303.
4. Flores F., M. Ben Amor, B. Jones, J.C. Pech, M. Bouzayen, A. Latché, F. Romojaro. 2001. The use of ethylene-supressed lines to asses differential sensitivity to ethylene of the vairous ripening pathways in Cantaloupe melons. Physiologia Plantarum 113:128-133.
5. Food and Agriculture Organization of the United Nations. FAOSTAT data. 2016. URL: http://faostat.fao.org/.
6. Nishiyama K., M. Guis, J.K.C. Rose, Y. Kubo, K.A. Bennett, L. Wangjin, K. Kato, K. Ushijima, R. Nakano, A. Inaba, M. Bouzayen, A. Latche, J.C. Pech, A.B. Bennett. 2007. Ethylene regulation of fruit softening and cell wall disassembly in Charantais melon. Journal of Experimental Botany 58(6):1281-1290.
7. Pech J.C., M. Bouzayen, A. Latché. 2008. Climacteric fruit ripening: Ethylene-dependent and independent regulation or ripening pathways in melon fruit. Plant Science 175(1-2):114-120.
8. Perpiñá G., C. Esteras, Y. Gibon, A.J. Monforte, B. Picó. 2016. A new genomic library of melon introgression lines in a cantalupe genetic background for dissecting desirable agronomical traits. BMC Plant Biology 16:154.
9. Pitrat M., P. Hanelt, K. Hammer. 2000. Some comments on intraspecific classification of cultivar melon. Acta Horticulturae 510:29-36.

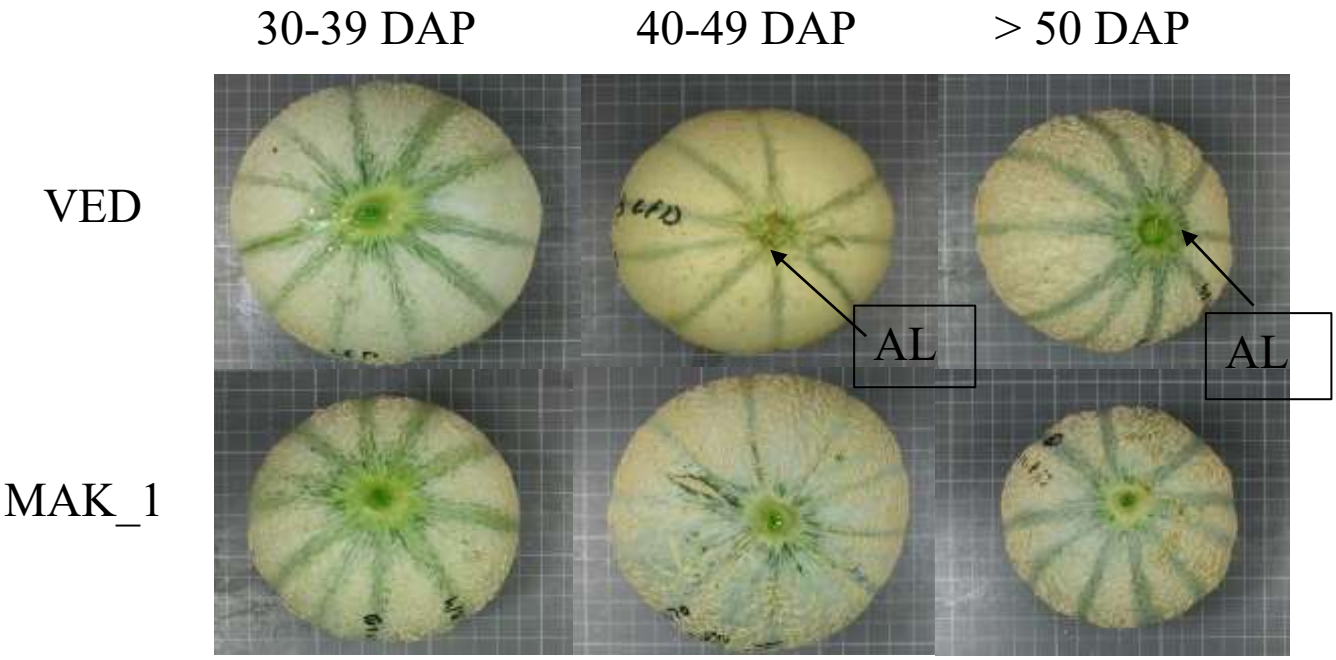

Figure 1. Fruits of VED (top) and line MAK_10 (bottom) harvested at different number of days after pollination (DAP). An abscission layer (AL) formed on VED fruits.

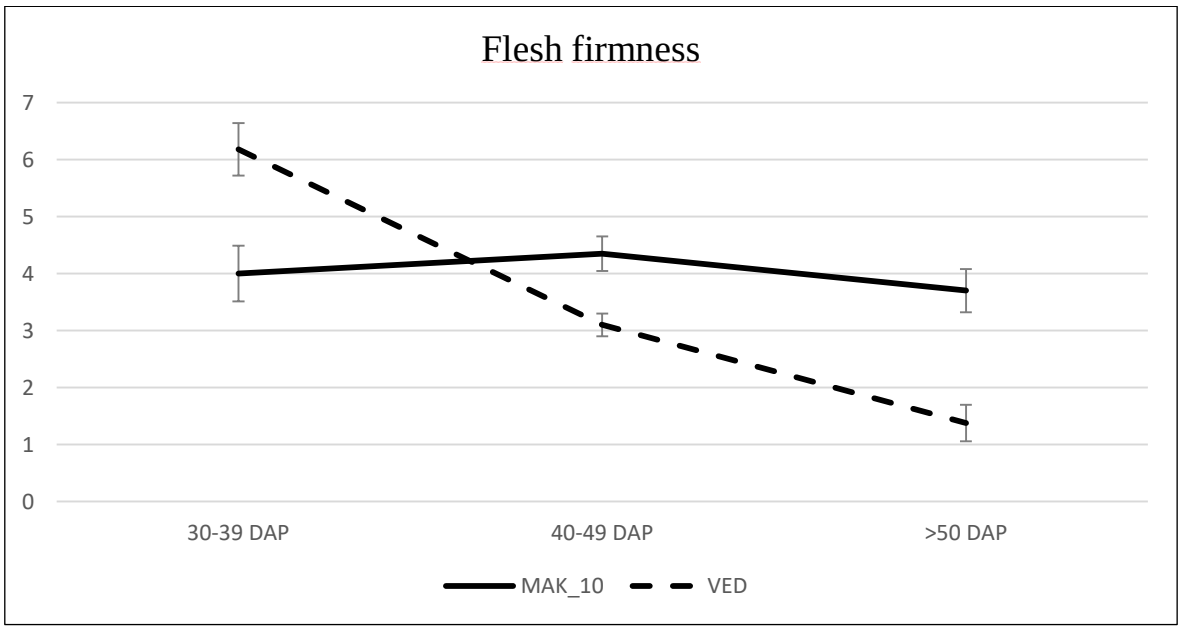

Figure 2. Tendency of flesh firmness (kg/cm^2) in fruits harvested at different times after pollination (DAP)

Table 1. Mean and standard error of presence of abscission layer and flesh firmness in fruits harvested at different times after pollination. * Significant difference (P<0.05) between VED and MAK_10.

Days after pollination	Abscission layer				Flesh firmness			
	VED		MAK_10		VED		MAK_10	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
30-39	0.00	0.00	0.00	0.00	6.18*	0.46	4.00*	0.49
40-49	0.50*	0.10	0.00*	0.00	3.19*	0.20	4.35*	0.30
>50	1.00*	0.00	0.00*	0.00	1.38*	0.32	3.71*	0.39

Table 2. Mean of external aroma occurrence (AR), netting (NET), fruit weight (FW), fruit length (FL), fruit diameter (FD), fruit shape (FS), cavity width (CW), flesh thickness (Fth), rind thickness (Rth), soluble solids content (SSC), flesh color parameter (FCHl, FCa, FCb) in fruits collected at 40-49 days after pollination. Letters a and b indicate significant differences (P<0.05) between VED and MAK_10.

	AR	NET	FW	FL	FD	CW	Fth	Rth	SSC	FCHL	FCa	FCb
MAK_10	0.00 a	1.00 a	532.55 a	9.06 a	10.33 a	51.46 a	4.16 a	20.68 a	11.42 a	59.28 a	7.35 a	23.49 a
VED	0.53 b	0.88 a	523.00 a	9.34 a	10.11 a	48.85 a	3.73 a	21.35 a	11.78 a	54.92 a	7.90 a	22.95 a

Table 3. Mean and standard error of flesh firmness in fruits collected at 40-49 days after pollination (DAP) conserved at room temperature 5/10 days after harvesting (DAH).* Significant differences (P<0.05) between VED and MAK_10.

Days after pollination and harvesting	Flesh firmness			
	VED		MAK_10	
	Average	SE	Average	SE
40-49DAP+5 DAH	0.60*	0.05	2.50*	1.00
40-49DAP+10DAH	1.06*	0.14	2.10*	0.05

Performance of Grafted Galia and Ananas Melon Types under Different Salinity Concentrations

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Abstract

Salinity is a major factor in reduced crop productivity in many arid and semiarid regions. An environmentally friendly approach to avoid or reduce salinity impairment in crop production is grafting of salt-sensitive plants onto salt-tolerant rootstocks. To evaluate the response of grafted Galia and Ananas type melons to salinity, two greenhouse experiments were conducted in National Center for Agricultural Research and Extension (NCARE), Baqa', Jordan. Two melon cultivars, 'Raymond' (Ananas type) and 'Ra'anan' (Galia type), were grafted onto two *Cucurbita* rootstocks; '53009' and '53004'. The grafted melons were grown in 10 L pots filled with perlite. The plants were irrigated with saline water concentrations of 1.5, 3, 6 and 9 dS m^{-1}. In general, increasing salinity decreased plant growth parameters. Fresh shoot weight and leaf area were the most sensitive parameters that were affected by increasing salinity stress. Non-grafted "Ananas" melon was more salt tolerant compared to "Galia" type, however, this salt tolerance had no significant effect on improving salt tolerance of the rootstocks. Rootstock '53009' appeared more salt tolerant compared to '53004'. Reduction of dry shoot weight and leaf area under salinity stress may be alleviated by grafting.

Introduction

Salinity is a major factor in reduced crop productivity in many arid and semiarid regions. Currently, at least 20% of the world's irrigated land is salt-affected and/or irrigated with water containing elevated salt levels (Qadir *et al.,* 2008). An environmentally friendly approach to avoid or reduce salinity impairment in crop production is grafting of salt-sensitive plants onto salt-tolerant rootstocks (e.g., Sykes, 1985; Colla *et al*., 2010; Yin *et al*., 2010; Edelstein *et al*., 2011).

Recently, grafting of vegetable plants has become more common, and various methods and machines for vegetable grafting have been developed. Although the main purpose of vegetable grafting has been to control soilborne diseases and nematodes, improved tolerance to environmental stresses such as low soil temperatures (Okimura *et al*., 1986), flooding (Liao and Lin, 1996), salinity (Romero *et al*., 1997), and high boron concentrations (Edelstein *et al*., 2005, 2007) has been shown.

Colla *et al*. (2006a, 2006b), and Edelstein *et al.* (2005) showed that melon and watermelon plants that were grafted on salt-tolerant cucurbit rootstocks resulted in higher fruit yield in the grafted plants. It was shown that sodium exclusion and retention by *Cucurbita* rootstock (Edelstein et al., 2011) markedly decreased leaf Na concentration in the scion. The objective of the present research was to study whether there is a difference between grafted Galia type and Ananas type melon response under different salt concentrations. This work was conducted within the framework of the MERC (Middle East Regional Cooperation) program conducted by Egyptian, Jordanian and Israeli collaborators. The material used included *Cucurbita* rootstocks created in Israel, and melon types that are common in the Middle East.

Materials and Methods

The experiments were conducted in March 2014 in the greenhouse at NCARE, Jordan, in 10 L pots filled with perlite, irrigated to excess, five times a day, so that 35% of the irrigation water drained as leachate of excess salts. Nitrogen, phosphorous and potassium fertilizers enriched with micronutrients were applied through the irrigation system at levels used in local commercial cultivation. Two melon cultivars 'Ra'anan' (Galia type) and 'Raymond' (Ananas type) were grafted onto two *Cucurbita* rootstocks: '53004' (Shimshon), and '53009' (Gad). All the genetic material used, rootstock and scions are products of Hazera Seeds, Israel. Non-grafted melon plants were used as controls. Each treatment consisted of eight plants with four replicates (totaling 32 plants per treatment). Treatments were subjected to four salinity levels (1.5 fresh water used as a control, 3, 6, and 9 dS m^{-1} salt concentrations). Plant height, shoot dry weights, and leaf areas were measured 24 days after salt exposure. After harvest, the shoot of each plant was weighed, washed gently in deionized water, dried at 60 ^{0} C for 48 h, and reweighed.

Results

In general, increasing salinity caused a decrease in plant growth parameters, when shoot dry weight and leaf area were considered the most sensitive plant vegetative parameters in response to salt stress (Table 1). Grafting of the two melon types onto the two rootstocks significantly increased root and shoot dry weights, plant height and leaf area, compared to non-grafted plants (Table 2). Non-grafted Galia melons are more sensitive to salinity then Ananas melons (Table 3). For example, the highest salinity concentration (9 dS m^{-1}), reduced shoot dry weight to 78% and 55%, compared to control for Galia and Ananas, respectively. Rootstock '53004' appeared more sensitive to salinity compared to '53009' (Table 3). When Galia was grafted onto '53004' and '53009' rootstocks, there was a decrease (in response to 9 dS m^{-1}) in shoot dry weight of 80.6% and 61%, respectively. The same pattern was observed for leaf area, decreasing by 82.8 and 55.8 % for '53004' and '53009', respectively. These results indeed confirm that rootstock '53009' is more tolerant to salinity than '53004'. Similar results were observed when Ananas was grafted onto '53009' and '53004'. It was also observed that the scion had no significant effect on improving salt tolerance of the rootstocks (Table 3).

Conclusions

- Shoot fresh weight and leaf area were the most sensitive parameters that were affected by increasing salinity stress as compared to root growth or plant height
- Non-grafted "Ananas" melon was more salt tolerant as compared to "Galia" type, however, this salt tolerance had no significant effect on improving salt tolerance of the rootstocks.
- Rootstock '53009' (Gad) is more salt tolerant than '53004' (Shimshon).
- Reduction of shoot dry weight and leaf area under salinity stress might be alleviated by grafting.

Acknowledgments

This work was supported by the Bureau for Economic Growth, Agriculture, and Trade, U.S. Agency for International Development, under the terms of the Middle East Regional Cooperation Program Award No. TA-MOU-10-M30-055.

Literature Cited

1. Colla, G., Rouphael, Y., Cardarelli, M., Massa, D., Salerno, A. and Rea, E. 2006a. Yield, fruit quality and mineral composition of grafted melon plants grown under saline conditions. *Journal of Horticultural Science and Biotechnology* 81:146-152.
2. Colla, G., Rouphael, Y., Cardarelli, M. and Rea, E. 2006b. Effect of salinity on yield, fruit quality, leaf gas exchange, and mineral composition of grafted watermelon plants. *HortScience* 41:622-627.
3. Colla, G., Rouphael, Y., Leonardi, C. and Bie, Z. 2010. Role of grafting in vegetable crops under saline conditions. *Scientia Hort*. 127:147-155.
4. Edelstein, M., Ben-Hur, M., Cohen, R., Burger, Y. and Ravina, I. 2005, Boron and salinity effects on grafted and non-grafted melon plants, *Plant and Soil* 269:273–284.
5. Edelstein, M., Ben-Hur, M. and Plaut, Z. 2007. Grafted melons irrigated with fresh or effluent water tolerate excess boron. *J. Amer. Soc. Hort. Sci.* 132:484-491.
6. Edelstein, M., Plaut, Z. and Ben-Hur, M. 2011. Sodium and chloride exclusion and retention by non-grafted and grafted melon and *Cucurbita* plants. *J. Exp. Bot.* 62:177-184.
7. Liao, C.T., Lin, C.H. 1996. Photosynthetic response of grafted bitter melon seedling to flood stress. *Environmental and Experimental Botany* 36:167–172.
8. Okimura, M., Matso, S., Arai, K. and Okistu, S. 1986. Influence of soil temperature on the growth of fruit vegetable grafted on different stocks. *Bull. Veg. Ornam. Crops Res. Stn. Jpn*. C9:43-58.

9. Qadir, M., Tubeileh, A., Akhtar, J., Larbi, A., Minhas, P.S. and Khan, M.A. 2008. Productivity enhancement of salt–affected environments through crop
10. diversification. *Land Degradation and Development* 19:429-453.
11. Romero, L., Belakbir, A., Ragala, l. and Ruiz, J.M. 1997. Response of plant yield and leaf pigments to saline conditions: Effectiveness of different rootstocks in melon plants (*Cucumis melo* L.). *Soil Sci. Plant Nutr*. 43:855-862.
12. Sykes, S.R. 1985. A glasshouse screening procedure for identifying citrus hybrid which restrict chloride accumulation in shoot tissue. *Aust. J. Agric. Res*. 36:779-789.
13. Yin, R., Bai, T.H., and Ma, F.W. 2010. Physiological responses and relative tolerance by Chinese apples rootstocks to NaCl stress. *Scientia Hort*. 126:247-252.

Table 1. Main effect of salinity on different plant growth parameters

Salinity	RDW* (g/plant)	SDW** (g/plant)	Root/shoot	Plant height (cm)	Leaf area (cm^2)
1.5 dS m^{-1} (control)	59.9 a	930.6 a	6.7 a	234.4 a	1568 a
3 dS m^{-1}	61.0 a	624.7 b	9.7 a	198.7 b	1093 b
6 dS m^{-1}	60.2 a	462.1 bc	12.0 a	186.0 c	768 bc
9 dS m^{-1}	38.3 a	305.0 c	11.7 a	161.5 d	508 c
LSD	37.7	205.3	7.489	8.0	375

*RDW=Root dry weight; **SDW=Shoot dry weight. Statistical analysis was applied separately to each column. Within a column, values accompanied with the same later are not significantly different.

Table 2. Main effect of grafting treatments on different plant growth parameters

Grafting Treatments	RDW* (g/plant)	SDW* (g/plant)	Root/shoot	Plant height (cm)	Leaf area (cm^2)
Galia/53004	48.5 c	6070 b	9.352 b	205.0 a	1113 ab
Galia/53009	68.5 a	5871 b	12.30 a	211.2 a	922 c
Ananas/53004	71.3 a	6860 a	12.10 a	202.8 a	1221 a
Ananas/53009	59.4 b	6620 a	9.144 b	202.6 a	1052 b
Galia/non-grafted	35.0 d	4664 c	7.626 c	164.2 c	845 cd
Ananas/non-grafted	46.4 c	4751 c	9.826 b	185.2 b	756 d
LSD	7.21	27.41	0.9262	12.76	112

*RDW=Root dry weight; **SDW=Shoot dry weight. Statistical analysis was applied separately to each column. Within a column, values accompanied with the same later are not significantly different.

Table 3. Interactive effects of salinity and grafting treatments on plant growth parameters

Salinity (dS m^{-1})	Grafting combination	RDW* (g/plant)	SDW* (g/plant)	Root/shoot	Plant height (cm)	Leaf area (cm^2)
1.5	Galia/53004	68.0 cd	1354.0 a	5.1 lm	245.8 abc	2550 a
	Galia/53009	59.0 cdef	891.7 c	6.8 jkl	259.2 ab	1308 cd
	Ananas/53004	55.0 cdef	987.7 b	5.5 klm	271.7 a	1713 b
	Ananas/53009	63.7 cde	862.5 cd	7.6 hijk	240.0 bc	1417 c
	Galia NG	60.0 cdef	789.5 e	7.7 hij	179.5 h	1315 cd
	Ananas NG	53.7 def	698.7 f	7.8 hij	210.5 defg	1108 def
3	Galia/53004	65.0 cde	516.1 hij	11.9 def	218.9 cde	973 efg
	Galia/53009	71.0 c	464.9 jk	14.5 c	180.5 h	1023 efg
	Ananas/53004	69.0 cd	913.9 c	7.1 ijk	212.2 def	1648 b
	Ananas/53009	68.0 cd	814.4 de	7.9 hij	201.6 efgh	1197 cde
	Galia NG	45.0 f	552.3 h	7.7 hij	189.1 fgh	919 fgh
	Ananas NG	48.0 ef	486.7 ijk	9.3 gh	189.9 fgh	800 ghi
6	Galia/53004	43.0 f	294.7 no	13.9 cd	180.5 h	490 jk
	Galia/53009	91.0 b	640.3 g	13.5 cde	230.4 cd	778 ghi
	Ananas/53004	109.0 a	545.6 hi	19.0 a	179.5 h	1029 efg
	Ananas/53009	52.0 def	540.5 hi	9.2 ghi	187.2 fgh	904 fgh
	Galia NG	16.0 h	350.5 mn	4.6 m	144.0 i	819 ghi
	Ananas NG	50.0 ef	400.9 lm	11.9 def	194.1 efgh	589 ij
9	Galia/53004	18.0 h	263.3 o	6.5 jklm	174.7 h	438 jk
	Galia/53009	53.0 def	351.3 mn	14.4 c	174.7 h	578 ijk
	Ananas/53004	52.0 def	297.0 no	16.7 b	147.8 i	494 jk
	Ananas/53009	54.0 def	430.7 kl	12.0 ef	181.4 gh	688 hij
	Galia NG	19.0 h	173.4 p	10.4 fg	144.0 i	327 k
	Ananas NG	34.0 g	313.9 no	10.3 fg	146.5 i	525 jk
LSD		14.4	548	1.852	25.52	223

*RDW=Root dry weight; **SDW=Shoot dry weight. Statistical analysis was applied separately to each column. Within a column, values accompanied with the same later are not significantly different.

Cushaw Squashes (*Cucurbita argyrosperma*) as pollinators for *C. maxima* x *C. moschata* hybrids.

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Introduction

Interspecific *Cucurbita maxima* × *C. moschata* F_1 hybrid winter squashes are commonly grown in Japan and Brazil (5), with 'Tetsukabuto' being the most well-known cultivar. *Cucurbita maxima* × *C. moschata* F_1 hybrids have a high degree of male sterility and are planted with one of the parental species as a pollinator to induce fruit set. Both *C. maxima* and *C. moschata* are known to form hybrids with a third species *C. argyrosperma*, commonly known as the cushaw squashes (1,2,3,4,6,7,9). Because both parents of the interspecific hybrid cultivars are known to form hybrids with *C. argyrosperma* easily, it was hypothesized that *C. argyrosperma* could serve as a third pollinator option for the male sterile cultivars. To the authors' knowledge, *C. argyrosperma* has never been reported as an effective pollinator for *Cucurbita maxima* × *C. moschata* F_1 hybrids.

Materials and Methods

During the summer of 2014 in Mansfield Center, Connecticut USA 10 female flowers of the interspecific cultivar 'Tetsukabuto' were pollinated with male flowers of 'Green Striped Cushaw' *C. argyrosperma*. Also in 2014, additional interspecific lines were generated by crossing *C. moschata* 'JWS 6823' x C. maxima 'Speckled Hound', and *C. moschata* 'Metro' x *C. maxima* 'Rouge Vif D' Etampes'. In 2015, 73 hand pollinations were conducted, 25 female flowers of the three different *C. maxima* x *C. moschata* hybrids were pollinated by cultivars of *C. argyrosperma*. Furthermore, as a comparison, 48 female interspecific flowers were pollinated with pollen from parental species, 24 with *C. maxima* pollen and 24 with *C. moschata* pollen. All hand pollinations were done using the standard masking tape pollinator exclusion method (8).

Results and Discussion

In 2014, four of the 10 interspecific hybrid x *C. argyrospera* hand pollinations resulted in fruit. In 2015, 12 of 25 pollinations or 48% of the female flowers set with *C. argyrosperma* as the pollen parent (Table 1). Additionally, 13 of 24 or 54% of the flowers pollinated with *C. maxima* were successful. Similarly, 13 of 24 or 54% of the pollinations involving *C. moschata* also formed fruits. Only fully developed mature fruit were counted as set fruits. All 12 fruits that resulted from *C. argyrosperma* as a pollen parent did not contain any viable seeds. The fruits that resulted from using *C. maxima* or *C. moschata* as a pollinator were not systematically searched for seeds but from casual observation they generally contained 1-5 seeds that appeared viable with fully developed embryos.

From this small 2 year study it appears that *C. argyrosperma* can serve as an effective pollinator for male sterile *C. maxima* x *C. moschata* F_1 cultivars, and that fruit set rates are similar to using the typical pollinators *C. maxima* and *C. moschata*. This information could be useful in a few horticultural situations where the grower desires a harvest of *C. maxima* x *C. moschata* F_1 cultivars and *C. argyrosperma* fruit only.

Literature Cited

1. Connolly, B. 2007. Viable seed production of temperate *Cucurbita moschata* germplasm when pollinated by *C. argyrosperma*. Cucurbit Genetics Cooperative Report 30:47-49.
2. Cuevas-Marrero, H., and L. Wessel-Beaver. 2008. Morphological and RAPD marker evidence of gene flow in open pollinated populations of *Cucurbita moschata* interplanted with *C. argyrosperma*. Cucurbitaceae 2008, Proceedings of the IXth EUCARPIA meeting on genetics and breeding of Cucurbitaceae (Pitrat M, ed), INRA, Avignon (France).
3. Merrick, L.C. 1990. Systematics and evolution of a domesticated squash, *Cucurbita argyrosperma*, and its wild and weedy relatives. In: D.M. Bates, R.W. Robinson and C. Jeffrey, eds., Biology and Utilization of the Cucurbitaceae. Cornell University Press, Ithaca.
4. Merrick, L.C. 1991. Systematics, Evolution, and Ethnobotany of a Domesticated Squash, *Cucurbita argyrosperma*. Ph.D. dissertation, Cornell University. 323 pp.
5. Uretsky, J. 2012. Development and evaluation of interspecific *Cucurbita maxima* x *Cucurbita moschata*

hybrids for processing squash. M.S., University of New Hampshire.
6. Wessel-Beaver, L. 2000. *Cucurbita argyrosperma* sets fruit in fields where *C. moschata* is the only pollen Source. Cucurbit Genetics Coop Rpt. 23:62-63
7. Wessel-Beaver L., H.E. Cuevas, T.C. Andres, and D.R. Piperno. 2004. Genetic compatibility between *Cucurbita moschata* and *C. argyrosperma*. In: Progress in Cucurbit Genetics and Breeding Research, Proceedings of Cucurbitaceae 2004, the 8th EUCARPIA Meeting on Cucurbit Genetics and Breeding, (Lebeda A, Paris HS, eds.), Palacky University, Olomouc (CZ) pp 393-400.
8. White, R. and B. Connolly. 2011. Breeding Organic Vegetables; A Step by Step Guide for Growers. Northeast Organic Farming Association of New York Inc. Rochester, NY.
9. Yongan, C., Z. Bingkui, Z. Enhui, and Z. Zunlian. 2002. Germplasm innovation by interspecific crosses in pumpkin. Cucurbit Genetics Cooperative Report 25: 56-57.

Table 1. Fruit set in interspecific F1 hybrids (*Cucurbita moschata* x *C. maxima* or *C. maxima* x *C. moschata*) using *C. argyrosperma, C. maxima* or *C. moschata* as pollen parents.

Maternal parent (interspecific hybrid)[1]	Pollen parent		No. of pollinations	No. of fruit Set	Fruit Set (%)
	Species	Cultivar			
JWS 6823 x Speckled Hound	*C. argyrosperma*	Gold Striped Cushaw	1	1	100.00
JWS 6823 x Speckled Hound	*C. argyrosperma*	Green Striped Cushaw	4	3	75.00
JWS 6823 x Speckled Hound	*C. argyrosperma*	Jonathon	3	2	66.67
Metro x Rouge Vif D' Etampes	*C. argyrosperma*	Gold Striped Cushaw	4	1	25.00
Metro x Rouge Vif D' Etampes	*C. argyrosperma*	Green Striped Cushaw	1	0	0.00
Metro x Rouge Vif D' Etampes	*C. argyrosperma*	Jonathon	1	0	0.00
Tetsukabuto	*C. argyrosperma*	Gold Striped Cushaw	3	0	0.00
Tetsukabuto	*C. argyrosperma*	Green Striped Cushaw	5	3	60.00
Tetsukabuto	*C. argyrosperma*	Jonathon	3	2	67.67
		Pollen species total	**25**	**12**	**48.00**
JWS 6823 x Speckled Hound	*C. maxima*	Blue Hubbard	13	7	53.85
JWS 6823 x Speckled Hound	*C. maxima*	Silver Moon	1	1	100.00
Metro x Rouge Vif D' Etampes	*C. maxima*	Blue Hubbard	2	1	50.00
Metro x Rouge Vif D' Etampes	*C. maxima*	Silver Moon	4	3	75.00
Tetsukabuto	*C. maxima*	Blue Hubbard	4	1	25.00
		Pollen species total	**24**	**13**	**54.17**
JWS 6823 x Speckled Hound	*C. moschata*	Autumn Buckskin	2	1	50.00
JWS 6823 x Speckled Hound	*C. moschata*	Butterbush	6	1	16.67
JWS 6823 x Speckled Hound	*C. moschata*	Honeynut x Long Island Cheese	1	0	0.00
JWS 6823 x Speckled Hound	*C. moschata*	JWS 6823	2	2	100.00
JWS 6823 x Speckled Hound	*C. moschata*	Tahitian	1	1	100.00
JWS 6823 x Speckled Hound	*C. moschata*	Waltham Butternut	4	4	100.00

(continued on next page)

Table 1 (continued)

Interspecific hybrid	Pollen species	Pollen cultivar	No. of pollinations	No. of fruit Set	Fruit Set (%)
Metro x Rouge Vif D' Etampes	*C. moschata*	Butterbush	1	1	100.00
Metro x Rouge Vif D' Etampes	*C. moschata*	JWS 6823	1	1	100.00
Metro x Rouge Vif D' Etampes	*C. moschata*	Waltham Butternut	3	1	33.33
Tetsukabuto	*C. moschata*	Waltham Butternut	3	1	33.33
		Pollen species total	**24**	**13**	**54.17**

[1] All interspecific F_1s are *C. moschata x C. maxima* except Tetsukabuto which is *C. maxima x C. moschata*.

Cucumber Gene Catalog 2017

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Introduction

This is an update of the 2010 version of Cucumber Gene List (Call and Wehner 2010). Since the public release of the cucumber draft genome in 2009, significant progress has been made in developing cucumber genetic and genomics resources. Many mutants have been identified and a number of genes or QTL have been tagged with molecular markers or cloned, which provides a better understanding of the inheritance and underlying genetic mechanisms of horticulturally important traits in cucumber. Major revisions have been made in this 2017 version of the cucumber gene catalog to reflect progress made in last several years. The following are some important changes made in this latest version of cucumber gene list.

A. This 2017 version focuses only on cucumber mutations with well defined, visible phenotypic changes, or of horticultural importance. Genes for isoenzymes were removed from the list.
B. Only simply inherited genes and QTL with large effects for disease resistances or other horticulturally important traits are listed.
C. Eight simply inherited genes were retired including *c* (*creamy fruit color*), *cd* (*chlorophyll deficient*), *P* (*Prominent tubercles*), *I* (*Intensifier of P*), *pr* (*protruding ovary*), *s* (*spine size and frequency*), *s-2* (*spine-2*), and *s-3* (*spine-3*). Reasons for this treatment: the reported mutants have lost and similar mutants have not been recovered; new evidence does not support the existence of such genes; the observed mutation may be the result of pleiotropy of another gen; or new evidence has provided better explanation of the early findings.
D. The watermelon mosaic resistance gene *wmv-1-1* was retired because it is the same as *prsv-1* for resistance to the watermelon strain of papaya ringspot virus.
E. The three genes for powdery mildew resistance, *pm-1*, *pm-2*, and *pm-3*, were retired because QTL mapping studies have identified major-effect QTL with more accurate information.
F. Two genes were renamed: *l* (for *locule number*) was replaced with *cn* (*carpel number*); *bl* (*blinded*) was replaced with *bld*; *bl* is now assigned for "*bitter leaf*".
G. Three genes were assumed to be synonymous, respectively to three new genes: *bi-1* = *bi* (*bitterfree foliage and fruits*); *bi-2* = *bl* (bitter leaf); *Bt-1* = *Bt* (*bitter fruits*).
H. For 11 genes, gene symbols were not available in the original publications. For convenience, we assigned a gene symbol for each gene or QTL in this revision. They are *a-1* for androecy, *sf* for small flower, *bf* for big flower, *lgp* for light green peel, *lgf* for light green fruit, *sfr* for short fruit, *lfr* for long fruit, *qFoc* for resistance QTL to Fusarium wilt, *qCYSDV* for resistance to CYSDV, *qCVYV* for resistance to CVYV, and *qMYSV* for resistance to MYSV.
I. In total, **73** new genes or major-effect QTL were added to the 2017 version bringing total number of genes in the 2017 Cucumber Gene List to **199**. Below are descriptions of the **199** genes in the 2017 Version which were listed, in order, in the following categories:

1. Hypocotyl and stem mutants
2. Cotyledon and leaf mutants
- 2.1 Leaf color
- 2.2 Leaf shape
- 2.3 Leaf size, petiole length and position
- 2.4 Trichomes

3. Flower mutants
- 3.1 Sex determination
- 3.2 Flower color
- 3.3 Flower number, size and positon
- 3.4 Flowering time
- 3.5 Male sterility

4. Fruit mutants
- 4.1 Fruit skin texture and color
- 4.2 Fruit spine number, size and color
- 4.3 Fruit internal structure
- 4.4 Fruit size and shape

4.5 Fruit flesh color and tastes
4.6 Fruit shelf life
4.7 Parthenocarpic fruit set

5. **Plant architecture**
6. **Disease and insect resistances**
   6.1 Resistance to bacterial and fungal pathogens
   6.2 Resistance to viral pathogens
   6.3 Resistance to root knot nematodes
   6.4 Insect resistance
7. **Abiotic stress tolerance**
8. **Miscellaneous mutants**

The alphabetic order of all genes is presented in **Table 1** including the year each gene was listed. The approximate locations of genes in seven cucumber chromosomes, when available, are shown in **Figure 1**. Researchers are encouraged to send the seeds of the mutant lines to either the cucumber gene curator (Yiqun Weng) or deposit in a publicly accessible germplasm storage facility or gene bank. Researchers are also encouraged to report new genes to the cucumber gene curator. To avoid inadvertent duplication of gene names and symbols, we hope that scientists will consult this list as well as the rules of gene nomenclature for the Cucurbitaceae before selecting a gene name and symbol, which can be found in each CGC Report. Please inform us any omissions or errors in this gene list. For any comments or suggestion, please contact Yiqun Weng at yiqun.weng@wisc.edu.

1. Hypocotyl and stem mutants

Blind (***bld***): lack of growing point in terminal bud; effect of gene affected with environment factors (Carlsson, 1961). The previously assigned gene symbol "*bl*" for this mutant is assigned to "*bitter leaf*".

Fasciated (***fa***)): Fasciated plants have with wide, flattened stems and increased numbers of leaves, tendrils, and flowers per node (Robinson, 1978a; Shifriss, 1950). Expression is influenced by environmental conditions.

Green stem (***Gs***): dark green stem, leaf and fruits due to increased chlorophyll content; dark green fruit has longer shelve life; dark green is monogenic, dominant or incomplete dominant over regular green; AFLP markers are available for this gene (Haaring, 2014).

Yellow stem (***ys***): yellow cotyledons that gradually turns creamy; creamy stems, leaf petioles and leaf veins; shorter hypocotyl, internode and vine length (Rucinska et al., 1991).

Tendrilless (***td***): Irradiation induced mutant with no tendrils on plant (Rowe and Bowers, 1965).

Tendrilless-1 (***td-1***): no tendrils on B007 mutant plant, dwarf, trichome-free, identified from an EMS mutagenesis population from a North China type cucumber line CCMC (Li YH, personal communication).

Tendrilless (***ten***): tendril-less spontaneous mutation from CG9192, a landrace from the semi-wild Xishuangbanna cucumber (*C. sativus* var. *xishuangbannesis*) of subtropical Southwest China. The mutant plant forms branches instead of tendrils. The affected gene *TEN* encodes a TCP transcription factor (Wang et al., 2015)

Opposite tendrils on stem (***ots***): EMS induced mutation from a North China type cucumber line "Shannong No 5", tendrils on opposite positions (Wang et al., 2014a).

Long hypocotyl (***lh***): increased hypocotyl and internode length (Robinson and Shail, 1981; Koornneef and van der Knaap, 1983).

Short hypocotyl (***sh1***): short hypocotyl compared with regular cultivated cucumber, identified in the semi-wild Xishuangbanna accession SWCC8 (*C. sativus* var. *xishuangbannanesis*); mapped in chromosome 3; encodes a human SMARCA3-like chromatin remodeling factor (Bo et al., 2015; Bo et al., 2016).

2. Cotyledon and leaf mutants

2.1 Leaf color

Golden cotyledon (***gc***)**:** monogenic, recessive, lethal, cotyledons butter-colored, seedlings died after 6-7d (Whelan and Chubey, 1973).

Albino cotyledon (***al***): Irradiation induced mutation from 'Nishiki Suyo'; cotyledons white, hypocotyl light green (Iida and Amano, 1991).

Light green cotyledon-1 (***lg-1***). Irradiation induced mutation from 'Nishiki Suyo'; initially, cotyledons and young leaves light green, becoming normal green later (Iida and Amano, 1991); phenotypically similar to *v*, *v-1* mutants.

Light green cotyledon-2 (***lg-2***). Irradiation induced mutation from 'Nishiki Suyo'; initially, cotyledons and young leaves light green, becoming normal green earlier than *lg-1* (Iida and Amano, 1991); allelism with *lg-1* unknown; phenotypically similar to *v*, *v-1* mutants.

Yellow cotyledon-1 (***yc-1***)**:** yellow seedling develops green color one week after germination (Aalders, 1959). In NCG-042, cotyledons and true leaves all start with yellow, and turn to green gradually; *yc-1* and *v-1* are two independent loci with 9 to 7 segregation in F_2 for leaf color (Miao et al., 2010a).

Yellow cotyledon-2 (***yc-2***): pale-yellow cotyledons became normal green when exposed to light of normal

intensity; *yc-1* and *yc-2* are two different loci (Whelan and Chubey, 1973; Whelan et al., 1975).

***Golden leaf* (*g*):** gold color lower leaves (Tkachenko, 1935); presumably the same as *virescent leaf*.

***Virescent leaf* (*v*):** yellow leaves change to green (Tkachenko, 1935; Poole, 1944).

Virescent leaf-1 (v-1): Yellow cotyledons change to green; first 3-4 true leaves start with yellow then turn to green; from 9110Gt; mapped in chromosome 6 with the candidate gene *CsaCNGCs* encoding a cyclic-nucleotide-gated ion channel protein (Miao et al., 2011a, 2016).

***Variegated virescence* (*vvi*):** Yellow cotyledons turn green in 7-10d; true leaves start with pale yellow that become strongly variegated in a green and white pattern. Hypocotyl, stem and petioles white to light green; corolla lighter yellow than normal; plant grows slower and smaller in size (Abul-Hayja and Williams, 1976). The allelic relationship among *v*, *v-1* and *vvi* is unknown.

Yellow plant (***yp***): Plant is light yellow green throughout life with slow growth and small plant size (Abul-Hayja and Williams, 1976). A mutant (C528) with similar phenotype was recovered from EMS mutagenesis population from a North China type cucumber CCMC. The chlorophyll-deficient golden leaf mutation in C528 is due to a single nucleotide substitution in *CsChlI* for magnesium chelatase I subunit (Li et al., 2015a; Gao et al., 2016)

***Light sensitive* (*ls*):** Monogenic, recessive, cotyledons smaller than normal; viable except under full sun (Whelan, 1972b; Whelan and Chubey, 1973).

***Pale lethal* (*pl*):** Monogenic, recessive, lethal, cotyledons paler than normal; recognized 2d after emergence; seedling died after 6-7d (Whelan and Chubey, 1973).

2.2 Leaf shape

Blunt leaf apex (***bla***): leaf apex is more obtuse than normal reduced leaf lobing and serration; easily recognized throughout whole development stage (Robinson, 1987a).

Cordate leaf-1 (cor-1): spontaneous mutation with normal flower structure and seed production (Gornitskaya, 1967).

Cordate leaf-2 (cor-2): late flowering, calyx segments tightly clasp corolla, hindering flower opening and insect pollination; parthenocarpic fruit setting (Robinson, 1987b).

***Crinkled leaf* (*cr*)**: leaves are wrinkled, only recognizable in true leaves (Odland and Groff, 1963a).

Divided leaf (dvl): True leaves are partly or fully divided or dissected, often resulting in compound leaves with 2-5 leaflets; recognizable by first true leaf; corollas have deep incisions (den Nijs and Mackiewicz, 1980).

Divided leaf-2 (***dvl-2***): Chemically induced mutation from "Borszczagowski"; divided leaves after the 2nd true leaf; flower petals free; similar to *dvl*, but allelism not checked (Rucinska et al., 1992b).

***Umbrella leaf* (*ul*)**: Under certain temperature and relative humidity, new leaves expand unevenly with leaf margin growing less than leaf blade resulting in downward or upward curled leaves reminiscent of an umbrella (den Nijs and de Ponti, 1983).

Ginkgo leaf (***gi***): spontaneous mutant; branched leaves resembling leaves of ginkgo; male sterile (John and Wilson, 1952).

Ginkgo leaf-2 (***gi-2***): chemically induced mutation from Borszczagowski; spatulate leaf blade with reduced lobing and altered veins; recognizable at the 2nd true leaf stage; similar to *gi*, fertile instead of sterile (Rucinska et al., 1992b).

Heart shaped leaf (***hsl***): Irradiation induced mutation from 'Nishiki Suyo'; leaves round-heart shaped; tendrils often branched (Iida and Amano, 1991).

Heart leaf (***hl***): Heart shaped leaves in WI 2757 (Vakalounakis, 1992).

Non-serrated leaf (***nsl***): an EMS-induced mutant from Poinsett 76 cucumber; leaf edge appears smooth (Fraenkel et al., 2014). We propose gene symbol '*nsl*' for this mutant.

Delayed growth (***dl***): reduce length of hypocotyl and first few internodes; slow growth; weakly linked with *de* (Miller and George, 1979).

Shrunken leaf (***shl***): Irradiation induced mutation from 'Nishiki Suyo'; first leaf shrunken, but later leaves progressively more normal (Iida and Amano, 1991).

Clustered leaves (***cll***): EMS induced mutation from a North China type cucumber line "Shannong No 5", true leaves clustered (Wang et al., 2014a).

Wilty leaf (***wi***): Irradiation induced mutation from 'Nishiki Suyo'; rim of leaves wilted (Iida and Amano, 1991).

Fused cotyledon (fc): an EMS-induced mutant from Poinsett 76 cucumber; cotyledons fused together (Fraenkel et al., 2014). We propose gene symbol '*fc*' for this mutant.

Horn-like cotyledon (***hn***): Irradiation induced mutation from 'Nishiki Suyo'; cotyledons warped like the thorns of a bull, but transverse section of stem was circular (Iida and Amano, 1991).

Revolute cotyledon (***rc***): cotyledons are short, narrow, and cupped downward (Whelan et al., 1975).

Revolute cotyledon-2 (***rc-2***): Recessive gene for revolute cotyledons; *rc-2* from NCG-0093 (short petiole mutant) (Wehner et al., 1998b).

Stunted cotyledon (***sc***): cotyledons short, narrow, and cupped downwards; enlarged perianth (Shanmugasundarum et al., 1972).

Wavy rimmed cotyledons **(*wy*)**: Irradiation induced mutation from 'Nishiki Suyo'; center of cotyledons occasionally white and rims green, later becoming wavy (Iida and Amano, 1991).

Necrotic lesions on cotyledons (***nlc***): an EMS-induced mutant from Poinsett 76 cucumber; spontaneous necrotic spots appear on cotyledons (Fraenkel et al., 2014).

2.3 Leaf size, petiole length and position

***Littleleaf (ll*)**: a spontaneous mutant found in the field; carried by H-19 (Goode et al., 1980; Wehner et al., 1987); mapped in chromosome 6 (Weng et al., 2010).

Littleleaf-2 (***ll2***): a major-effect QTL for small leaf size in the wild cucumber (*C. sativus* var. *hardwickii*) (PI 183967); mapped in chromosome 7 (Shi et al., 2014).

Short petiole-1 (***sp***): very short petioles of first true leaf, leaf blade smoothly narrows to the petiole; later leaves have petioles shorter than wild type; opposite arrangement of the first leaves due to very short internode (den Nijs and Boukema, 1985).

Short petiole-2 (***sp-2***): from mutagenesis of 'Borszczagowski'; small statue, shorter hypocotyl and petioles, crinkled leaves, short or no branch (Rucinska et al., 1992a).

Dwarf cotyledons-1 (***dwc-1***): Irradiation induced mutation from 'Nishiki Suyo'; cotyledons small and hypocotyl short; leaves not expanding (Iida and Amano, 1991).

Dwarf cotyledons-2 (***dwc-2***): Irradiation induced mutation from 'Nishiki Suyo'; cotyledons small and hypocotyl short; leaves not expanding; allelism with *dwc-1* unknown (Iida and Amano, 1991).

Gigantism (***gig***): Chemically induced mutation from Borszczagowski; first true leaf larger than normal (Kubicki et al., 1984).

Opposite leaf arrangement (***opp***): a single recessive gene linked with *m* and *cn*; incomplete penetrance; difficult to score (Robinson, 1987d).

2.4 Trichomes

Glabrous (***gl***): chemically induced mutation; glossy foliage and fruit, link with the yellow cotyledon (*yc*) gene (Inggamer and de Ponti, 1980; Robinson and Mishanec, 1964).

Glabrous 1 (***gl-1***, syn. ***Csgl1, mict***): spontaneous mutant from a North China type cucumber cultivar Daqingba. All aerial parts (leaves, stems, tendrils, floral organs, and fruits) are glabrous; mapped in chromosome 3; encodes a member of the homeodomain-leucine zipper I (HD-Zip I) proteins; *CsGL1* may be involved in foliar trichome development but not initiation (Cao et al., 2001; Li et al., 2015b).

***Micro-trichome (mict, Csgl1*)**: A spontaneous mutant from North China inbred line 06-1, glabrous leaves, stems, flowers, tendrils and fruits; trichomes only visible under microscope with >20× magnifications; same mutant as *gl-1*; the loss-of-function *csgl1* is due to a 2649-bp genomic DNA deletion spanning the first and second exons of *CsGL1* non-allelic with *gl-2* (Zhao et al., 2015).

Tiny branched hair (***tbh,*** syn. ***Csgl1***): spontaneous mutant from North China cucumber line R1407, glabrous foliage and fruits; no visible trichomes under light microscope (Chen et al., 2014).

Glabrous-2 **(*Csgl-2*)**: NCG-042 with few small fine hairs on fruit peduncle, pedicel and calyx of flowers, but stem, leaf and leaf petioles are smooth; mapped in chromosome 2 (Yang et al., 2011).

Glabrous-3 (Csgl-3; Syn. ***tril)***: A spontaneous glabrous mutant *csgl3* was identified in WI7412, a recombinant inbred line progeny from the cross between WI2757 and True Lemon cucumber inbred lines. WI7412 is completely trichome-free on all above-ground organs. *Csgl3* encodes a class IV homeodomain-associated leucine zipper (HD-ZIP) transcription factor. The loss-of-function of *CsGL3* in the mutant is due to the insertion of a 5-kb long terminal repeat retrotransposon in the 4th exon of *CsGL3*. (Pan et al., 2015). The glabrous mutant NCG157 is caused by mutations within the same gene (Cui et al., 2016).

Trichome-less (***tril;*** Syn. ***CsGl3***): mutant that was completely free from trichomes on all aerial organs, which is true even under an SEM suggesting the *Tril* gene may function in trichome cell fate determination (Wang et al., 2016b).

Glabrate (glb)*:* glabrous, but not completely hairfree (Whelan, 1973); similar to *gl-2* mutant NCG-042 (Yang et al., 2011).

3. Flower mutants

3.1 Sex determination

Cucumber has long been served as a model for study of sex determination in plants (Galun, 1961; Kubicki, 1969a, b, c, d). Three types of flowers can be present in a cucumber plant: staminate (male), pistillate (female) and hermaphrodite (bisexual/perfect). By default, all floral buds contain staminate and pistillate primordia at early stages of development; selective arrest of either staminate or pistillate flower development results in female or male flowers, respectively, and no abortion of either staminate or pistillate primordia allows development of hermaphroditic flowers (Galun, 1961). Three genes *F*, *m*, and *a* have been proposed to be the main mechanisms in sex determination in cucumber (Rosa, 1928; Tkachenko, 1935; Galun, 1961; Shifriss, 1961; Wall, 1967; Kubicki, 1969a, b, c, d; Mibus and Tatlioglu, 2004; Li et al., 2012). Based on this three-gene model, a cucumber plant may be monoecious (*MMffAA*, with both male and female flowers), gynoecious (*MMFFAA* or *MMFFaa* with only female flowers), andromonoecious (*mmffAA* with bisexual flowers and male flowers), hermaphroditic (*mmFFAA*, or *mmFFaa*, with only perfect flowers), or androecious (*MMffaa* or *mmffaa* with only male flowers) (Mibus and Tatlioglu, 2004). However, genetic control of sex expression in cucumber seems to be more complicated than the three-gene model. Additional genes or modifiers are possible. Environmental factors such as photoperiod, temperature can also influence sex expression in cucumber plants.

***Femaleness* (*F*):** partially dominant; several studies (Kamachi et al., 1997, 2000; Trebitsh et al., 1997; Yamasaki et al., 2003; Mibus andTatlioglu, 2004; Knopf and Trebitsh, 2006) have identified *CsACS1G* in chromosomes 6 as the most possible candidate gene of the *F/f* locus. Gynoecy is due to a duplication of *CsACS1*. Molecular markers tagging the *F* allele are available (Zhang et al., 2015; Win et al., 2015).

Andromonoecious (m): Lemon cucumber plant produces bisexual flowers; plant s are andromonoecious; located in chromosome 1 and encodes *CsACS2* (Boualem et al., 2009, 2014; Li et al., 2008, 2009); the *mm* genotype is pleiotropic, and the fruits are often round shaped with protruding ovaries (Robinson, 1978c).

***Androecy* (*a-1*):** An EMS mutant, 406a bearing only male flowers on the main stem and lateral shoots identified from the monoecious line 406. The androecy phenotype is conditioned by a single recessive gene *CsACO2*, which encodes an ACC oxidase gene (Chen et al., 2016). We designated this gene as *a-1*.

***Andromonoecious-1* (*m-1*)**: new allele of the *m* locus; identified in hermaphroditic H38 (Tan et al., 2015). H38 has elongated fruit.

Andromonoecious (***m-2***): a recessive gene in a chemically induced mutant from cv. Borszczagowski; andromonoecious plants; bisexual flower set elongated fruits (instead of round or oval fruits like in Lemon cucumber); independent of *F* and *m* genes; trimonoecious under certain conditions; the gene was originally named '*h*' (Kubicki, 1974).

Trimonoecious (***Tr***): plants with staminate, bisexual and pistillate flowers; bisexual flowers form superior ovaries, single dominant major gene; independent of *F* and *m* genes (Kubicki, 1969d).

Trimonoecious-1 (***tr-1***): The line 'GW' (selfed progeny of cucumber variety 'Hi-green') is trimonoecious with elongated fruits from hermaphrodite flowers; hermaphrodite flowers usually turn into female flowers in higher nodes; expression affected by temperature conditions; controlled by a single recessive gene; originally name '*h*' (Fujieda and Fujita, 1978). Phenotypically similar to the mutant by Kubicki (1974), but is recessive.

Subgynoecious-1 (***Mod-F1***): in cucumber line S-2-98, incomplete dominance; enhances intensity of femaleness; high ratio of female to male flowers with continuous female flower nodes at high node positions; independent of *F* and *M* loci (Chen et al., 2011). The subgynoecious sex expression in S-2-98 is determined by three QTL, *sg3.1*, *sg6.1*, and *sg6.2* with *sg3.1* having the largest effect (Bu et al., 2016),

Subgynoecious-2 (***mod-F2***): in cucumber line 97-17, recessive, enhances intensity of femaleness, high ratio of female to male flowers with continuous female flower nodes at high node positions; independent of *F* and *M* loci (Chen et al., 2011).

Androecious (***a***): increases maleness; *A* is suppressed by the dominant *F* allele, however the recessive *a* allele intensifies the male tendency in *ff* genotypes (Kubicki, 1969c). The androecious gene (*A*) is *CsACS11* on Chromosome 2 (Boualem et al., 2015).

Intensifier of F (In-F): intensifier of the *F* gene to increase femaleness (Kubicki, 1969b).

Gynoecious (gy): recessive gene for high degree of pistillate sex expression, chemically induced mutant from cv. Borszczagowski; the gene was originally named '*g*' (Kubicki, 1974).

Gooseberry fruit (***gb***): Oval shape of fruit of Klin cucumber (trimonoecious), small size of fruit, long

dense hairs on the surface of ovary, smooth tight rind not liable to become covered with a network of fissures, dark stripes in the place where the principal meridional veins pass through the fruit flesh, luxuriant growth of the receptacle, tendency of the flesh to deep splitting (Tkachenko, 1935).

Male pygmy **(*mpy*)**: Dwarf plant with only staminate flowers in Gnome 1, a selection of 'Rochford's Improved' (Pyzhenkov and Kosareva, 1981).

3.2 Flower color

Green corolla (***co***): green petals; has enlarged but sterile pistils (Hutchins, 1935).

Orange-yellow corolla (***o***): pale yellow corolla, recessive, but observed only in single instance (Tkachenko, 1935); Poole (1944) suspected the '*green corolla* (*co*)' (Hutchins, 1935) might be the same as the '*orange-yellow corolla* (*o*).

3.3 Flower number, size and positon

Negative geotropic peduncle response (***n***): flower stem/fruit peduncle grow downward; *n* linked with *m* (Odland and Groff, 1963b).

Multiple pistillate flowers (***mp***): multiple pistillate flowers per node; single recessive gene (Nandgaonkar and Baker, 1981)

Multiple pistillate flower-2 (***Mp-2***): clustering of pistillate flowers; single dominant gene assigned by Pierce and Wehner (1990); modifier genes influence the amount of clustering; clustering of perfect flowers is controlled by genes different from clustering of gynoecious flowers (Thaxton, 1974).

Plural pistillate flower (***pf***): plural pistillate flowering controlled by 3 alleles with single pistillate being incompletely dominant over multiple pistillate: pf^{+} for single pistillate, pf^{d} for double pistillate and pf^{m} for multiple pistillate (>2 per node) (Fujieda et al., 1982). Miao et al. (2010b) identified six QTLs for control of twin female flowers in North China type cucumber 9930 with major-effect QTLs in chromosomes 3 and 6.

Choripetalous (***chp***): Chemically induced mutant from "Borszczagowski"; small first true leaf; choripetalous flowers; glossy ovary; small fruits; few seeds (Kubicki and Korzeniewska, 1984).

Twin fused fruit (***tf***)**:** spontaneous mutant from cucumber line B5263; single recessive; two separate pistallate flowers with partially joined ovaries on a single peduncle at a node develop into twin fused fruit; only observed on gynoecious plants (Klosinka et al., 2006).

Small flower (***sf***): EMS induced mutation from a North China type cucumber line "Shannong No 5", smaller flower size (both male and female) size than wild type (Wang et al., 2014a).

Big flower (bf): EMS induced mutation from a North China type cucumber line "Shannong No 5", bigger flower size (both male and female) size than wild type (Wang et al., 2014a).

3.4 Flowering time

Flowering time is a quantitative trait, but QTL mapping studies have revealed only one or two major QTL for flowering time in cucumber in each case (for example, Bo et al., 2015). Cultivated cucumber is typically day-neutral plants; some landraces or wild cucumbers require short days for flowering.

Delayed flowering (***df***): a single gene responsible for short-day response (Della Vecchia et al., 1982).

Days to anthesis (***Da1.1***): Using population from 9110Gt × 9930 RILs (with 2 days difference in flowering time), one QTL, *qDa1.1*, was detected in chromosome 1 (Miao et al., 2012).

Early flowering (***Ef1.1***): QTL mapping in a population from cross between Muromskij (early flowering) and 9930 (late flowering) identified a major QTL, *qEf1.1* on chromosome 1, which is a homolog of *FLOWERING LOCUS T* (*FT*) in *Arabidopsis* (Lu et al., 2014); physically very close to *qDa1.1* (Miao et al., 2012).

Flowering time (***qFt1.1, qFt5.1, qFt6.1* and *qFt6.2***): From a population derived from WI7200 (early flowering) and the semi-wild Xishuangbana cucumber line WI7167 (late flowering), three QTL, *qFt1.1 (Chr1), qFt5.1* (Chr5) and *qFt6.2* (Chr6) were identified for number of days to anthesis of both male and female flowers (Qu et al., 2014; Pan et al., 2017, unpublished data). The QTL *qFt1.1* and *qFt6.1* were identified from CC3 × SWCC8 RIL population for first female flowering time (Bo et al., 2015). The Chr1 QTL *qFt1.1* is probably the same as *qDa1.1*.

3.5 Male sterility

Male sterility (***ms-1***, ***ms-2***): pollen abortion before anthesis; *ms-1* plants are also partially female sterile (Robinson and Mishanec, 1965; Whelan, 1972a).

Male sterile-2 pollen sterile (*ms-2^{PS}*): Male-sterile; allelic to *ms-2*, but not to *ap*; *ms-2*$^{(PS)}$ from a mutant of Sunseeds 23B-X26 (Zhang et al., 1994)

Apetalous (***ap***): male sterile, anthers transformed into sepal-like structures (Grimbly, 1980).

Closed flower (***cl***): pollen is inaccessible to bees because the buds remain closed; both male and female sterile (Groff and Odland, 1963).

Flower bud abortion (***Fba***): *Fba* triggers flower bud abortion prior to anthesis in 10 to 100% of the buds (Miller and Quisenberry, 1978).

4. Fruit mutants

4.1 Fruit skin texture and color

A number of genes control skin-texture related traits on cucumber fruits. Specific allele combinations of these genes are characteristic of different market classes. For example, the European greenhouse cucumbers often have uniform immature fruit color (*u*), smooth (*tu*) and glossy (*d*) fruits with heavy fruit netting (*H*) and tender skin (*te*). Meanwhile, typical fresh market north China cucumbers have ribbed (*Fr*) and dull (*D*) fruits with non-netting (*h*), but many small spines (*ns*, *ss*). American cucumbers are generally warty (*Tu*), mottled (*U*) with dull (*D*), tough skin (*Te*) and few, large spines (*Ns*, *Ss*), but no ribs (*fr*). Several genes for fruit skin texture were found tightly linked which include heavy netting (*H*), smooth (*tu*), dull fruit skin (*D*), fruit ribbing (*Fr*), uniform immature fruit color (u), numerous spines (*ns*), small spines (*ss*), and tender fruit (*te*) (Fanourakis and Simon, 1987; Walters et al., 2001; Yuan et al., 2008; Miao et al., 2011a).

Tuberculated fruit (***Tu***): Tuberculated, warty fruit is dominant to smooth (glabrous) fruit (Wellington, 1913; Strong, 1931). *Tu* is located in chromosome 5 (Zhang et al., 2010b) and encodes a transcription factor with a single C_2H_2 zinc finger domain; *Gl* (*non-glabrous*) is epistatic over *Tu* (Yang et al., 2014a).

Tender fruit (***te***): Tender fruit skin vs tough is recessively inherited (Strong, 1931; Poole, 1944); linked with tough and warty fruits in chromosome 5 (Fanourakis and Simon, 1987). 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).

Dull fruit skin (***D***): dull fruit skin is dominant to glossy (*dd*) (Strong, 1931; Tkachenko, 1935; Poole, 1944); located in chromosome 5 (Yang et al., 2014b).

Heavy netting (***H***): occurs when fruit reaches maturity; netting is dominant to smooth (Tkachenko, 1935; Hutchins, 1940); mapped in chromosome 5 (Miao et al., 2011a; Wang et al., 2014b).

Fruits ribbing **(*Fr*):** fruits of 9930 have ribbing; fruits of 9110Gt have no ribbing at commercial maturity stage; ribbed is dominant to non-ribbing; *U*, *D*, *H* and *fr* are linked in chromosome 5 (Miao et al., 2011a).

Uniform immature fruit color (***u***): immature fruit has uniform color; mottled is dominant to uniform; located in chromosome 5 (Andeweg, 1956; Fanourakis and Simon, 1987; Miao et al., 2011a; Yang et al., 2014c).

Palisade epidermis (***pe***): Epidermal cells arranged perpendicular to the fruit surface; *pe* from WI 2757 (Fanourakis and Simon, 1987).

White immature fruit color (***w***): white immature skin color (*w*) is recessive to the normal green (Cochran, 1938); *w* is located in chromosome 3 (Dong et al., 2012). The w allele encodes a candidate gene for the '*two-component response regulator-like*' (*APRR2*) protein (Liu et al., 2015, 2016).

Yellow green immature fruit color (***yg***): yellow green (*yg*) is recessive to dark green and epistatic with light green (Youngner, 1952).

Red fruit color (***R***): The cucumber mature fruit colors are very diverse, but the majority could be classified broadly into two groups: yellow (orange, red, brown), and white (white, creamy, light green, green); yellow controlled by *R* is dominant to white (*rr*) (Li et al., 2013). The *B* gene for black spine is pleiotropic to or linked with *R* (Wellington, 1913). Hutchins (1940) classified matured fruits colors into four classes (red, orange, yellow, and cream) and suggested two genes, *R* and *C*, controlled these colors. Peterson and Pike (1992) studied the inheritance of green mature fruit color, and proposed two major genes (*R* and *Gn*) underlying the inheritance of colors under investigation. Using populations derived from crosses between WI7200 (black spine and orange fruit skin colors) and WI7201 (white spine and creamy fruit skin colors), Li et al. (2013) identified a transcription factor (R2R3MYB) candidate gene for black spine gene *B* in chromosome 4 which is pleiotropic that also controls orange, red, or brown mature color. Li et al. (2013) found that in the same population, the mature fruits could be yellow, brown, orange, or red depending on the environment conditions and development stages. Miao et al. (2011b) treat mature fruit color as quantitative trait (yellow-green, yellow, orange) and identified four QTL in three chromosomes (Chr3, Chr5 and Chr6).

Green mature fruit (gn): Green mature fruits when *rr gngn*; cream colored when *rr GnGn*; gn from TAMU 830397 (Peterson and Pike, 1992).

Light green peel (lgp): An EMS mutant showing light green exocarp as compared with donor line 406 with dark green exocarp, which is due to a mutation in the candidate gene *Csa7G051430* encoding ACCUMULATION AND REPLICATION OF CHLOROPLASTS 5 (ARC5) that plays a vital role in chloroplast division (Zhou et al., 2015).

Light green fruit (***lgf, CsYcf54***): An EMS-induced recessive mutant with light green fruits and leaves; from North China type cucumber line 406; due to a mutation in *Csa6G133820* that encodes an Ycf54-like protein which has been implicated in the cyclase step of chlorophyll biosynthesis (Lun et al., 2016). Here '*lgf*' was assigned as the gene symbol.

4.2 Fruit spine number, size and color

Black spine (***B***): In cultivated cucumber, black or brown spines are dominant to white (Strong, 1931; Tkachenko, 1935; Walters et al., 2001). The *B* gene has been mapped to chromosome 4; an R2R3MYB transcription factor seems to be the candidate gene; *B* is pleiotropic with red/orange mature fruit color (Li et al., 2013).

Black spine-1 (***B-1***) and ***Black spine-2*** (***B-2***): two complementary genes control spine colors (black vs. white) in the progeny from crosses of cucumber line 9362 with PI 212233 and Pixie (Shanmugasundarum et al., 1971a); Pierce and Wehner (1990) assigned gene symbols *B-1* and *B-2* (black is dominant); *B* probably belongs to either *B-1* or *B-2*.

Black spine-3 (B-3) and ***Black spine-4*** (***B-4***): Fruit spine color in F_2 from the cross of white-spined cultivated cucumber lines with black-spined wild cucumber line (*C. s*. var. *hardwickii*) LJ90430, the black spine color was controlled by two genes (9 black : 7 white) that were assigned *B-3* and *B-4* (Cowen and Helsel, 1983; Walters et al., 2001). But in a cross between a white-spined cultivated cucumber with the wild cucumber, Pitchaimuthu et al. (2012) found brown spine color in the *C. s.* var. *hardwickii* line was controlled by a single dominant gene.

Numerous spines (***ns***) and ***small spines*** (***ss***): spine number and density on fruit surface are controlled by two genes: many small spines on WI 2757 cucumber are recessive to few, large spines on SMR 18 (Fanourakis and Simon, 1987). Previously, 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) suggested that *s* and *f* were the same gene and proposed the joint symbol *s* for a high density of small spines. Piece and Wehner (1990) proposed that these genes be labeled *s-2* and *s-3* and *s-1* be used instead of *s* proposed by Poole (1944). Here we proposed to use *ns* for spine density and *ss* for spine size following Fanourakis and Simon (1987). Yuan et al. (2008) mapped *ss* in chromosome 5 that is closely linked with *D* and *u* loci. Miao et al. (2011b) treated spine density on immature fruits as quantitative trait (no, thin, medium, dense, denser), and mapped one QTL, *Fsd6.1* in chromosome 6. In a cross between NCG-122 with numerous spines and NCG-121 with few spines, the few spines trait was dominant over the numerous spines trait; *ns* was mapped to chromosome 2 (Zhang et al., 2016a).

Few spines 1 (***fs1***): A mutant from a North China type cucumber CNS2 with a high density of fruit spines. *Fs1* encodes "Few spines" is controlled by a single recessive gene; encodes a PDF2-related protein (Csa6M514870) which belongs to a homeodomain-leucine zipper IV transcription factor (CsHDZIV11/CsGL3) (Zhang et al., 2016b)

4.3 Fruit internal structure

Empty chamber-1 (***Es-1***) and ***Empty chambers-2*** (***Es-2***): The hollow inside fruit is due to carpel separation; controlled by two partially dominant genes with additive effects (Kubicki and Korzeniewska, 1983). Wilson and Baker (1976) showed that separation of carpels within the fruit is controlled by one to three dominant genes.

Carpel splitting **(*cs*):** Fruits develop deep longitudinal splits; *cs* from TAMU 1043 and TAMU 72210 (Carruth,, 1975; Pike and Carruth, 1977).

Carpel number (***cn***): This is a new gene symbol to replace previously used *l* for locule number (Youngner, 1952). Botanically, a locule in cucumber fruit should be a carpel. Most cucumbers have 3 carpels; the andromonoecious cucumber line 'True Lemon' has five carpels. Five-carpel is recessive to three; the *CsCLAVATA3* (*CsCLV3*) gene is underlying carpel number variations in cucumber (Li et al., 2016).

4.4 Fruit size and shape

Fruit size (length and diameter) in cucumber is quantitative in nature. QTLs for fruit length and diameter have been investigated in several QTL mapping studies. However, mutants with significant differences in fruit length have also been identified, which may correspond to major-effect fruit length QTL.

Fruit length (***fl***): a modifier of fruit length; *fl* was identified by its linkage with scab resistance (*Ccu*); expressed in an additive fashion, fruit length decreases incrementally from heterozygote to homozygote (*fl fl*) (Wilson, 1968; Pierce and Wehner, 1990). Fruit length was found to be linked with scab resistance (Munger and Wilkinson, 1975).

Fruit length-1 (***fl-1***): The North China cucumber line 409 is a spontaneous mutant of line 408; fruits on 409 are 7 cm shorter than those on line 408 (Jiang et al., 2015).

Short fruit (***sfr***): EMS induced mutation from a North China type cucumber line "Shannong No 5"; shorted fruit than wild type controlled by a single recessive gene (Wang et al., 2014a)

Long fruit (***lfr***): EMS induced mutation from a North China type cucumber line "Shannong No 5", longer fruit than wild type (Wang et al., 2014a)

4.5 Fruit flesh color and tastes

Orange flesh (***or***): The semi-wild Xishuangbanna cucumber (*C. sativus* var. *xishuangbannesis*) is characteristic of orange flesh in mature fruits due to accumulation of high level of beta carotene; orange is recessive to white; *or* was mapped in chromosome 3 (Bo et al., 2012), which encodes a β-carotene hydroxylase (Qi et al., 2013).

Yellow flesh (***yf***): The mature fruit of cucumber line PI 200815 exhibits yellow flesh. 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. Lu et al. (2015) suggested that the *yellow flesh* is recessive to *white flesh*, and *yf* was mapped on chromosome 7.

***White flesh (wf)*:** Intense white flesh color is recessive to dingy white; acts with *yf* to produce F_2 of 12 white (*WfWf YfYf* or *wfwf YfYf*) : 3 yellow (*WfWf yfyf*) : 1 orange (*wfwf yfyf*). *Wf* from EG and G6, each being dingy white (*WfWf YfYf*): *wf* from 'NPI ' which is orange (*wfwf yfyf*) (Kooistra, 1971).

Fragrance (fgr): the fruits and foliage of cucumber line PK2011T202 from Thailand have pandan-like fragrance; controlled by a single recessive gene, *fgr* (Pramnoi et al., 2013), which is located on chromosome 1 and encodes the betaine aldehyde dehydrogenase 2 (BADH2) (also known as aminoaldehyde dehydrogenase 2) (Yundaeng et al. 2015).

4.6 Fruit shelf life

Reduced ethylene sensitivity (***res***): single recessive gene from chemically induced mutagenesis; co-dominance in heterozygotes; reduced sensitivity to ethylene; no detrimental effect on sex expression and seed germination; maintain fruit firmness thus longer shelf life after fruit harvest; reduced hypocotyl length (Dirks et al., 2013).

4.7 Parthenocarpic fruit set

Parthenocarpic fruit set (***Pc***): Parthenocarpy is 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 for parthenocarpic fruit set. de Ponti and Garretsen (1976) explained the inheritance by 3 major isomeric genes with additive action. Molecular mapping studies support quantitative nature of parthenocarpic fruit setting in cucumber (Sun et al., 2006; Lietzow et al., 2016; Wu et al., 2016)

5. Plant architecture

Bushy (***by***): EMS mutant from Borszczagowski; short internodes; normal seed viability; linked with *F* and *gy*, but not with *B* or *bi* (Kubicki et al., 1986a)

Bush (***bu***): recessively inherited mutant from EMS treatment; half-length of internode compared with wild type (Kubicki et al., 1986b).

Compact (***cp***): The two plant introduction lines, PI 308915 and PI 308916, exhibit significantly reduced internode length (super dwarf) and was due to a recessive gene, *cp* (Kauffman and Lower, 1976); mapped in chromosome 4 (Li et al., 2011; Yong et al., 2013).

Compact-2 (***cp-2***): From EMS treated cucumber plants, Kubicki et al. (1986b) identified a second mutant with shortened internodes similar to PI 308916; allelism

between *cp* and *cp-2* is unknown, but *cp-2* is required to interact with the 'bushy' gene to produce the dwarf phenotype (Kubicki et al., 1986b).

Compact-3 (***cp-3***): a compact plant that is different from either *cp* or *cp-2* in chromosome locations; compact phenotype in homozygous and heterozygous states are different (Crienen et al., 2009). We propose a new gene symbol, *cp-3* for this mutant.

Super compact (***scp***): EMS-induced mutant with drastically reduced main stem length and no lateral branches; controlled by a recessive gene, *scp* (Niemirowicz-Szczytt et al., 1996); may be identical to the rosette (*ro*) mutant (de Ruiter et al., 1980).

Super compact-1 (***scp-1***): A dwarf mutant C257 was discovered from EMS mutagenesis of the North China cucumber line CCMC; the mutant exhibited a super compact (SCP) phenotype with drastically reduced internode length (<5 cm) and reduced number of internodes, no tendrils, more round shaped leaf with wrinkled surface and dark green color. The cytochrome P450 gene *CsCYP85A1* is a putative candidate for *Scp-1* (Wang et al., 2017).

Super compact-2 (***Scp-2***)**:** **S**pontaneous dwarf mutant AM204M with super compact phenotype identified in PI 618937. A mutation in the *CsDET2* gene leads to a systemic brassinosteriod deficiency and super compact phenotype in AM204M (Li Zheng, personal communication).

Determinate (***de***): A determinate plant has reduced plant height; growing point ends with clustered flowers (Hutchins, 1940; George, 1970; Denna, 1971); mapped in chromosome 6 close to the *F* gene (Weng et al., 2010).

Determinate-2 (***de-2***): Chemical induced mutation from 'Borszczagowski'; main stem stops growth after 3-10 nodes; end with flowers at the apex; smooth, fragile, dark-green leaves (Soltysiak et al., 1986); allelism with *de* unknown.

Determinate intensifier (***In-de***): an intensifier for *de* (George, 1970).

Dwarf (***dw***): spontaneous mutant with extremely short internode and very compact plant (Robinson and Mishanec, 1965).

Rosette (***ro***): a mutant with reduced plant height, shorter internodes, more obtuse leaf lobing; muskmelon-like leaves (de Ruiter et al., 1980).

Non-lateral branch (***nlb***): cucumber line 419 has no lateral branches, which is controlled a recessive gene *nlb* mapped in chromosome 1 (Jiang et al., 2008; Ren et al., 2013).

Tall plant (T): Tall incompletely dominant to short (Hutchins, 1940).

Reduced internode length (***Si***): The EMS-induced dwarf mutant exhibited shorter internode, smaller fruits, and wrinkled leaves as compared with its wild-type line 406, which is shown to be due to a mutation in an F-box gene (Lin et al., 2016).

6. Disease and insect resistances

6.1 Resistance to bacterial and fungal pathogens

Resistance to Cladosporium cucumerinum **(*Ccu*):** Resistance in cucumber to scab, *Cladosporium cucumerinum* Ell. & Arth, is dominant and controlled by *Ccu* (Bailey and Burgess, 1934; Andeweg, 1956; Abul-Hayja et al., 1975, 1978); mapped in chromosome 2, linked with resistance to *Fusarium* wilt (Vakalounakis, 1993; Zhang et al., 2010a; Kang et al., 2011)

Bacterial wilt resistance **(*Bw*):** resistance against *Erwinia tracheiphila* (E. F. Smith) Holland. *Bw* in PI 200818 is due to a single dominant gene (*Bw*) (Nuttall and Jasmin, 1958; Robinson and Whitaker, 1974). *Bw* seems to be linked with *m* (Iezzoni and Peterson, 1979, 1980). The disease is transmitted by the striped cucumber beetle and the spotted cucumber beetle. *Bw* confers resistance to the pathogen but not the beetles.

Resistance to Corynespora cassiicola **(*Cca*)**: A single dominant gene, *Cca*, in Royal Sluis 72502 cucumber line for resistance to target leaf spot (TLS) (syn. *Cercospora melonis* Cooke) (Abul-Hayja et al., 1978).

Resistance to Corynespora cassiicola-1 **(*cca-1*):** Resistance to target leaf spot (TLS) in cucumber line Q5, mapped to Chromosome 6 (Wang et al., 2010; Fu et al., 2012).

Resistance to Corynespora cassiicola-2 (cca-2): Yang et al. (2012) studied the inheritance of TLS resistance with populations derived from PI 183967 (resistant parent, wild cucumber *C. sativus* var. *hardwickii*) and Xintaimici (susceptible parent), and revealed that a single recessive gene *cca-2* controls TLS resistance in PI 183967. This gene was mapped in cucumber chromosome 6.

Resistance to Corynespora cassiicola-3 **(*cca-3*):** The TLS resistance in the resistant cucumber line D31 is controlled by a single recessive gene *cca-3* on chromosome 6. A CC-NB-ARC type resistance gene analog (*Csa6M375730*) is identified as the candidate gene (Wen et al., 2015).

Resistance to Fusarium oxysporum f. sp. cucumerinum (***qFoc2.1***): Resistance for *Fusarium* wilt (FW) races 1 and 2 in Wis248 is controlled by a single dominant gene (*Foc*) (Netzer et al., 1977; Vakalounakis, 1995). Vakalounakis (1996) found FW resistance genes in WI 2757, SMR18 and Wis 248 are allelic. Mao et al. (2008) found FW and scab resistance in WI 2757 was linked. Zhang et al. (2014) mapped a major QTL, *qFoc2.1*, for FW resistance from cucumber line 9110Gt to chromosome 2 that is very close to the *Ccu* locus for scab resistance.

Resistance to Fusarium oxysporum f. sp. cucumerinum (***qFoc6.1***and ***qFoc6.2***): The cucumber line URS 189 carries two FW QTLs for resistance against the causal agent of *Fusarium* stem and root rot *Fusarium oxysporum* f. sp. *radicis cucumerinum* (Forc) which are linked QTL loci in chromosome 6 (de Milliano et al., 2012). We propose gene symbols for the two QTLs *qFoc6.1*, *qFoc6.2*, respectively.

Gummy stem blight resistance **(*qGsb1.1*, *qGsb4.1*, *qGsb6.1*)**: No simply inherited genes have been identified for resistance to gummy stem blight (GSB), *Didymella bryoniae* (Auersw.) Rehm. Introgression lines derived from cross between cucumber and *Cucumis hystrix* were reported to exhibit GSB resistance, and QTL mapping identified three resistance QTLs, *qGsb1.1*, *qGsb4.1*, and *qGsb6.1* (Lou et al., 2013).

Anthracnose resistance **(*Ar*):** Anthracnose resistance in PI 197087 was controlled by a partially dominant gene (Barnes and Epps, 1952, 1955).

Resistance to Colletotrichum lagenarium race 1 **(*cla*):** anthracnose resistance in SC, 19B cucumber line is by a single recessive gene, *cla* (Abul-Hayja et al., 1978).

Resistance to Pseudomonas syringae pv. ***lachrymans*** (***psl***): angular leaf spot (ALS) resistance to the bacterial pathogen *Pseudomonas syringae* pv. *lachrymans* (Syn. *Pseudomonas lachrymans*); Dessert *et al.* (1982) found non-halo type resistance was governed by a single recessive gene *psl*. Olczak-Woltman et al. (2009) suggested resistance to ALS in H603 (*C. sativus* var. *hardwickii*) is quantitative; a RAPD marker linked to the gene conferring the chlorotic halo was identified.

Powdery mildew resistance **(*pm-h*, *pm5.1*)**: Powdery mildew (PM) is caused mainly by *Podosphaera fusca* (Fr.) Braun & Shishkoff (formerly *Sphaerotheca fuliginea* Schlech ex Fr. Poll.). PM resistance in cucumber is in general quantitative. Fujieda and Akiya (1962) proposed two resistance genes, *pm-1* and *pm-2*, controlling PM resistance in the Japanese cultivar 'Natsufushinari'. Kooistra (1968) identified *pm-3* in PI 200815 and PI 200818. Shanmugasundarum et al. (1971b) proposed a gene for hypocotyl resistance (*pm-h*) that played the major role in whole plant PM resistance. de Ruiter et al. (2008) classified PM resistance from PI 200815 source into leaf resistance (*pm-l*) and hypocotyl resistance (*pm-h*), which were linked loci in cucumber chromosome 5. Recent QTL mapping studies have identified major- and minor-effect QTLs for PM resistance from different sources (e.g., WI 2757, PI 197088) (Sakata et al., 2006; Liu et al., 2008; Fukino et al., 2013; He et al., 2013). Especially, He et al. (2013) identified a major-effect QTL in chromosome 5 (*pm5.2* or *pm-h*), which seems to be consistent with the *mlo*-type candidate gene (Nie et al., 2015a,b; Berg et al., 2015). From a North China type cucumber line Jin5-508, Xu et al. (2016) identified a dominantly inherited PM resistance major-effect QTL, *Pm1.1* that was located in a 41.1 kb region of cucumber Chromosome 1 harboring two tandemly arrayed cysteine rich receptor like protein kinase genes. In this revision, *Pm1.1* and *pm-h* (*pm5.1*) were included.

Downy mildew resistance**:** Downy mildew (DM) is caused by the obligate oomycete *Pseudoperonospora cubensis*. The DM resistance conferred by *dm-1* from PI 197087 had been very effective in the field until, 2004 when it was overcome due to the appearance of a new pathotype in the US. Resistance sources against the new DM strain have been identified (Criswell, 2008; Call et al., 2012a, b; Holdsworth et al., 2014). The inheritance patterns for DM resistance range from a single recessive to several genes (e.g., Shimizu et al., 1963; Van Vliet and Meysing, 1974, 1977; Fanourakis and Simon, 1987; Doruchowski and Lakowska-Ryk, 1992; Angelov, 1994), to one or two incompletely dominant genes (Petrov et al., 2000). Recent QTL mapping studies have revealed the recessive and quantitative nature of DM resistance in various resistance sources. QTLs for DM resistance were detected in K8, PI 197085, PI 197088 and PI 330628, and mapped in five (1, 2, 4, 5, and 6) of the seven cucumber chromosomes (Zhang et al., 2013a; Yoshioka et al., 2014; Szczechura et al. 2015; Wang et al. 2016a). Pang et al (2013) identified three QTL for DM resistance, which are presumably due to introgression from *Cucumis hystrix*.

In this revision, we only listed *dm-1*, which was originated from PI 197087, but is no longer effective for the post-2004 DM strain in the US. *dm-1* seems to

be located in chromosome 5 (van Vliet, 1977; Fanourakis and Simon, 1987; Kennard et al., 1994).

6.2 Resistance to viral pathogens

Several potyviruses infect cucurbit crops including the *watermelon strain of papaya ringspot virus* (PRSVW) (previously named *watermelon mosaic virus* 1), *Zucchini yellow mosaic virus* (ZYMV), *Watermelon mosaic virus* (WMV), the *Moroccan watermelon mosaic virus* (MWMV) and *Zucchini yellow fleck virus* (ZYFV). At least three resistance sources for potyviruses have been identified in cucumber: 'Surinam', 'TMG-1' and 'Dina-1'; Surinam is only resistant to PRSV-W; TMG-1 and 'Dina-1' both are also resistant to ZYMV, WMV and MWMV (Provvidenti, 1985; Wai and Grumet, 1995; Kabelka et al., 1997; Kabelka and Grumet, 1997; Wai et al., 1997). Resistances to PRSV-W, ZYMV, WMV and MWMV in TMG-1 are tightly linked (within 1 cM) suggesting that multiple potyvirus resistance in cucumber may be due to different alleles of a single gene with differing viral specificities, or that the multiple closely linked genes (Grumet et al., 2000).

Resistance to PRSV-1 (***prsv-1***): resistance in cucumber line 'Surinam' against PRSV-W was inherited as a recessive allele at a single locus (Wang et al., 1984a, b).

Resistance to PRSV-2 (***Prsv-2***): Wai and Grumet (1995) described a dominant locus (*Prsv-2*) in TMG-1 for PRSV-W resistance. Wai et al. (1997) reported genes for resistances to PRSV-W in Surinam (*prsv-1*) and TMG1 (*Prsv-2*) were allelic; located in chr6 (Park et al., 2000).

Resistance to PRSV (***prsv^{02245}***): resistance in cucumber line 02245 is controlled by a single recessive gene, *prsv^{0224}*; molecular mapped in cucumber chromosome 6, linked with but not the same as the ZYMV resistance locus (*zym*) (Tian et al., 2015).

***Resistance to ZYMV* (*zym^{Dina}, zym^{TMG}, zym$^{A192-18}$*):** In Dina-1 and TMG-1, resistance to ZYMV is conferred by single genes (Provvidenti, 1987) that are alleles of the same locus (Kabelka et al., 1997). The *zym*^{Dina} allele, which allows for viral spread and distinct veinal chlorosis that is limited to one leaf, is dominant to the *zym*^{TMG} allele, which appears to restrict virus accumulation more rapidly; both are recessive to the allele for susceptibility. Molecular mapping placed the two linked genes *prsv-2* and *zym* in chromosome 6 (Park et al., 2000). Amano et al. (2013) identified a candidate gene for the *zym*$^{A192-18}$ locus (resistance source: A192-18) which putatively encodes a vacuolar protein sorting-associated protein 4-like (VPS4-like) gene. The *zym*$^{A192-18}$ locus is physically very close to *zym*^{Dina} –linked markers, but the nature of allelic variations in Dina-1 or TMG-1 at this locus is not known.

***Resistance to ZYFV* (*zyf*)**: controlled by single recessive genes in TMG-1 and Dina-1(Kabelka and Grumet, 1997).

Resistance to MWMV (***mwm***): controlled by single recessive genes in TMG-1 and Dina-1 (Kabelka and Grumet, 1997).

Resistance to watermelon mosaic virus (***wmv***): Cohen et al. (1971) identified a dominant gene, *Wmv*, in the cultivar 'Kyoto 3 Feet', resistant to strain 2 of WMV.

Resistance to watermelon mosaic virus (***wmv-2, wmv-3, Wmv-4***): There are two independent factors governing WMV resistance in TMG-1 (Wai et al., 1997): *wmv-2* expressed at the cotyledon stage and throughout the plant; *wmv-3* (recessive*)* and *Wmv-4* (dominant) with epistatic interactions expressed only in true leaves. *Wmv-4* seems to be from the susceptible parental (WI2757); *wmv-2* is located in chromosome 6; *wmv-3* may be the same, or very tightly linked to the *zym*$^{TMG-1}$ locus (chromosome 6) (Wai et al., 1997).

Resistance to watermelon mosaic virus (***wmv^{02245}***): Tian et al. (2016) found that WMV resistance in the cucumber inbred line '02245' is controlled by a single recessive locus, *wmv^{02245}* on mapped to Chromosome 6.

Resistance to cucumber mosaic virus (***Cmv***): 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). The resistance gene *cmv* was identified in 'National Pickling' and 'Wis SMR 6' for resistance cucumber mosaic virus was reported by Wasuwat and Walker (1961).

Resistance to CYSDV (***qCYSDV5.1***): Three QTLs were identified for CYSDV resistance in PI 250147 (de Ruiter et al., 2008; Faber et al., 2010); the major QTL, which we designate *qCYSDV5.1*, was mapped in chromosome 5; this QTL is close to the major QTL for powdery mildew (de Ruiter et al., 2008).

Resistance to CVYV (q***CVYV***): Molecular markers for the Cucumber Vein Yellowing Virus (Ipomovirus) (CVYV) were identified; this CVYV resistant plant also confers a general resistance against tobamoviruses including the cucumber green mottle mosaic virus (CGMMV) and cucumber fruit mottle mosaic virus (CFMMV) (Mazereeuw et al., 2012; Faber et al., 2014).

Resistance to MYSV (strain FuCu05P-1) (*q**MYSV1.1**, q**MYSV3.1**, q**MYSV4.1**, q**MYSV7.1**,*): Resistance in

cucumber line 27028930 to the Melon yellow spot virus (MYSV) FuCu05P-1 strain is controlled two major QTLs, *qMYSV1.1* (*qSwf1.1*) (resistance to spotted wilt of FuCu05P-1) and *qMYSV3.1* (*qSwf3.1*) (Chr3), and one minor QTL *qMYSV7.1* (*qSwf7.1*) (Chr7) . A minor QTL, *qMYSV4.1* (*qSwf4.1*)(Chr4) was detected in the susceptible parent 'Tokiwa' (Sugiyama et al. 2015).

6.3 Resistance to root knot nematodes

Resistance to Meloidogyne javanica (***mj***): The wild cucumber line LJ90430 (*C. sativus* var. *hardwickii*) is resistant to the root knot nematode, *Meloidogyne javanica* (Walters et al., 1996; Walters and Wehner, 1998), which is controlled by a single recessive gene *mj* (Walters et al., 1997). Devran et al. (2011) identified two AFLP markers linked with *mj*.

6.4 Resistance to insects

Bitterfree (***bi***): No bitter foliage in cucumber (Andeweg and DeBruyn, 1959) is responsible for resistance to spotted and striped banded cucumber beetles (*Diabrotica* spp.), as well two-spotted spider mites (*Tetranychus urticae* Koch.) (Da Costa & Jones, 1971a,b; Soans et al., 1973; Chambliss, 1978), but it works inversely for the 2 species. *Bi* (higher foliage cucurbitacin levels) incites resistance to spider mites by an antibiotic effect of the cucurbitacin; *bibi* (bitterfree) results in resistance to cucumber beetles because cucurbitacins are attractants.

7. Abiotic stress tolerance

Seedling chilling resistance (***Ch***): Seedling stage chilling resistance in cucumber line NC-76, which was developed from PI 246930, is controlled by single dominant gene (Kozik and Wehner, 2006, 2008).

Resistance to sulfur dioxide air pollution (***Sd***): A single dominant gene, *Sd*, in the National Pickling is responsible for resistance to acute exposure of sulfur dioxide (Bressan et al., 1981)

Salt tolerance (***sa***): increased tolerance to high salt levels in PI 177361 is conditioned by a dominant gene, *Sa* (Jones, 1984).

Waterlogging tolerance (qARN6.1)**:** The waterlogging tolerant line Zaoer-N produces more hypocotyl-derived adventitious roots (AR) under waterlogging stress. The AR number (ARN) in Zaoer is controlled by 3 QTL, *ARN3.1*, *ARN5.1*, and *ARN6.1* with *ARN6.1* as the major-effect QTL (Xu et al., 2016).

8. Miscellaneous mutants

Bitterfree (***bi, bi-3***): No bitter plant (foliage and fruit) in cucumber (Andeweg and DeBruyn, 1959; Wehner et al., 1998a); mapped in Chr6. *Bi* encodes a cucurbitadienol synthase that catalyzes the cyclization of 2,3-oxidosqualene into the tetracyclic cucurbitane skeleton, the first committed step of CuC biosynthesis (Qi et al., 2013; Shang et al., 2014). The previous designated bitterfree gene *bi-1* seems to be synonymous to *bi*. In the 9110Gt × 9930 RIL population, Zhang et al. (2013b) found that two loci, *bi-1* (*bi*) and *bi-3* control fruit bitterness. The gene *bi-3* was linked with *bi* (*bi-1*) in Chr5.

Bitter fruit (***Bt***): control cucurbitacin levels in the fruit only (Barham, 1953). Bitter fruit requires both *Bi* and *Bt*. *Bt* is located in chromosome 5 (Qi et al., 2013) and has been cloned; *Bt* is a transcription factor that activates *Bi* and regulates CuC biosynthesis in the fruit (Shang et al., 2014). The bitter fruit gene *Bt-2* (Walters et al., 2001) is proposed to retire.

Bitter leaf (***Bl***): a newly discovered gene regulating bitterness biosynthesis in cucumber leaves by activating transcription of *Bi* in cucumber leaves. *Bl* is located in chromosome 5, and it encodes a putative basic helix loop-helix (bHLH) transcription factor (TF) expressed specifically in leaves. Abiotic stress may stimulate the bitterness biosynthesis in cucumber by up-regulation of *Bl* (Shang et al., 2014). The previous named gene *bi-2* seems to be synonymous to *bl*.

Paternal sorting of mitochondria (***Psm***): The single dominant gene *Psm* from MSC16 cucumber controls sorting of wild-type mitochondrial DNA from paternal parent (Havey et al., 2004). When a maternal plant homozygous for the wild-type (*Psm+*) allele is crossed with MSC16 as the pollen parent, progenies almost exclusively (>95%) show the MSC phenotype. A plant homozygous for the rarer *Psm* allele crossed with MSC16 as the pollen parent produces almost all wild-type progenies. QTL mapping placed a major QTL for the *Psm* locus in chromosome 3, and a candidate gene has been identified that encodes a pentatricopeptide repeat (PPR) 336 protein (Calderon et al., 2012; Del Valle-Echevarria et al., 2016).

References cited

1. Aalders, L. E. 1959. 'Yellow Cotyledon', a new cucumber mutation. Can. J. Genet. Cytol. 1:10-12.
2. Abul-Hayja, Z. and P. H. Williams. 1976. Inheritance of two seedling markers in cucumber. HortScience 11:145.
3. Abul-Hayja, Z., P. H. Williams, and E. D. P. Whelan. 1975. Independence of scab and bacterial wilt resistance and ten seedling markers in cucumber. HortScience 10:423- 424.
4. Abul-Hayja, Z., P. H. Williams, and C. E. Peterson. 1978. Inheritance of resistance to anthracnose and target leaf spot in cucumbers. Plant Dis. Rptr. 62:43-45.
5. Amano, M., A. Mochizuki, Y. Kawagoe, K. Iwahori, K. Niwa, J. Svoboda, T. Maeda, and Y. Imura. 2013. High-resolution mapping of *zym*, a recessive gene for Zucchini yellow mosaic virus resistance in cucumber. Theor. Appl. Genet. 126:2983–2993.
6. Andeweg, J. M. 1956. The breeding of scab-resistant frame cucumbers in the Netherlands. Euphytica 5:185-195.
7. Andeweg, J. M. and J. W. DeBruyn. 1959. Breeding non-bitter cucumbers. Euphytica 8:13-20.
8. Angelov, D. 1994. Inheritance of resistance to downy mildew, *Pseudoperonospora cubensis* (Berk. & Curt.) Rostow. Rep. 2nd Natl. Symp. Plant Immunity (Plovdiv) 3:99-105.
9. Bailey, R. M. and I. M. Burgess. 1934. Breeding cucumbers resistant to scab. Proc. Amer. Soc. Hort. Sci. 32:474-476.
10. Barham, W. S. 1953. The inheritance of a bitter principle in cucumbers. Proc. Amer. Soc. Hort. Sci. 62:441-442.
11. Barnes, W. C. and W. M. Epps. 1952. Two types of anthracnose resistance in cucumbers. Plant Dis. Rptr. 36:479-480.
12. Barnes, W. C. and W. M. Epps. 1955. Progress in breeding cucumbers resistant to anthracnose and downy mildew. Proc. Amer. Soc. Hort. Sci. 65: 409-415.
13. Berg, J.A., Appiano, M., Martínez, M.S., Hermans, F.W.K., Vriezen, W.H., Visser, R.G.F., Bai, Y.L., Schouten, H.J. 2015. A transposable element insertion in the susceptibility gene *CsaMLO8* results in hypocotyl resistance to powdery mildew in cucumber. BMC Plant Biol. 15: 243.
14. Bo, K.L., H. Song, J. Shen, C. T. Qian, J. E. Staub, P. W. Simon, Q. F. Lo, and J. F. Chen. 2012. Inheritance and mapping of the ore gene controlling the quantity of β-carotene in cucumber (*Cucumis sativus* L.) endocarp. Mol. Breed. 30: 335–344.
15. Bo, K. L., Z. Ma, J. F. Chen, and Y. Weng. 2015. Molecular mapping reveals structural rearrangements and quantitative trait loci underlying traits with local adaptation in semi-wild Xishuangbana cucumber (*Cucumis sativus* L. var. *Xishuangbannanesis* Qi et Yuan). Theor. Appl. Genet. 128: 25-39.
16. Bo, K.L., Wang, H., Pan, Y.P., Behera, T.K., Pandey, S., Wen, C.L., Wang, Y.H., Simon, P.W., Li, Y.H., Chen, J.F., Weng, Y. 2016. Cucumber *Short Hypocotyl1* (*Sh1*) encodes a human SMARCA3-like chromatin remodeling factor regulating hypocotyl elongation. Plant Physiol.172: 1273-1292.
17. Boualem, A., C. T. Kovalski, M. A. Sari, R. Perl-Treves, and A. Bendahmane. 2009. A conserved ethylene biosynthesis enzyme leads to andromonoecy in two *Cucumis* species. PLoS ONE 4: e6144.
18. Boualem, A., S. Fleurier, C. Troadec, P. Audigier, A. P. K. Kumar, M. Chatterje, A. A. Alsadon, M. T. Sadder, M. A. Wahb-Allah, A. A. Al-Doss, A. Bendahmane. 2014. Development of a *Cucumis sativus* TILLinG platform for forward and reverse genetics. PLoS ONE 9: e97963.
19. Boualem, A., Troadec, C., Camps, C., Lemhemdi, A., Morin, H., Sari, M.A., Fraenkel-Zagouri, R., Kovalski, I., Dogimont, C., Perl-Treves, R., Bendahmane, A. 2015. A cucurbit androecy gene reveals how unisexual flowers develop and dioecy emerges. Science 350: 688-691.
20. Bressan, R. A., L. LeCureux, L. G. Wilson, P. Filner, and L. R. Baker. 1981. Inheritance of resistance to sulfur dioxide in cucumber. HortScience 16:332-333.
21. Bu, F., Chen, H., Shi, Q., Zhou, Q., Gao, D., Zhang, Z., Huang, S. 2016. A major quantitative trait locus conferring subgynoecy in cucumber. Theor Appl Genet 129: 97-104.
22. Calderon, C. I., B. S. Yandell, and M. J. Havey. 2012. Genetic mapping of paternal sorting of mitochondria in cucumber. Theor. Appl. Genet. 125: 11-18.
23. Call, A. D. and T. C. Wehner. 2010. Search for resistance to the new race of downy mildew in cucumber, p. 112-115. Cucurbitaceae 2010 Proceeding. ASHS Press, Alexandria, VA
24. Call, A. D., A. D. Criswell, T. C. Wehner, K. Ando, and R. Grumet. 2012a. Resistance of cucumber cultivars to a new strain of cucurbit downy mildew. HortSci 47: 171-178.
25. Call, A. D., A. D. Criswell, T. C. Wehner, U. Klosinska, and E. U. Kozik. 2012b. Screening cucumber for resistance to downy mildew caused by Pseudoperonospora cubensis (Berk. and Curt.) Rostov. Crop Sci. 52: 577-592.
26. Cao, C. X., S. Zhang, and H. Y. Guo. 2001. Genetic relationship between glabrous foliage character and warty fruit character of cucumber. Acta Hort. Sinica 28: 565-566.
27. Carlsson, G. 1961. Studies of blind top shoot and its effect on the yield of greenhouse cucumbers. A recessive gene, t, with a physiologically released effect. Acta Agr. Scand. 11:160-162.
28. Carruth, T. F. 1975. A genetic study of the inheritance of rupturing carpel in fruit of cucumber, *Cucumis sativus* L. Master thesis, Texas A&M Univ., College Station.
29. Chambliss, O. L. 1978. Cucumber beetle resistance in the Cucurbitaceae: Inheritance and breeding. HortScience 13:366 (Abstract).

30. Chen, C. H., M. L. Liu, L. Jiang, X. F. Liu, J. Y. Zhao, S. S. Yan, and X. L. Zhang. 2014. Transcriptome profiling reveals roles of meristem regulators and polarity genes during fruit trichome development in cucumber (*Cucumis sativus* L.). J. Expt. Bot. 65: 4943–4958.
31. Chen, H. M., Y. Tian, X. Y. Lu, and X. H. Liu. 2011. The inheritance of two novel subgynoecious genes in cucumber (Cucumis sativus L.). Scientia Horticulturae 127: 464–467.
32. Chen, H., Sun, J., Li, S., Cui, Q., Zhang, H., Xin, F., Wang, H., Lin, T., Gao, D., Wang, S., Li, X., Wang, D., Zhang, Z., Xu, Z., Huang, S. 2016. An ACC oxidase gene essential for cucumber carpel development. Mol. Plant. 9, 1315–1327.
33. Cochran, F. D. 1938. Breeding cucumbers for resistance to downy mildew. Proc. Amer. Soc. Hort. Sci. 35:541-543.
34. Cohen, S., E. Gertman, and N. Kedar. 1971. Inheritance of resistance to melon mosaic virus in cucumbers. Phytopathology 61:253-255.
35. Cowen, N. M. and D. B. Helsel. 1983. Inheritance of 2 genes for spine color and linkages in a cucumber cross. J. Hered. 74:308-310.
36. Crienen, J., G. Reuling, B. Segers, and M. van de Wal. 2009. New cucumber plants with a compact growth habit. Patent, International publication number WO 2009/059777 A1.
37. Criswell, A. D. 2008. Screening for downy mildew resistance in cucumber. M. S. Thesis, North Carolina State Univ., Raleigh.
38. Cui, J.Y., Miao, H., Ding, L.H., Wehner, T.C., Liu, P.N., Wang, Y., et al. 2016. A new glabrous gene (c*sgl3*) identified in trichome development in cucumber (*Cucumis sativus* L.). PLoS ONE 11: e0148422.
39. Da Costa, C. P. and C. M. Jones. 1971a. Cucumber beetle resistance and mite susceptibility controlled by the bitter gene in *Cucumis sativus* L. Science 172:1145-1146.
40. Da Costa, C. P. and C. M. Jones. 1971b. Resistance in cucumber, *Cucumis sativus* L., to three species of cucumber beetles. HortScience 6:340-342.
41. de Milliano, M. J. K., R. T. Folkertsma, M. Q. M. van Paassen, J. S. de Vries, M. B. Sela. 2012. *Fusarium* resistant cucumber plants. US patent US 2012/0066790 A1.
42. de Ponti, O. M. and F. Garretsen. 1976. Inheritance of parthenocarpy in pickling cucumbers (*Cucumis sativus* L.) and linkage with other characters. Euphytica 25:633642.
43. de Ruiter, A. C., B. J. van der Knapp, and R. W. Robinson. 1980. *Rosette*, a spontaneous mutant arising from cucumber-muskmelon pollen. Cucurbit Genet. Coop. Rpt. 3:4.
44. de Ruiter, W., R. Hofstede, J. de Vries, and H. van den Heuvel H. 2008. Combining QTL for resistance to CYSDV and powdery mildew in a single cucumber line. In: Proc 9th EUCARPIA meeting on genetics and breeding of Cucurbitaceae (Pitrat, M., ed), INRA, Avignon (France), May 21–24, 181–188.
45. Del Valle-Echevarria, A.R., Sanseverino, W., Garcia-Mas, J., Havey, M.J. 2016. *Pentatricopeptide repeat 336* as the candidate gene for *paternal sorting of mitochondria* (*Psm*) in cucumber. Theor Appl Genet 129: 1951–1959.
46. Della Vecchia, P. T., C. E. Peterson, J. E. Staub. 1982. Inheritance of short-day response to flowering in crosses between a *Cucumis sativus* var. *hardwickii* (R.) Alef. line and *Cucumis sativus* L. lines. Cucurbit Genet. Coop. Rpt. 5:4.
47. den Nijs, A. P. M. and H. O. Mackiewicz. 1980. "Divided leaf", a recessive seedling marker in cucumber. Cucurbit Genet. Coop. Rpt. 3:24.
48. den Nijs, A. P. M. and O. M. B. de Ponti. 1983. Umbrella leaf: a gene for sensitivity to low humidity in cucumber. Cucurbit Genet. Coop. Rpt. 6:24.
49. den Nijs, A. P. M. and I. W. Boukema. 1985. Short petiole, a useful seedling marker for genetic studies in cucumber. Cucurbit Genet. Coop. Rpt. 8: 7-8.
50. Denna, D. W. 1971. Expression of determinate habit in cucumbers. J. Amer. Soc. Hort. Sci. 96:277-279.
51. Dessert, J. M., L. R. Baker, and J. F. Fobes. 1982. Inheritance of reaction to *Pseudomonas lachrymans* in pickling cucumber. Euphytica 31: 847-856.
52. Devran, Z., A. F. Firat, M. Tor, N. Mutlu, and I. H. Elekcioglu. 2011. AFLP and SRAP markers linked to the mj gene for root-knot nematode resistance in cucumber. Scientia Agricola 68: 115-119.
53. Dirks, R. H. G., C. M. P. van Dun, J. S. Vel Terop, J. W. Kloet. 2013. Resistance to post harvest deterioration in cucumber. US Patent # US 2013/0074223 A1.
54. Dong, S. Y., H. Miao, S. P. Zhang, M. M. Liu, Y. Wang, and X. F. Gu. 2012. Genetic analysis and mapping of white fruit skin color in cucumber. Acta Bot Boreal-Occident Sinica 32: 2177–2181 (in Chinese)
55. Doruchowski, R. W. and E. Lakowska-Ryk. 1992. Inheritance of resistance to downy mildew (*Pseudoperonospora cubensis* Berk & Curt) in *Cucumis sativus*. Proc. 5th EUCARPIA Cucurbitaceae Symp. p. 66-69, Warsaw, Poland.
56. Faber, N.M., Torres, L.M., Sanchez, L.O. 2010. Method of breeding cysdv-resistant cucumber plants. Patent WO 2010071431 A1.
57. Faber, N., J. Mazereeuw, B. Van Kampen, and R. Wilterdink. 2014. Cucumber vein yellowing virus (CVYV) resistant cucumber plants (*Cucumis sativus* L.). US Patent # 08779241.
58. Fanourakis, N. E. and P. W. Simon. 1987A. Analysis of genetic linkage in the cucumber. J. Hered. 78:238-242.
59. Fraenkel, R., I. Kovalski, C. Troadec, A. Bendahmane, R. Perl-Treves. 2014. Development and evaluation of a cucumber TILLING population. BMC Res Notes 7: 846.
60. Fu, H.P., Wei, J., Li, S.J., Yang, R.H., Guan, W., Wang, H.Z. 2012. EST-SSR markers and artificial inoculation identification of leaf spot resistance in cucumber germplasm. Chin Hortic Abstract 2:1–3.

61. Fujieda, K. and R. Akiya. 1962. Genetic study of powdery mildew resistance and spine color on fruit in cucumber. J. Jpn. Soc. Hort. Sci. 31:30-32.
62. Fujieda, K. and Y. Fujita. 1978. New trimonoecious strain in cucumber, *Cucumis sativus* L. J. Fat. Agr., Kyushu Univ., 22: 221-226.
63. Fujieda, K., V. Fujita, Y. Gunji, and K. Takahashi. 1982. The inheritance of plural-pistillate flowering in cucumber. J. Jap. Soc. Hort. Sci. 51:172-176.
64. Fukino, N., Y. Yoshioka, M. Sugiyama, Y. Sakata, and S. Matsumoto. 2013. Identification and validation of powdery mildew (*Podosphaera xanthii*) resistant loci in recombinant inbred lines of cucumber (*Cucumis sativus* L.). Mol. Breed. 32:267–277.
65. Galun, E. 1961. Study of the inheritance of sex expression in the cucumber. The interaction of major genes with modifying genetic and non-genetic factors. Genetica 32:134-163.
66. Gao, M.L., Hu, L.L., Li, Y.H., Weng, Y. 2016. The chlorophyll-deficient golden leaf mutation in cucumber is due to a single nucleotide substitution in *CsChlI* for magnesium chelatase I subunit. Theor Appl Genet 129: 1961-1973.
67. George, W. L., Jr. 1970. Genetic and environmental modification of determinant plant habit in cucumbers. J. Amer. Soc. Hort. Sci. 95:583-586.
68. Goode, M. J., J. L. Bowers, and A. Bassi, Jr. 1980. Little-leaf, a new kind of pickling cucumber plant. Ark. Farm Res. 29:4.
69. Gornitskaya, I. P. 1967. A spontaneous mutant of cucumber variety Nezhinskii 12. Genetika 3:169.
70. Grimbly, P. E. 1980. An apetalous male sterile mutant in cucumber. Cucurbit Genet. Coop. Rpt. 3:9.
71. Groff, D. and M. L. Odland. 1963. Inheritance of closed-flower in the cucumber. J. Hered. 54:191-192.
72. Grumet, R., E. Kabelka, S. McQueen, T. Wai, R. Humphrey. 2000. Characterization of sources of resistance to the watermelon strain of *Papaya ringspot virus* in cucumber: allelism and co-segregation with other potyvirus resistances. Theor. Appl. Genet. 101: 463-472.
73. Haaring, C. 2014. New cucumber plant of species *Cucumis sativus* carrying genetic determinant that leads to darker green stem in seedling stage that is predictive of darker green color of fruits compared to isogenic cucumber plant not carrying determinant. European patent # EP2777386-A1
74. Havey, M. J., Y. H. Park, and G. Bartoszewski. 2004. The *Psm* locus controls paternal sorting of the cucumber mitochondrial genome. J. Hered. 95:492497.
75. He, X. M., Y. H. Li, S. Pandey, B. S. Yandell, M. Pathak, and Y. Weng. 2013. QTL mapping of powdery mildew resistance in WI 2757 cucumber (*Cucumis sativus* L.). Theor. Appl. Genet. 126: 2149-2161.
76. Holdsworth, W. L., C. F. Summers, M. Glos, C. D. Smart, and M. Mazourek, M. 2014. Development of downy mildew-resistant cucumbers for late-season production in the Northeastern United States. HortSci, 49: 10-17.
77. Hutchins, A. E. 1935. The inheritance of a green flowered variation in *Cucumis sativus*. Proc. Amer. Soc. Hort. Sci. 33:513.
78. Hutchins, A. E. 1940. Inheritance in the cucumber. J. Agr. Res. 60:117-128.
79. Iezzoni, A. F. and C. E. Peterson. 1979. Linkage of bacterial wilt resistance and sex expression genes in cucumber. Cucurbit Genet. Coop. Rpt. 2:8.
80. Iezzoni, A. F. and C. E. Peterson. 1980. Linkage of bacterial wilt resistance and sex expression in cucumber. HortScience 15:257-258.
81. Iida, S. and E. Amano. 1991. Mutants induced by pollen irradiation in cucumber. Cucurbit Genet. Coop. Rpt. 14:32-33.
82. Inggamer, H. and O. M. B. de Ponti. 1980. The identity of genes for glabrousness in *Cucumis sativus* L. Cucurbit Genet. Coop. Rpt. 3:14.
83. Jiang, S., X. J. Yuan, J. S. Pan, H. L. He, and R. Cai. 2008. Quantitative trait locus analysis of lateral branch–related traits in cucumber (*Cucumis sativus* L.) using recombinant inbred lines. Sci. China Ser. C - Life Sci. 51: 833-841.
84. Jiang, L., S. S. Yan, W. C. Yang, Y. Q. Li, M. X. Xia, Z. J. Chen, Q. Wang, L. Y. Yan, X. F. Song, R. Y. Liu, and X. L. Zhang. 2015. Transcriptomic analysis reveals the roles of microtubule-related genes and transcription factors in fruit length regulation in cucumber (*Cucumis sativus* L.). Sci. Rep. 5, 8031.
85. John, C. A. and J. D. Wilson. 1952. A "*ginko leafed*" mutation in the cucumber. J. Hered. 43:47-48.
86. Jones, R. W. 1984. Studies related to genetic salt tolerance in the cucumber, *Cucumis sativus* L. Ph.D. Diss., Texas A&M Univ., College Station.
87. Kabelka, E. and R. Grumet. 1997. Inheritance of resistance to the Moroccan watermelon mosaic virus in the cucumber line TMG-1 and cosegregation with zucchini yellow mosaic virus resistance. Euphytica 95:237-242.
88. Kabelka, E., Z. Ullah and R. Grumet. 1997. Multiple alleles for zucchini yellow mosaic virus resistance at the *zym* locus in cucumber. Theor. Appl. Genet. 95:9971004.
89. Kamachi, S., H. Sekimoto, N. Kondo, and S. Sakai. 1997. Cloning of a cDNA for a 1-aminocyclopropane-1-carboxylate synthase that is expressed during development of female flowers at the apices of *Cucumis sativus* L. Plant Cell Physiol. 38: 1197-1206.
90. Kamachi, S., H. Mizusawa, S. Matsuura, and S. Saki. 2000. Expression of two 1-aminocyclopropane-1-carboxylate synthase genes, *CS-ACS1* and *CS-ACS2*, correlated with sex phenotypes in cucumber plants (*Cucumis sativus* L.). Plant Biotechnol. 17: 69-74.
91. Kang, H., Y. Weng, Y. Yang, Z. Zhang, S. Zhang, Z. Mao, G. Cheng, X. Gu, S. Huang S, and B. Xie. 2011. Fine genetic mapping localizes cucumber scab resistance gene *Ccu*

into an R gene cluster. Theor. Appl. Genet. 122: 795–803.
92. Kauffman, C. S. and R. L. Lower. 1976. Inheritance of an extreme dwarf plant type in the cucumber. J. Amer. Soc. Hort. Sci. 101:150-151.
93. Kennard, W. C., K. Poetter, A. Dijkhuizen, V. Meglic, J. E. Staub, and M. J. Havey. 1994. Linkages among RFLP, RAPD, isozyme, disease-resistance, and morphological markers in narrow and wide crosses of cucumber. Theor. Appl. Genet. 89:42-48.
94. Klosinska, U., E. U. Kozik, and T. C. Wehner. 2006. Inheritance of a new trait - twin fused fruit - in cucumber. HortScience 41: 313-314.
95. Knopf, R. R. and T. Trebitsh. 2006. The female-specific *CS-ACS1G* gene of cucumber. A case of gene duplication and recombination between the non-sex-specific 1-aminocyclopropane-1-carboxylate synthase gene and a branched-chain amino acid transaminase gene. Plant Cell Physiol. 47: 1217-1228.
96. Kooistra, E. 1968. Powdery mildew resistance in cucumber. Euphytica 17:236244.
97. Kooistra, E. 1971. Inheritance of flesh and skin colors in powdery mildew resistant cucumbers (*Cucumis sativus* L.). Euphytica 20:521-523.
98. Koornneef, M., and B. J. van der Knaap. 1983. A second long hypocotyl mutant at the *lh* Locus. Cucurbit Genet Coop Rpt 6:13 (article 6).
99. Kozik, E. U. and T. C. Wehner. 2006. Inheritance of chilling resistance in cucumber seedlings. Proc. Cucurbitaceae 2006, p. 121-124 (ed. G. J. Holmes). Universal Press, Raleigh, North Carolina.
100. Kozik, E. U. and T. C. Wehner. 2008. A single dominant gene *Ch* for chilling resistance in cucumber seedlings. J. Amer. Soc. Hort. Sci. 133: 225-227
101. Kubicki, B. 1974. New sex types in cucumber and their uses in breeding work. Proc. XIX Intl. Hort. Congr. 3:475-485.
102. Kubicki, B. 1969a. Investigations of sex determination in cucumber (*Cucumis sativus* L.). IV. Multiple alleles of locus Acr. Genetica Polonica 10:23-68.
103. Kubicki, B. 1969b. Investigations of sex determination in cucumber (*Cucumis sativus* L.). V. Genes controlling intensity of femaleness. Genetica Polonica 10:69-86.
104. Kubicki, B. 1969c. Investigations on sex determination in cucumbers (*Cucumis sativus* L.). VI. Androecism. Genetica Polonica 10:87-99.
105. Kubicki, B. 1969d. Investigations of sex determination in cucumber (*Cucumis sativus* L.). VII. Trimonoecism. Genetica Polonica 10:123-143.
106. Kubicki, B. and A. Korzeniewska. 1983. Inheritance of the presence of empty chambers in fruit as related to the other fruit characters in cucumbers (*Cucumis sativus* L.). Genetica Polonica 24:327-342.
107. Kubicki, B. and A. Korzeniewska. 1984. Induced mutations in cucumber (*Cucumis sativus* L.) III. A mutant with choripetalous flowers. Genetica Polonica 25:53-60.
108. Kubicki, B., I. Goszczycka, and A. Korzeniewska. 1984. Induced mutations in cucumber (*Cucumis sativus* L.) II. Mutant of gigantism. Genetica Polonica 25:41-52.
109. Kubicki, B., U. Soltysiak, and A. Korzeniewska. 1986b. Induced mutations in cucumber (*Cucumis sativus* L.) V. Compact type of growth. Genetica Polonica 27:289-298.
110. Kubicki, B., U. Soltysiak, and A. Korzeniewska. 1986a. Induced mutations in cucumber (*Cucumis sativus* L.) IV. A mutant of the bush type of growth. Genetica Polonica 27:273-287.
111. Li, Z., J. S. Pan, Y. Guan, Q. Y. Tao, H. L. He, L. T. Si, and R. Cai. 2008. Development and fine mapping of three co-dominant SCAR markers linked to the *M/m* gene in the cucumber plant (*Cucumis sativus* L.). Theor. Appl. Genet. 117: 1253-1260.
112. Li. Z, S. W. Huang, S. Q. Liu, et al. 2009. Molecular isolation of the *M* gene suggests that a conserved-residue conversion induces the formation of bisexual flowers in cucumber plants. Genetics 182: 1381–1385.
113. Li, Y. H., L. M. Yang, M. Pathak, D. W. Li, X. M. He, and Y. Weng. 2011. Fine genetic mapping of *cp*, a recessive gene for *compact* (dwarf) plant architecture in cucumber, *Cucumis sativus* L. Theor .Appl. Genet. 123:973-983.
114. Li, Z., S. Wang, Q. Y. Tao, J. S. Pan, L .T. Si, Z. H. Gong, and R. Cai. 2012. A putative positive feedback regulation mechanism in *CsACS2* expression suggests a modified model for sex determination in cucumber (*Cucumis sativus* L.). J. Exp. Bot. 63: 4475-4484.
115. Li, Y.H., C. L. Wen, and Y. Weng. 2013. Fine mapping of the pleiotropic locus *B* for black spine and orange mature fruit color in cucumber identifies a 50 kb region containing a R2R3-MYB transcription factor. Theor. Appl. Genet. 126: 2187–2196.
116. Li, W.Q., Gao, B., Yang, J., Chen, P., Li, Y.H. 2015a. Physiological characterization of a new yellow leaf mutant. Acta Agri Boreal Occident Sin 24:98–103 (in Chinese)
117. Li, Q., C. X. Cao, C. J. Zhang, X. X. Zheng, Z. H. Wang, L. N. Wang, and Z. H. Ren. 2015b. The identification of *Cucumis sativus Glabrous 1* (*CsGL1*) required for the formation of trichomes uncovers a novel function for the homeodomain-leucine zipper I gene. J Expt. Bot. 65: 4943–4958.
118. Li, S., Pan, Y.P., Wen, C.L., Li, Y.H., Liu, X.F., Zhang, X.L., Behera, T.K., Xing, G.M., Weng, Y. 2016. Integrated analysis in bi-parental and natural populations reveals *CsCLAVATA3* (*CsCLV3*) underlying carpel number variations in cucumber. Theor Appl Genet 129: 1007-1022.
119. Lietzow, C.D., Zhu, H.Y., Pandey, S., Havey, M.J., Weng, Y. 2016. QTL mapping of parthenocarpic fruit set in North American processing cucumber. Theor Appl Genet 129: 2387–2401.
120. Lin, T., Wang, S.H., Zhong, Y., Gao, D.L., Cui, Q.Z., Chen, H.M., Zhang, Z.H., Shen, HL, Weng Y, Huang SW. 2016.

A truncated F-box protein confers the dwarfism in cucumber. J Genetics Genomics 43: 223-226
121. Liu, L. Z., X. j. Yuan, R. Cai, J. S. Pan, H. L. He, L. H. Yuan, Y. Guan, and L. H. Zhu. 2008. Quantitative trait loci for resistance to powdery mildew in cucumber under seedling spray inoculation and leaf disc infection. J. Phytopathol. 156: 691–697.
122. Liu, H., Meng, H., Pan, Y., Liu, J., Chen, S.X. et al. 2015. Fine genetic mapping of the white immature fruit color gene *w* to a 33.0-kb region in cucumber (*Cucumis sativus* L.). Theor Appl Genet 128:2375–2385.
123. Liu, H.Q., Jiao, J.Q., Liang, X.J., Liu, J., Meng, H.W., Chen, S.X., Li, Y.H., Cheng, Z.H. 2016. Map-based cloning, identification and characterization of the w gene controlling white immature fruit color in cucumber (*Cucumis sativus* L.). Theor Appl Genet 129:1247–1256.
124. Lou, L. N., H. Y. Wang, C. T. Qian, J. Liu, Y. L. Bai, and J. F. Chen. 2013. Genetic mapping of gummy stem blight (Didymella bryoniae) resistance genes in *Cucumis sativus-hystrix* introgression lines. Euphytica 192: 359-369.
125. Lu, H. F., Lin, T., Klein, J., Wang, S.H., Qi, J.J., Zhou, Q., Sun, J.J., Zhang, Z.H., Weng, Y., Huang, S.W. 2014. QTL-Seq identifies a major early flowering QTL corresponding to the *FT* locus in cucumber. Theor Appl Genet 127:1491-1499.
126. Lu, H. W., H. Miao, G. L. Tian, T. C. Wehner, X. F. Gu, and S. P. Zhang. 2015. Molecular mapping and candidate gene analysis for yellow fruit flesh in cucumber. Mol. Breed. 35:64.
127. Lun, Y.Y., Wang, X., Zhang, C.Z., Yang, L., Gao, D.L., Chen, H.M., Huang, S.W. 2016. A *CsYcf54* variant conferring light green coloration in cucumber. Euphytica 208:509–517.
128. Mao, A. J., F. Zhang, L. R. Zhang, and Y. J. Wang. 2008. Analysis on the inheritance of resistance to *Fusarium* wilt race 4 and scab and their linkage in WI 2757 cucumber. Sci. Agri. Sinica 41:3382-3388.
129. Mazereeuw, J., B. Van Kampen, R. Wilterdink, and N. Faber. 2012. Cucumber vein yellowing virus (CVYV) resistant cucumber plants (*Cucumis sativus* L.). US Patent # 20120137388 A1.
130. Miao, H., X. F. Gu, S. P. Zhang, Z. Y. Fang, and Z. X. Zhang. 2010a. Comparison and analysis of two yellow-green mutants in cucumber (*Cucumis sativus* L.). 1(22): 16-20 (In Chinese).
131. Miao, H., X. F. Gu, S. P. Zhang, J. Wu, and Z. Y. Fang. 2010b. Mapping QTLs for multiple pistillate flowers in cucumber. Acta Hort Sinica 37: 1449–1455 (in Chinese)
132. Miao, H., S. P. Zhang, X .W. Wang, Z. H. Zhang, M. Li, S. Q. Mu, et al. 2011a. A linkage map of cultivated cucumber（ *Cucumis sativus* L. ）with 248 microsatellite marker loci and seven genes for horticulturally important traits. Euphytica 182: 167–176.
133. Miao, H., X. F. Gu, S. P. Zhang, Z. H. Zhang, S. W. Huang, Y. Wang, Z. C. Cheng, et al. 2011b. Mapping QTLs for fruit-associated traits. Sci. Agri. Sinica 44: 5031–5040 (in Chinese).
134. Miao, H., X. F. Gu, S. P. Zhang, Z. H. Zhang, S. W. Hunag, Y. Wang, and Z. Y. Fang. 2012. Mapping QTLs for seedling-associated traits in cucumber. Acta Hort. Sinica 39: 879–887 (in Chinese)
135. Miao, H., Zhang, S.P., Wang, M., Wang, Y., Weng, Y., Gu, X.F. 2016. Fine mapping of virescent leaf gene *v-1* in cucumber (*Cucumis sativus* L.). Int. J. Mol. Sci. 17: 1602
136. Mibus, H, and t. Tatlioglu. 2004. Molecular characterization and isolation of the *F/f* gene for femaleness in cucumber (*Cucumis sativus* L.). Theor. Appl. Genet. 109: 1669-1676.
137. Miller, G. A. and W. L. George, Jr. 1979. Inheritance of dwarf determinate growth habits in cucumber. J. Amer. Soc. Hort. Sci. 104:114-117.
138. Miller, J. C., Jr. and J. E. Quisenberry. 1978. Inheritance of flower bud abortion in cucumber. HortScience 13:44-45.
139. Munger, H. M. and R. E. Wilkinson. 1975. Scab resistance in relation to fruit length in slicing cucumbers. Veg. Imp. Nwsl. 17:2.
140. Nandgaonkar, A. K. and L. R. Baker. 1981. Inheritance of multi-pistillate flowering habit in gynoecious pickling cucumber. J. Amer. Soc. Hort. Sci. 106:755-757.
141. Netzer, D., S. Niegro, and F. Galun. 1977. A dominant gene conferring resistance to Fusarium wilt in cucumber. Phytopathology 67:525-527.
142. Nie, J. T., H. L. He, J. L. Peng, X. Q. Yang, B. B. Bie, J. L. Zhao, Y. L. Wang, L. T. Si, J. S. Pan, and R. Cai. 2015a. Identification and fine mapping of *pm5.1*: a recessive gene for powdery mildew resistance in cucumber (*Cucumis sativus* L.). Mol. Breed. 35: 7.
143. Nie, J.T., Wang, Y.L., He, H.L., Guo, C.L., Zhu, W.Y., Pan, J., Li, D.D., Lian, H.L., Pan, J.S., Cai, R. 2015b. Loss-of-function mutations in *CsMLO1* confer durable powdery mildew resistance in cucumber (*Cucumis sativus* L.). Front. Plant Sci. 6: 1155.
144. Niemirowicz-Szczytt, A., M. Rucinska, and A. Korzeniewsia. 1996. An induced mutation in cucumber (*Cucumis sativus* L.): super compact. Cucurbit Genet. Coop. Rept. 19:1-3.
145. Nuttall, W. W. and J. J. Jasmin. 1958. The inheritance of resistance to bacterial wilt (*Erwinia tracheiphila* [E. F. Sm.] Holland) in cucumber. Can. J. Plant Sci. 38:401-404.
146. Odland, M. L. and D. W. Groff. 1963a. Inheritance of crinkled-leaf cucumber. Proc. Amer. Soc. Hort. Sci. 83:536-537.
147. Odland, M. L. and D. W. Groff. 1963b. Linkage of vine type and geotropic response with sex forms in cucumber Cucumis sativus L. Proc. Amer. Soc. Hort. Sci. 82:358-369.
148. Olczak-Woltman, H., G. Bartoszewski, W. Madry, and K. Niemirowicz-Szczytt. 2009. Inheritance of resistance to angular leaf spot (*Pseudomonas syringae* pv. *lachrymans*) in cucumber and identification of

molecular markers linked to resistance. Plant Pathology 58: 145–151.
149. Pan, Y.P., Bo, K.L., Cheng, Z.H., Weng, Y. 2015. The loss-of-function *GLABROUS 3* mutation in cucumber is due to LTR-retrotransposon insertion in a class IV HD-ZIP transcription factor gene *CsGL3* that is epistatic over *CsGL1*. BMC Plant Biology 2015 15: 302.
150. Pang, X., X. H. Zhou, H. J. Wan, and J. F. Chen. 2013. QTL Mapping of downy mildew resistance in an introgression line derived from interspecific hybridization between cucumber and *Cucumis hystrix*. J. Phytopathol 161: 536-543.
151. Park, Y. H., S. Sensoy, C. Wye, R. Antonise, J. Peleman, and M. J. Havey. 2000. A genetic map of cucumber composed of RAPDs, RFLPs, AFLPs, and loci conditioning resistance to papaya ringspot and zucchini yellow mosaic viruses. Genome 43:1003-1012.
152. Peterson, G. C. and L. M. Pike. 1992. Inheritance of green mature seed-stage fruit color in *Cucumis sativus* L. J. Amer. Soc. Hort. Sci. 117:643-645.
153. Petrov, L., K. Boogert, L. Sheck, A. Baider, E. Rubin, and Y. Cohen. 2000. Resistance to downy mildew, Pseudoperonospora cubensis, in cucumbers. In VII Eucarpia Meeting on Cucurbit Genetics and Breeding 510, pp 203-210.
154. Pierce, L. K. and T. C. Wehner. 1990. Review of genes and linkage groups in cucumber. HortScience 25:605-615.
155. Pike L. M. and T. F. Caruth. 1977. A genetic study of the inheritance of rupturing carpel in fruit of cucumber, *Cucumis sativus* L. HortScience 12:235 (Abstract).
156. Pike, L. M. and C. E. Peterson. 1969. Inheritance of parthenocarpy in the cucumber (*Cucumis sativus* L.). Euphytica 18:101-105.
157. Pitchaimuthu, M., O. P. Dutta, K. P. M. Swamy, and K. Souravi. 2012. Mode of inheritance of bitterness and spine color in cucumber fruits (*Cucumis sativus* L.). In: Sari, N., I. Solmaz, and V. Aras (eds) Cucurbitaceae 2012, Proc. 10th EUCARPIA meeting on Genetics and Breeding of Cucurbitaceae, Antalya, Turkey, 15–18 October 2012, pp 70–73
158. Poole, C. F. 1944. Genetics of cultivated cucurbits. J. Hered. 35:122-128.
159. Pramnoi, P., P. Somta, S. Chankaew, R. Juwattanasomran, and P. Srinives. 2013. A single recessive gene controls fragrance in cucumber (Cucumis sativus L.). J. Genetics 92: 147-149.
160. Provvidenti, R. 1985. Sources of resistance to viruses in two accessions of *Cucumis sativus*. Cucurbit Genet. Coop. Rpt. 8:12.
161. Provvidenti, R. 1987. Inheritance of resistance to a strain of zucchini yellow mosaic virus in cucumber. HortScience 22:102-103.
162. Pyzhenkov, V. I. and G. A. Kosareva. 1981. Description of features and their inheritance pattern in a new cucumber mutant. Biull. Vses. Inst. Rastenievod 109:5-8 (Plant Breeding Abstracts 1983, 53:478).
163. Qi, J. J., X. Liu, D. Shen, H. Miao, B. Y. et al. 2013. A genomic variation map provides insights into the genetic basis of cucumber domestication and diversity. Nat Genet. 45: 1510–1515
164. Qu, S. P., Y. P. Pan, and Y. Weng. 2014. QTL Mapping of flowering time and fruit shape in Xishuangbana cucumber (*Cucumis sativus* L. var. *xishuangbannanesis* Qi et Yuan). Proc Cucurbitaceae 2014, pp 54-56.
165. Ren GL, Yang XQ, He HL, Cai R, Pan JS (2013) Molecula rmapping of non-lateral gene in cucumber. Acta
166. Hort Sinica 40: 1375-1381
167. Robinson, R. W. 1978a. Fasciation in the cucumber. Cucurbit Genet. Coop. Rpt. 1:11a.
168. Robinson, R. W. 1978b. Association of fruit and sex expression in the cucumber. Cucurbit Genet. Coop. Rpt. 1:10.
169. Robinson, R. W. 1987a. Blunt leaf apex, a cucumber mutant induced by a chemical mutagen. Cucurbit Genet. Coop. Rpt. 10:6.
170. Robinson, R. W. 1987b. Chlorosis induced in glabrous cucumber by high temperature. Cucurbit Genet. Coop. Rpt. 10:7.
171. Robinson, R. W. 1987c. Cordate, a leaf shape gene with pleiotropic effects on flower structure and insect pollination. Cucurbit Genet. Coop. Rpt. 10:8.
172. Robinson, R. W. 1987d. Inheritance of opposite leaf arrangement in *Cucumis sativus* L. Cucurbit Genet. Coop. Rpt. 10:10.
173. Robinson, R. W. and W. Mishanec. 1964. A radiation-induced seedling marker gene for cucumbers. Veg. Imp. Nwsl. 6:2.
174. Robinson, R. W. and W. Mishanec. 1965. A new dwarf cucumber. Veg. Imp. Nwsl. 7:23.
175. Robinson, R. W. and J. W. Shail. 1981. A cucumber mutant with increased hypocotyl and internode length. Cucurbit Genet. Coop. Rpt. 4:19-20.
176. Robinson, R. W. and T. W. Whitaker. 1974. *Cucumis*, p. 145-150. In: R. C. King (ed), Handbook of Genetics. vol. 2. Plenum, New York.
177. Rosa, J. T. 1928. The inheritance of flower types in *Cucumis* and *Citrullus*. Hilgardia 3:233-250.
178. Rowe, J. T. and J. L. Bowers. 1965. The inheritance and potential of an irradiation induced tendrilless character in cucumbers. Proc. Amer. Soc. Hort. Sci. 86:436-441.
179. Rucinska, M., K. Niemirowicz-Szczytt, and A. Korzeniewska. 1991. A cucumber (*Cucumis sativus* L.) mutant with yellow stem and leaf petioles. Cucurbit Genet. Coop. Rpt. 14:8-9.
180. Rucinska, M., K. Niemirowicz-Szczytt, and A. Korzeniewska. 1992a. Cucumber (*Cucumis sativus* L.) induced mutations. II. A second short petiole mutant. Cucurbit Genet. Coop. Rpt. 15:33-34.
181. Rucinska, M., K. Niemirowicz-Szczytt, and A. Korzeniewska. 1992b. Cucumber (*Cucumis sativus* L.) induced mutations. III and IV. Divided and gingko

leaves. Proc. 5th EUCARPIA Cucurbitaceae Symp. p. 66-69, Warsaw, Poland.
182. Sakata, Y., N. Kubo, M. Morishita, E. Kitadani, M. Sugiyama, and M. Hirai. 2006. QTL analysis of powdery mildew resistance in cucumber (*Cucumis sativus* L). Theor Appl Genet 112: 243-250.
183. Shang, Y., Y. S. Ma, Y. Zhou, H. M. Zhang, L. X. Duan, et al. 2014. Biosynthesis, regulation, and domestication of bitterness in cucumber. Science 346: 1084-1088.
184. Shanmugasundarum, S., P. H. Williams, and C. E. Peterson. 1971a. Inheritance of fruit spine color in cucumber. HortScience 6:213-214.
185. Shanmugasundarum, S., P. H. Williams, and C. E. Peterson. 1971b. Inheritance of resistance to powdery mildew in cucumber. Phytopathology 61:1218-1221.
186. Shanmugasundarum, S., P. H. Williams, and C. E. Peterson. 1972. A recessive cotyledon marker gene in cucumber with pleiotropic effects. HortScience 7:555-556.
187. Shi, T. T., S. H. Wang, T. Lin, Q. Yang, and S. W. Huang. 2014. Genetic mapping of *little leaf 2* (*ll2*), a major QTL controlling leaf area in cucumber (*Cucumis sativus* L.). J Agri. Biotech 22: 415-421
188. Shifriss, O. 1950. Spontaneous mutations in the American varieties of *Cucumis sativus* L. Proc. Amer. Soc. Hort. Sci. 55:351-357.
189. Shifriss, O. 1961. Sex control in cucumbers. J. Hered. 52:5-12.
190. Shifriss, O., C. H. Myers, and C. Chupp. 1942. Resistance to mosaic virus in cucumber. Phytopathology 32:773-784.
191. Shimizu, S., K. Kanazawa, and A. Kato. 1963. Studies on the breeding of cucumber for resistance to downy mildew. Part 2. Difference of resistance to downy mildew among the cucumber varieties and the utility of the cucumber variety resistance to downy mildew (in Japanese). Bul. Hort. Res. Sta. Jpn. Ser. A, No. 2:80-81.
192. Soans, A. B., D. Pimentel, and J. S. Soans. 1973. Cucumber resistance to the two-spotted spider mite. J. Econ. Entomol. 66:380-382.
193. Soltysiak, U. and B. Kubicki. 1988. Induced mutations in the cucumber (*Cucumis sativus* L.). VII. Short hypocotyl mutant. Genetica Polonica 29:315-321.
194. Soltysiak, U., B. Kubicki, and A. Korzeniewska. 1986. Induced mutations in cucumber (*Cucumis sativus* L.). VI. Determinate type of growth. Genetica Polonica 27:299-308.
195. Strong, W. J. 1931. Breeding experiments with the cucumber (*Cucumis sativus* L.). Sci. Agr. 11:333-346.
196. Sugiyama, M., Y. Kawazu. N. Fukino, Y. Yoshioka, K. Shimomura, Y. Sakata, M. Okuda. 2015. Mapping of quantitative trait loci for Melon yellow spot virus resistance in cucumber (*Cucumis sativus* L.). Euphytica 205:615–625
197. Sun, Z., J. E. Staub, S. M. Chung, and R. L. Lower. 2006. Identification and comparative analysis of quantitative trait loci associated with parthenocarpy in processing cucumber. Plant Breed. 125: 281-287.
198. Szczechura, W., Staniaszek, M., Klosinska, U., Kozik, E.U. 2015. Molecular analysis of new sources of resistance to *Pseudoperonospora cubensis* (Berk. et Curt.) Rostov. in cucumber. Russian J Genet 51: 974–979.
199. Tan, J.Y., Tao, Q.Y., Niu, H.H., Zhang, Z., Li, D.D., Gong, Z.H., Weng, Y., Li, Z. 2015. A novel allele of monoecious (*m*) locus is responsible for elongated fruit shape and perfect flowers in cucumber (*Cucumis sativus* L.) Theor Appl Genet 128: 2483-2493.
200. Thaxton, P. M. 1974. A genetic study of the clustering characteristics of pistallate flowers in cucumber, *Cucumis sativs* L. M.S. Thesis, Texas A&M University, College Station.
201. Tian G.L., Y.H. Yang, S. P. Zhang, H. Miao, H. W. Lu, Y. Wang, B. Y. Xie, X.F. Gu. 2015. Genetic analysis and gene mapping of papaya ring spot virus resistance in cucumber. Mol. Breed. 35: 110.
202. Tian, G.L., Miao, H., Yang, Y.H., Zhou, J., Lu, H.W., Wang, Y., Xie, B.Y., Zhang, S.P., Gu, X.F. 2016. Genetic analysis and fine mapping of watermelon mosaic virus resistance gene in cucumber. Mol Breed. 36:131
203. Tkachenko, N. N. 1935. Preliminary results of a genetic investigation of the cucumber, *Cucumis sativus* L. Bul. Applied Bot. Genet. Plant Breed. 9:311-356.
204. Trebitsh, T., J. E. Staub, and S. D. O'Neill. 1997. Identification of a 1aminocyclopropane-1-carboxylic acid synthase gene linked to the female (*F*) locus that enhances female sex expression in cucumber. Plant Physiol. 113: 987-995.
205. Vakalounakis, D. J. 1992. *Heart leaf*, a recessive leaf shape marker in cucumber: linkage with disease resistance and other traits. J. Heredity 83:217-221.
206. Vakalounakis, D. J. 1993. Inheritance and genetic linkage of *fusarium* wilt (*Fusarium oxysporum* f. sp. *cucumerinum* race 1) and scab (*Cladosporium cucumerinum*) resistance genes in cucumber (*Cucumis sativus*). Annals of Applied Biology 123:359-365.
207. Vakalounakis, D. J. 1995. Inheritance and linkage of resistance in cucumber line SMR18 to races 1 and 2 of *Fusarium oxysporum* f. sp. *cucumerinum*. Plant Pathology 44:169-172.
208. Vakalounakis, D. J. 1996. Allelism of the *Fcu-1* and *Foc* genes conferring resistance to *Fusarium* wilt in cucumber. European J. Plant Pathology 102:855-858.
209. Van Vliet, G. J. A. and W. D. Meysing. 1974. Inheritance of resistance to Pseudoperonospora cubensis Rost. in cucumber (Cucumis sativus L.). Euphytica 23:251-255.
210. Van Vliet, G. J. A. and W. D. Meysing. 1977. Relation in the inheritance of resistance to *Pseudoperonospora cubensis* Rost. and *Sphaerotheca fuliginea* Poll. in cucumber (*Cucumis sativus* L.). Euphytica 26:793-796.
211. Wai, T. and R. Grumet. 1995. Inheritance of resistance to the watermelon strain of papaya ringspot virus in the cucumber line TMG-1. HortScience 30:338-340.

212. Wai, T., J. E. Staub, E. Kabelka and R. Grumet. 1997. Linkage analysis of potyvirus resistance alleles in cucumber. J. Heredity. 88: 454-458.
213. Wall, J. R. 1967. Correlated inheritance of sex expression and fruit shape in *Cucumis*. Euphytica 23:251-255.
214. Walters, S. A. and T. C. Wehner. 1998. Independence of the *mj* nematode resistance gene from 17 gene loci in cucumber. HortScience 33:1050-1052.
215. Walters, S. A., T. C. Wehner, and K. R. Barker. 1996. NC-42 and NC-43: Root-knot nematode-resistant cucumber germplasm. HortScience 31:1246-1247.
216. Walters, S. A., T. C. Wehner, and K. R. Barker. 1997. A single recessive gene for resistance to the root-knot nematode (*Meloidogyne javanica*) in *Cucumis sativus* var. *hardwicki*i. J. Hered. 88: 66-69.
217. Walters, S. A., N. V. Shetty and T. C. Wehner. 2001. Segregation and linkage of several genes in cucumber. J. Amer. Soc. Hort. Sci. 126: 442-450.
218. Wang, Y. J., R. Provvidenti, and R. W. Robinson. 1984a. Inheritance of resistance to watermelon mosaic virus 1 in cucumber. HortScience 19:587-588.
219. Wang, Y. J., R. Provvidenti, and R. W. Robinson. 1984b. Inheritance of resistance in cucumber to watermelon mosaic virus. Phytopathology 51:423-428.
220. Wang, H. Z., S. J. Li, R. H. Yang, and W. Guan. 2010. EST-SSR marker linked to cucumber target leaf spot resistance-related gene. Acta Hort. 871, ISHS 2010 871: 49-53.
221. Wang, L. N., B. Zhang, J. R. Li, X. Y. Yang, and Z. H. Ren. 2014a. Ethyl Methanesulfonate (EMS)-mediated mutagenesis of cucumber (*Cucumis sativus* L.). Agri. Sci. 5:716 -721.
222. Wang, M., X. F. Gu, H. Miao, S. L. Liu, Y. Wang, T. C. Wehner, and S. P. Zhang. 2014b. Molecular mapping and candidate gene analysis for heavy netting gene (*H*) of mature fruit of cucumber (*Cucumis sativus* L.). Scientia Agri. Sinica 47: 1550-1557.
223. Wang, S., Yang, X., Xu, M., Lin, X., Lin, T., Qi, J., Shao, G., Tian, N., Yang, Q., Zhang, Z., Huang, S. 2015. A rare SNP identified a TCP transcription factor essential for tendril development in cucumber. Mol. Plant. 8: 1795–1808.
224. Wang, Y.H., VandenLangenberg, K., Wehner, T.C., Kraan, P.A.G., Suelmann, J., Zheng, X.Y., Owens, K., Weng, Y. 2016a. QTL mapping for downy mildew resistance in cucumber inbred line WI7120 (PI 330628). Theor Appl Genet 129: 1493-1505.
225. Wang, Y.L., Nie, J.T., Chen, H.M., Guo, C.L., Pan, J., He, H.L., Pan, J.S., Cai, R. 2016b Identification and mapping of *Tril*, a homeodomain-leucine zipper gene involved in multicellular trichome initiation in *Cucumis sativus*. Theor Appl Genet 129: 305-316.
226. Wang, H., Li, W., Qin, Y., Pan, Y., Wang, X., Weng, Y., Chen, P., Li, Y. 2017. The cytochrome P450 gene *CsCYP85A1* is a putative candidate for *super compact-1* (*scp-1*) plant architecture mutation in cucumber (*Cucumis sativus* L.). Front Plant Sci doi: 10.3389/fpls.2017.00266
227. Wasuwat, S. L. and J. C. Walker. 1961. Inheritance of resistance in cucumber to cucumber mosaic virus. Phytopathology 51:423-428.
228. Wehner, T. C., J. E. Staub, and C. E. Peterson. 1987. Inheritance of *littleleaf* and multi-branched plant type in cucumber. Cucurbit Genet. Coop. Rpt. 10:33.
229. Wehner, T. C., J. S. Liu, and J. E. Staub. 1998a. Two-gene interaction and linkage for bitterfree foliage in cucumber. J. Amer. Soc. Hort. Sci. 123: 401-403.
230. Wehner, T. C., J. E. Staub, and J. S. Liu. 1998b. A recessive gene for revolute cotyledons in cucumber. J. Hered. 89: 86 87.
231. Wellington, R. 1913. Mendelian inheritance of epidermal characters in the fruit of *Cucumis sativus*. Science 38:61.
232. Wellington, R. and L. R. Hawthorn. 1928. A parthenocarpic hybrid derived from a cross between and English forcing cucumber and the Arlington White Spine. Proc. Amer. Soc. Hort. Sci. 25:97-100.
233. Wen, C.L., Mao, A.J., Dong, C.J., Liu, H.Y., Yu, S.C., Guo, Y.D., Weng, Y., Xu, Y. 2015. Fine genetic mapping of target leaf spot resistance gene *cca-3* in cucumber, *Cucumis sativus* L. Theor Appl Genet 128: 2495-2506.
234. Weng, Y., S. Johnson, J. E. Staub, and S. W. Huang. 2010. An extended microsatellite genetic map of cucumber, *Cucumis sativus* L. HortSci 45: 880-886.
235. Whelan, E. D. P. 1972a. A cytogenetic study of a radiation-induced male sterile mutant of cucumber. J. Amer. Soc. Hort. Sci. 97:506-509.
236. Whelan, E. D. P. 1972b. Inheritance of a radiation-induced light sensitive mutant of cucumber. J. Amer. Soc. Hort. Sci. 97:765767.
237. Whelan, E. D. P. 1973. Inheritance and linkage relationship of two radiation-induced seedling mutants of cucumber. Can. J. Genet. Cytol. 15:597-603.
238. Whelan, E. D. P. and B. B. Chubey. 1973. Chlorophyll content of new cotyledon mutants of cucumber. HortScience 8:30-32.
239. Whelan, E. D. P., P. H. Williams, and A. Abul-Hayja. 1975. The inheritance of two induced cotyledon mutants of cucumber. HortScience 10:267-269.
240. Wilson, J. M. 1968. The relationship between scab resistance and fruit length in cucumber, *Cucumis sativus* L. M.S. Thesis, Cornell Univ., Ithaca, NY.
241. Wilson, J. E., and L. R. Baker. 1976. Inheritance of carpel separation in mature fruits of pickling cucumbers. J. Am. Soc. Hort. Sci., 101: 66-69.
242. Win, K.T., Zhang, C.Y., Song, K.W., Lee, J.H., Lee, S.H. 2015. Development and characterization of a co-dominant molecular marker via sequence analysis of a genomic region containing the *Female* (*F*) locus in cucumber (*Cucumis sativus* L.). Mol Breeding 35:229.
243. Wu, Z., Zhang, T., Li, L., Xu, J., Qin, X.D,, Zhang, T.L,, Cui, L., Lou, Q.F,, Li, J., Chen, J.F. 2016. Identification of a stable major-effect QTL (*Parth 2.1*) controlling parthenocarpy in cucumber and associated candidate

gene analysis via whole genome re-sequencing. BMC Plant Biol 16:182.
244. Xu, X.W., Yu, T., Xu, R.X., Shi, Y., Lin, X.J., Xu, Q., Qi, X.H., Weng, W., Chen, X.H. 2015. Fine mapping of a dominantly inherited powdery mildew resistance major-effect QTL, *Pm1.1*, in cucumber identifies a 41.1 kb region containing two tandemly arrayed cysteine-rich receptor-like protein kinase genes. Theor Appl Genet 129:507-516.
245. Xu, X., Ji, J., Xu, Q., Qi, X., Chen, X. 2016, Inheritance and quantitative trail loci mapping of adventitious root numbers in cucumber seedlings under waterlogging conditions. Mol Genet Genomics doi:10.1007/s00438-016-1280-2
246. Yamasaki S., N. Fujii, H. Takahashi. 2003. Characterization of ethylene effects on sex determination in cucumber plants. Sexual Plant Reprod. 16: 103-111.
247. Yang, S. J., H. Miao, S. P. Zhang, Z. C. Cheng, S. Y. Dong, T. C. Wehner, and X. F. Gu. 2011. Genetic analysis and mapping of *gl-2* gene in cucumber (*Cucumis sativus* L.). Acta Hort Sinica 38: 1685–1692 (in Chinese)
248. Yang, S.J., Gu, X.F., Zhang, S.P., Miao, H., Li, B.J. 2012. Research progress on cucumber target leaf spot (*Corynespora cassiicola*). China Veg 4:1–9. (in Chinese)
249. Yang, X. Q., W. Zhang, H. L. He, J. T. NieT, B. B. Bie, J. L. Zhao, G. L. Ren, Y. Li, D. B. Zhang, J. S. Pan, and R. Cai. 2014a. Tuberculate fruit gene *Tu* encodes a C2H2 zinc finger protein that is required for the warty fruit phenotype in cucumber (*Cucumis sativus* L.). Plant J. 78: 1034-1046.
250. Yang, X. Q., W. W. Zhang, Y. Li, H. L. He, B. B. Bie, G. L. Ren, J. L. Zhao, Y. L. Wang, J. T.
251. Yang, X. Q., Y. Li, W. W. Zhang, H. L. He, J. S. Pan, and R. Cai. 2014c. Fine mapping of the uniform immature fruit color gene *u* in cucumber. Euphytica 196: 341-348.
252. Yong, J. P., Y. H. Li, Y. J. Meng, Y. H. Zhong, Z. H. Cheng, and P. Chen. 2013. Microsatellite and STS markers for the compact (*cp*) locus in cucumber. J. Agri. Biotech. 21: 2152-2158.
253. Yoshioka, Y., Y. Sakata, M. Sugiyama, and N. Fukino. 2014. Identification of quantitative trait loci for downy mildew resistance in cucumber (*Cucumis sativus* L.). Euphytica (in press)
254. Youngner, V. B. 1952. A study of the inheritance of several characters in the cucumber. Ph.D. Diss. Univ. of Minnesota, St. Paul.
255. Yundaeng, C., P. Somta, S. Tangphatsornruang, S. Chankaew, P. Srinives. 2015. A single base substitution in BADH/AMADH is responsible for fragrance in cucumber (*Cucumis sativus* L.), and development of SNAP markers for the fragrance. Theor. Appl. Genet. 128:1881-92.
256. Yuan, X.J., X. Z. Li, J. S. Pan, G. Wang, S. Jiang, X. H. Li, S. L. Deng, H. L. He, M. X. Si, L. Lai, A. Z. Wu, L. H. Zhu, and R. Cai. 2008. Genetic mapping and QTL analysis of fruit and flower related traits in cucumber (*Cucumis sativus* L.) using recombinant inbred lines. Euphytica 164:473–491.
257. Zhang, Q., A. C. Gabert, and J. R. Baggett. 1994. Characterizing a cucumber pollen sterile mutant: inheritance, allelism, and response to chemical and environmental factors. J. Amer. Soc. Hort. Sci. 119: 804-807.
258. Zhang, S. P., H. Miao, X. F. Gu, Y. H. Yang, B. Y. Xie, X. W. Wang, S. W. Huang, Y. C. Du, and R. F. Sun. 2010a. Genetic mapping of the scab resistance gene in cucumber. J. Amer. Soc. Hort. Sci. 135:53–58.
259. Zhang, W. W., H. L. He, Y. Guan, H. Du, L. H. Yuan, Z. Li, D. Q. Yao, J. S. Pan, and R. Cai. 2010b. Identification and mapping of molecular markers linked to the tuberculate fruit gene in the cucumber (*Cucumis sativus* L.). Theor. Appl. Genet. 120: 645–654.
260. Zhang, S. P., M. M. Liu, H. Miao, S. Q. Zhang, Y. H. Yang, B. Y. Xie, T. C. Wehner, and X. F. Gu. 2013a. Chromosomal mapping and QTL analysis of resistance to downy mildew in *Cucumis sativus*. Plant Dis. 97:245–251.
261. Zhang, S. P., H. Miao, R. F. Sun, X. W. Wang, S. W. Huang, T. C. Wehner, and X. F. Gu. 2013b. Localization of a new gene for bitterness in cucumber. J. Hered. 104:134–139.
262. Zhang, S. P., H. Miao, Y. H. Yang, B. Y. Xie, Y. Wang, and X. F. Gu. 2014. A major quantitative trait locus conferring resistance to *Fusarium* wilt was detected in cucumber by using recombinant inbred lines. Mol. Breed. 34:1805–1815.
263. Zhang, Z., Mao, L., Chen, H., Bu, F., Li, G., Sun, J., et al. 2015. Genome-wide mapping of structural variations reveals a copy number variant that determines reproductive morphology in cucumber. *Plant Cell* 27: 1595-1604.
264. Zhang, S.P., Liu, S.L,, Miao, H., Wang, M., Liu, P.N., Wehner, T.C,, Gu, X.F, 2016a, Molecular mapping and candidate gene analysis for numerous spines on the fruit of cucumber. J Hered 107: 471–477.
265. Zhang, H., Wang, L., Zheng, S., Liu, Z., Wu, X., Gao, Z., Cao, C., Li, Q., Ren, Z. 2016b. A fragment substitution in the promoter of *CsHDZIV11/CsGL3* is responsible for fruit spine density in cucumber (*Cucumis sativus* L.). Theor Appl Genet 129: 1289-301.
266. Zhao, J. L., Pan, J.S., Guan, Y., Zhang, W.W., Bie, B.B., Wang, Y.L., He, H.L., Lian, H.L., Cai, R. 2015. *Micro-trichome* as a class I homeodomain-leucine zipper gene regulates multicellular trichome development in *Cucumis sativus*. J Integr Plant Biol 57: 925-35.
267. Zhou, Q., S. H. Wang, B. W. Hu, H. M. Chen, Z. H. Zhang, S.W. Huang. 2015. *An ACCUMULATION AND REPLICATION OF CHLOROPLASTS 5* gene mutation confers light green peel in cucumber. J. Integ. Plant Biol. 57: 936–942.

	Gene	*Syn*	**Full name**	**Description**	**References**	**Year listed**
1	***a***		*Androecious*	Increases maleness; *A* is suppressed by the dominant *F* allele, however the recessive *a* allele intensifies the male tendency in *ff* genotypes. The androecious gene (A) is CsACS11 on Chromosome 2.	Kubicki, 1969c; Boualem et al., 2015.	1976, 2017
2	***a-1***	*CsACO2*	*Androecy 1*	An EMS mutant, 406a bearing only male flowers on the main stem and lateral shoots identified from the monoecious line 406. The androecy phenotype is conditioned by a single recessive gene *CsACO2*, which encodes an ACC oxidase gene	Chen et al., 2016	2017
3	***al***		*Albino cotyledon*	Irradiation induced mutation from 'Nishiki Suyo'; cotyledons white, hypocotyl light green; dying before first true leaf.	Iida and Amano, 1991	1993
4	***ap***		*Apetalous*	Male sterile, anthers transformed into sepal-like structures. *Ap* from 'Butcher's Disease Resisting'; *ap* from 'Butcher's Disease Resisting Mutant'.	Grimbly, 1980	1982
5	***Ar***		*Anthracnose resistance*	Anthracnose resistance in PI 197087 was controlled by a partially dominant gene.	Barnes and Epps, 1952, 1955	1976
6	***B***	*B-1*	*Black spine*	In cultivated cucumber, black or brown spines are dominant to white; *B* is pleiotropic with red/orange mature fruit color. Shanmugasundarum et al., (1971a) identified two complementary genes, *B-1* and *B-2*, control spine colors (black vs. white) in the progeny from crosses of cucumber line Wis. 9362 with PI 212233 and 'Pixie'; Pierce and Wehner (1990) assigned gene symbols *B-1* and *B-2* (black is dominant); one of *B-1* or *B-2* is probably *B*.	Strong, 1931; Tkachenko, 1935; Pierce and Wehner, 1990; Vakalounakis, 1992; Shanmugasundarum et al., 1971a; Li et al., 2013	1976
7	***B-2***		*Black spine-2*	Two complementary genes control spine colors (black vs. white) in the progeny from crosses of cucumber line Wis. 9362 with PI 212233 and 'Pixie'; assigned gene symbols *B-1* and *B-2* (black is dominant) by Pierce and Wehner (1990).	Shanmugasundarum et al., 1971a	1976
8	***B-3***		*Black spine-3*	Fruit spine color in F_2 from the cross of white-spined cultivated cucumber line MSU41 with black-spined wild cucumber line (*C. s.* var. *hardwickii*) LJ90430 segregated in 9 black : 7 white; the two gene were assigned *B-3* and *B-4*.	Cowen and Helsel, 1983; Walters et al., 2001	1990
9	***B-4***		*Black spine-4 (B-4)*	Fruit spine color in F_2 from the cross of white-spined cultivated cucumber line MSU41 with black-spined wild cucumber line (*C. s.* var. *hardwickii*) LJ90430 segregated in 9 black : 7 white; the two gene were assigned *B-3* and *B-4*.	Cowen and Helsel, 1983; Walters et al., 2001	1990
10	***bf***		*Big flower*	EMS induced mutation from a North China type cucumber line "Shannong No 5", bigger flower size than wild type.	Wang et al., 2014	2017
11	***bi***	*bi-1*	*Bitterfree*	No bitter plant (foliage and fruit) in cucumber; mapped in Chr6 and encodes a cucurbitadienol synthase in the pathway for cucurbitacin biosynthesis.	Andeweg and DeBruyn, 1959; Shang et al. 2014	1976
12	***bi-3***		*bitterfree fruits*	In 9110Gt x 9930 RIL population, two loci, *bi-1* (*bi*) and *bi-3* control fruit bitterness. The gene *bi-3* was linked with *bi* (*bi-1*) in Chr5.	Zhang et al. 2013	2017

13	***Bl***	*bi-2*	*Bitter leaf*	*Bl* controls cucurbitacin levels in the leaves; located in chromosome 5 and encodes a transcription factor that activates *Bi* and regulates cucurbitacin biosynthesis in leaves.	Shang et al., 2014	2017
14	***bla***		*Blunt leaf apex*	Leaf apex is more obtuse than normal reduced leaf lobing and serration; easily recognized throughout whole development stage; *bla* from a mutant of 'Wis. SMR 18'.	Robinson, 1987a	1990
15	***bld***	*t, bl*	*Blind*	Lack of growing point in terminal bud; effect of gene affected by environment factors; *bld* from 'Hunderup' and inbred HP3. Previous used gene symbol "*bl*" which is now for "*bitter leaf*".	Carlsson, 1961	1976
16	***Bt***	*Bt-1*	*Bitter fruit*	*Bt* controls cucurbitacin levels in the fruit only; located in chromosome 5 and encodes a transcription factor that activates *Bi* and regulates cucurbitacin biosynthesis in the fruit.	Barham, 1953; Qi et al., 2013; Shang et al., 2014	1976
17	***bu***		*Bush*	EMS induced mutant; half-length of internode compared with wild type.	Kubicki et al., 1986b	1982
18	***Bw***		*Bacterial wilt resistance*	Resistance against *Erwinia tracheiphila*in PI 200818 is due to a single dominant gene, *Bw*.	Nuttall and Jasmin, 1958; Robinson and Whitaker, 1974	1976
19	***by***	*bu*	*Bushy*	EMS mutant from Borszczagowski; short internodes; normal seed viability; linked with *F* and *gy*, but not with *B* or *bi.*	Kubicki et al., 1986a	1993
20	***Cca***		*Resistance to Corynespora cassiicola*	A single dominant gene, *Cca*, in Royal Sluis 72502 cucumber for resistance to target leaf spot (TLS) (syn. *Cercospora melonis* Cooke).	Abul-Hayja et al., 1978	1997
21	***cca-1***		*Resistance to Corynespora cassiicola*	Resistance to target leaf spot (TLS) in cucumber line Q5, mapped to Chromosome 6	Wang et al., 2010; Fu et al. 2012	2017
22	***cca-2***		*Resistance to Corynespora cassiicola*	A single recessive gene *cca-2* controls TLS resistance in PI 183967. This gene was mapped in cucumber chromosome 6.	Yang et al. 2012	2017
23	***cca-3***		*Resistance to Corynespora cassiicola*	The TLS resistance in the resistant cucumber line D31 is controlled by a single recessive gene *cca-3* on chromosome 6. A CC-NB-ARC type resistance gene analog (*Csa6M375730*) is identified as the candidate gene.	Wen et al. 2015	2017
24	***Ccu***		*Resistance to Cladosporium cucumerinum*	Resistance in cucumber to scab is dominant; mapped in chromosome 2.	Bailey and Burgess, 1934; Andeweg, 1956; Abul-Hayja et al., 1978; Zhang, et al. 2011; Kang, et al. 2012	1976
25	***Ch***		*Seedling chilling resistance*	Seedling stage chilling resistance in cucumber line NC-76, which was developed from PI 246930, is controlled by single dominant gene	Kozik and Wehner, 2008	2010
26	***chp***	-	*choripetalous*	Chemically induced mutant from "Borszczagowski"; small first true leaf; choripetalous flowers; glossy ovary; small fruits; few seeds.	Kubicki and Korzeniewska, 1984	1993

27	***cl***		*Closed flower*	Pollen is inaccessible to bees because the buds remain closed; both male and female sterile.	Groff and Odland, 1963	1976
28	***cla***		*Resistance to Colletotrichum lagenarium race 1*	Anthracnose resistance in SC 19B cucumber line is by a single recessive gene, *cla*.	Abul-Hayja et al., 1978	1990
29	***cll***		*Clustered leaves*	EMS induced mutation from a North China type cucumber line "Shannong No 5", true leaves clustered, controlled by a single recessive gene.	Wang et al., 2014	2017
30	***Cm***	-	*Corynespora melonis* resistance.	*Corynespora melonis resistance*. Resistance to *C. melonis* dominant to susceptibility. *Cm* from 'Spotvrie'; *cm* from 'Esvier'.	van Es, 1958	1990
31	***Cmv***		*Resistance to cucumber mosaic virus*	Wasuwat and Walker (1961) found a single dominant gene, *Cmv*, for resistance to cucumber mosaic virus; *Cmv* from 'Wis. SMR 12', 'Wis. SMR 15', and 'Wis. SMR 18'; *cmv* from 'National Pickling' and 'Wis. SR 6'. Others have reported more complex inheritance.	Shifriss et al., 1942; Wasuwat and Walker, 1961	1976
32	***cn***	*l*	*Carpel number*	Most cucumbers have 3 carpels; the andromonoecious cucumber line 'Lemon' has five carpels; five-carpel is recessive to three; previously named '*l*'	Youngner, 1952; Li et al., 2016	2017
33	***co***		*Green corolla*	Green petals that turn white with age and enlarged reproductive organs; female-sterile. *co* from a selection of 'Extra Early Prolific'.	Hutchins, 1935	1976
34	***cor-1***		*Cordate leaf-1*	Spontaneous mutation; leaves are cordate; *cor-1* from 'Nezhinskii'; mutant with normal flower structure and seed production.	Gornitskaya, 1967	1990
35	***cor-2***		*Cordate leaf-2*	Late flowering, calyx segments which tightly clasp corolla, hindering flower opening and insect pollination; parthenocarpic fruit setting; *cor-2* from an induced mutant of 'Lemon'.	Robinson, 1987c	1990
36	***cp***		*Compact*	PI 308916 exhibits significantly reduced internode length (super dwarf) and was due to a recessive gene, *cp*; mapped in chromosome 4.	Kauffman and Lower, 1976; Li et al., 2011; Yong et al., 2013	1976
37	***cp-2***		*Compact-2*	EMS mutant from 'Borszczagowski'; shortened internodes similar to PI 308916; allelism between *cp* and *cp-2* is unknown; *cp-2* is required to interact with the 'bushy' gene to produce the dwarf phenotype.	Kubicki et al., 1986b	1993
38	***cp-3***		*Compact-3*	A compact plant that is different from either *cp* or *cp-2* in chromosome locations; compact phenotype in homozygous and heterozygous states are different. We propose a new gene symbol, *cp-3* for this mutant.	Crienen et al., 2009	2017
39	***cr***		*Crinkled leaf*	Leaves are wrinkled, only recognizable in true leaves.	Odland and Groff, 1963a	1976
40	***cs***		*Carpel splitting*	Fruits develop deep longitudinal splits; *cs* from TAMU 1043 and TAMU 72210.	Carruth, 1975; Pike and Carruth, 1977	1990
41	***D***	*g*	*Dull fruit skin*	Dull fruit skin is dominant to glossy (dd) located in chromosome 5.	Strong, 1931; Tkachenko, 1935; Poole, 1944; Zhang et al., 2011; Yang et al., 2014b	1976

42	***Da1.1***	*qDa1.1, qFt1.1, qfft1.1*	*Days to anthesis*	Using population from 9110Gt × 9930 RILs (with 2 days difference in flowering time), one QTL, *qDa1.1*, was detected in chromosome 1.	Miao et al., 2012; Bo et al. 2015; Pan et al. ubpublished data	2017
43	***de***	*I*	*Determinate*	A determinate plant have reduced plant height; growing point ends with clustered flowers; mapped in chromosome 6 close to the *F* gene.	Hutchins, 1940; George, 1970; Denna, 1971; Weng et al., 2010	1976
44	***de-2***		*Determinate-2*	Chemical induced mutation from 'Borszczagowski'; main stem stops growth after 3-10 nodes; end with flowers at the apex; smooth, fragile, dark-green leaves.	Soltysiak et al., 1986	1993
45	***df***		*Delayed flowering*	Flowering delayed by long photoperiod; associated with dormancy; *df* from PI 212896 and PI 215589 (*Cucumis sativus* var. *hardwickii*).	Shifriss and George, 1965; Della Vecchia et al., 1982	1976
46	***dl***		*Delayed growth*	Reduced growth rate; shortening of hypocotyl and first internodes. *dl* from 'Dwarf Marketmore' and 'Dwarf Tablegreen', both deriving dwarfness from 'Hardin's PG-57'.	Miller and George, 1979	1990
47	***dm-1***	*P, dm*	*Downy mildew resistance*	Downy mildew (DM) is caused by the obligate oomycete *Pseudoperonospora cubensis*. The DM resistance locus in PI 197087 is *dm-1*mapped in chromosome 5. In the U.S., resistance conferred by *dm-1* was overcome by a new strain in 2004.	van Vliet and Meysing, 1974; Criswell, 2008; Klosinska et al., 2010	1976
48	***dvl***		*Divided leaf*	True leaves are partly or fully divided or dissected, often resulting in compound leaves with 2-5 leaflets; recognizable by first true leaf; corollas have deep incisions	den Nijs and Mackiewicz, 1980	1982
49	***dvl-2***	*dl-2*	*divided leaf-2*	Divided leaves after the 2nd true leaf; flower petals free; similar to *dvl*, but allelism not checked. Wild type *Dvl-2* from 'Borszczagowski'; *dvl-2* from mutant induced by ethylene-imine from 'Borszczagowski'.	Rucinska et al., 1992b	1990
50	***dw***		*Dwarf*	Spontaneous mutant with extremely short internode and very compact plant; *dw* from an induced mutant of 'Lemon'.	Robinson and Mishanec, 1965	1976
51	***dwc-1***		*Dwarf cotyledons-1*	Irradiation induced mutation from 'Nishiki Suyo'; cotyledons small and hypocotyl short; leaves not expanding; died after 3rd true leaf.	Iida and Amano, 1991	1993
52	***dwc-2***		*Dwarf cotyledons-2*	Irradiation induced mutation from 'Nishiki Suyo'; cotyledons small and hypocotyl short; leaves not expanding; allelism with *dwc-1* unknown.	Iida and Amano, 1991	1993
53	***Ef1.1***		*Early flowering*	QTL mapping in a population from cross between Muromskij and 9930 identified a major QTL, *qEf1.1* on chromosome 1	Lu et al., 2014	2017
54	***Es-1***	-	*Empty chamber-1*	*Empty chambers-1*. Carpels of fruits separated from each other, leaving a small to large cavity in the seed cell. *Es-1* from PP-2-75; *es-1* from Gy-30-75.	Kubicki and Korzeniewska, 1983	1990
55	***Es-2***	-	*Empty chambers-2*	*Empty chambers-2*. Carpels of fruits separated from each other, leaving a small to large cavity in the seed cell. *Es-2* from PP-2-75; *es-2* from Gy-30-75.	Kubicki and Korzeniewska, 1983	1990

56	***F***	*Acr, acr^{F}, D, st*	*Femaleness*	Partially dominant; several studies (Kamachi et al., 1997, 2000; Trebitsh et al., 1997; Yamasaki et al., 2003; Mibus andTatlioglu, 2004; Knopf and Trebitsh, 2006) have identified *CsACS1G* in chromosomes 6 as the most possible candidate gene of the *F/f* locus. Gynoecy is due to a duplication of *CsACS1*. Molecular markers tagging the *F* allele are available	Tkachenko, 1935; Poole, 1944; Galun, 1961; Shifriss, 1961; Kubicki, 1965, 1969a;; Kamachi et al., 1997, 2000; Trebitsh et al., 1997; Yamasaki et al., 2003; Mibus andTatlioglu, 2004; Knopf and Trebitsh, 2006; Zhang et al. 2015; Win et al., 2015	1976
57	***fa***		*Fasciated*	Fasciated plants have with wide, flattened stems and increased numbers of leaves, tendrils, and flowers per node; Expression is influenced by environmental conditions; *fa* was from a selection of 'White Lemon'.	Robinson, 1978a; Shifriss, 1950	1990
58	***Fba***		*Flower bud abortion*	*Fba* triggers flower bud abortion prior to anthesis in 10-100% of the buds; *fba* from MSU 0612.	Miller and Quisenberry, 1978	1990
59	***fc***		*Fused cotyledon*	An EMS-induced mutant from Poinsett 76 cucumber; cotyledons fused together. We propose gene symbol '*fc*' for this mutant.	Fraenkel et al., 2014	2017
60	***fgr***		*Fragrance*	The fruits and foliage of cucumber line PK2011T202 from Thailand have pandan-like fragrance; controlled by a single recessive gene *fgr*; a candidate in chromosome 1 for betaine aldehyde dehydrogenase 2 (*BADH2*) (also known as aminoaldehyde dehydrogenase 2) has been identified.	Pramnoi et al., 2013; Yundaeng et al. 2015	2017
61	***fl***		*Fruit length*	A modifier of fruit length; *fl* was identified by its linkage with scab resistance Ccu; expressed in an additive fashion, fruit length decreases incrementally from heterozygote to homozygote	Wilson, 1968; Pierce and Wehner, 1990	1990
62	***fl-1***		*Fruit length-1*	The North China cucumber line 409 is a spontaneous mutant of line 408; fruits on 409 are 7 cm shorter than those on line 408	Jiang et al., 2014	2017
63	***Foc***	*Fcu-1; qFoc2.1*	*Resistance to Fusarium oxysporum f. sp. cucumerinum*	Resistance for *Fusarium* wilt (FW) races 1 and 2 in Wis 248 is controlled by a single dominant gene (*Foc*); Zhang et al. (2014) mapped a major QTL, *qFoc2.1*, for FW resistance from cucumber line 9110Gt.	Netzer et al., 1977; Vakalounakis, 1995; Zhang et al., 2014	2017
64	***Fr***		*Fruits ribbing*	Fruits of 9930 have ribbing; fruits of 9110Gt have no ribbing at commercial maturity stage; ribbed is dominant to no-ribbing; *U, D, H* and *fr* are linked in chromosome 5.	Miao et al., 2011	2017
65	***fs1***		*few spines1*	A mutant from a North China type cucumber CNS2 with a high density of fruit spines. *Fs1* for "few spines" is controlled by a single recessive gene; encodes a PDF2-related protein (Csa6M514870) which belongs to a homeodomain-leucine zipper IV transcription factor (CsHDZIV11/CsGL3)	Zhang et al. 2016b	2017
66	***g***		*Golden leaf*	Gold color lower leaves; *G* and *g* are both from different selections of 'Nezhin'; presumably the same as virescent leaf.	Tkachenko, 1935	1976

67	***gb***	*n*	*Gooseberry fruit*	Oval shape of fruit of Klin cucumber; trimonoecious, small size of fruit, long dense hairs on the surface of ovary, smooth tight rind not liable to become covered with a network of fissures, dark stripes in the place where the principal meridional veins pass through the fruit flesh, luxuriant growth of the receptacle, tendency of the flesh to deep splitting	Tkachenko, 1935	1976
68	***gc***		*Golden cotyledon*	Monogenic, recessive, lethal, cotyledons butter-colored, seedlings died after 6-7d; *gc* from a mutant of 'Burpless Hybrid'.	Whelan and Chubey, 1973	1976
69	***gi***		*Ginkgo leaf*	Spontaneous mutant; Leaves reduced and distorted, resembling leaves of Ginkgo; male- and female-sterile.	John and Wilson, 1952	1976
70	***gi-2***		*Ginkgo leaf-2*	Chemically induced mutation from Borszczagowski; spatulate leaf blade with reduced lobing and altered veins; recognizable at the 2nd true leaf stage; similar to *gi*, fertile instead of sterile	Rucinska et al., 1992b	1993
71	***gig***		*Gigantism*	Chemically induced mutation from Borszczagowski; first true leaf larger than normal	Kubicki et al., 1984	1993
72	***gl***		*Glabrous*	Chemically induced mutation; glossy foliage and fruit, link with the yellow cotyledon (*yc* gene).	Inggamer and de Ponti, 1980; Robinson and Mishanec, 1964	1976
73	***gl-1***	*Csgl1, mict, tbh*	*Glabrous 1*	Spontaneous mutant from a North China type cucumber cultivar Daqingba. All aerial parts (leaves, stems, tendrils, floral organs, and fruits) are glabrous; mapped in chromosome 3; encodes a member of the homeodomain-leucine zipper I (HD-Zip I) proteins; *CsGL1* may be involved in foliar trichome development but not initiation.	Cao et al., 2001; Li et al., 2015b	2017
74	***gl-2***		*Glabrous-2*	NCG-042 with few small fine hairs on fruit peduncle, pedicel and calyx of flowers, but stem, leaf and leaf petioles are smooth.	Yang et al., 2011	2017
75	***gl-3***	*tril*	*Glabrous-3*	A spontaneous glabrous mutant csgl3 was identified in WI7412, a recombinant inbred line progeny from the cross between WI2757 and True Lemon cucumber inbred lines. WI7412 is completely trichome-free on all above-ground organs. *Csgl3* encodes a class IV homeodomain-associated leucine zipper (HD-ZIP) transcription factor. The loss-of-function of *CsGL3* in the mutant is due to the insertion of a 5-kb long terminal repeat retrotransposon in the 4th exon of *CsGL3*. The glabrous mutant NCG157 is caused by mutations within the same gene.	Pan et al., 2015; Cui et al., 2016	2017
76	***glb***		*Glabrate*	Stem and petioles glabrous, laminae slightly pubescent. *glb* from 'Burpless Hybrid'.	Whelan, 1973	1976
77	***gn***		*Green mature fruit*	Green mature fruits when *rr* gngn; cream colored when *rr GnGn*; gn from TAMU 830397.	Peterson and Pike, 1992	1993
78	***Gs***		*Green stem*	Dark green stem, leaf and fruits due to increased chlorophyll content; dark green is dominant or incomplete dominant over regular green.	Haaring, 2014	2017
79	***gy***	*g*	*Gynoecious*	High degree of pistillate sex expression; chemically induced mutant from "Borszczagowski".	Kubicki, 1974	1976

80	***H***		*Heavy netting*	Fruit netting occurs when fruit reaches maturity; netting is dominant to smooth.	Tkachenko, 1935; Hutchins, 1940	1976
81	***hl***		*Heart leaf*	Heart shaped leaves in WI 2757	Vakalounakis, 1992	1993
82	***hn***		*Horn-like cotyledon*	Irradiation induced mutation from 'Nishiki-suyo'; cotyledons shaped like bull horns; true leaves round shaped; circular stem cross section; divided petals; spineless fruits; pollen fertile.	Iida and Amano, 1991	1993
83	***hsl***		*Heart shaped leaf*	Irradiation induced mutation from 'Nishiki Suyo'; leaves round-heart shaped; tendrils often branched.	Iida and Amano, 1991	1993
84	***In-de***	*In(de)*	*Determinate intensifier*	Reduces internode length and branching of *de* plants. *In-de* and *in-de* are from different selections (S_5-1 and S_5-6, respectively) from a determinant inbred S_2-1.	George, 1970	1976
85	***In-F***	*F*	*Intensifier of F*	*Intensifier of female sex expression*. Increases degree of pistillate sex expression of *F* plants. *In-F* from monoecious line 18-1; *in-F* from MSU 713-5.	Kubicki, 1969b	1976
86	***lfr***		*Long fruit*	EMS induced mutation from a North China type cucumber line "Shannong No 5", longer fruit than wild type controlled by a single recessive gene.	Wang et al., 2014	2017
87	***lg-1***		*Light green cotyledon-1*	Irradiation induced mutation from 'Nishiki Suyo'; initially, cotyledons and young leaves light green, becoming normal green later; phenotypically similar to *v, v-1* mutants.	Iida and Amano, 1991	1993
88	***lg-2***		*Light green cotyledon-2*	Irradiation induced mutation from 'Nishiki Suyo'; initially, cotyledons and young leaves light green, becoming normal green	Iida and Amano, 1991	1993
89	***lgf***	*CsYcf54*	*light green fruit*	An EMS-induced recessive mutant with light green fruits and leaves; from North China type cucumber line 406; due to a mutation in *Csa6G133820* that encodes an *Ycf54*-like protein that has been implicated in the cyclase step of chlorophyll biosynthesis.	Lun et al., 2016	2017
90	***lgp***		*light green peel*	An EMS mutant with light green peel, which is due to a mutation in *ACCUMULATION AND REPLICATION OF CHLOROPLASTS 5*.	Zhou et al., 2015	2017
91	***lh***		*Long hypocotyl*	As much as a 3-fold increase in hypocotyl length. *lh* from a 'Lemon' mutant.	Robinson and Shail, 1981; Koornneef and van der Knaap, 1983	1982
92	***ll***		*Littleleaf*	A spontaneous mutant found in the field; The H-19 mutant has little leaves, flowers, fruits, and seeds; multiple lateral branches; mapped in chromosome 6.	Goode et al. 1980; Weng et al. 2010	1990
93	***ll-2***		*Littleleaf-2*	A major QTL for small leaf size in wild cucumber, *C. sativus* var. *hardwickii*	Shi et al., 2014	2017
94	***ls***		*Light sensitive*	Monogenic, recessive, cotyledons smaller than normal; viable except under full sun	Whelan and Chubey, 1973	1976
95	***m***	*a, g*	*Andromonoecious*	The Lemon cucumber with *mm* genotype has are andromonoecious; encodes *CsACS2*; the *mm* genotype is pleiotropic, and the fruits are often round shaped with protruding ovaries.	Rosa, 1928; Tkachenko, 1935; Youngner, 1952; Shifriss, 1961; Wall, 1967; Boualem et al., 2009; Li et al., 2008, 2009	1976

96	***m-1***		*Andromonoecious-1*	A new allele of the *m* locus; identified in hermaphroditic; H38 has elongated fruit.	Tan et al., 2015	2017
97	***m-2***	*h*	*Andromonoecious-2*	A recessive gene in a chemically induced mutant from cv. Borszczagowski; andromonoecious plants; bisexual flower set elongated fruits.	Kubicki, 1974	1976
98	***mict***	*Csgl1*	*Micro-trichome*	A spontaneous mutant from North China inbred line 06-1, glabrous leaves, stems, flowers, tendrils and fruits; trichomes only visible under microscope with >20× magnifications; same mutant as *gl-1*; the loss-of-function csgl1 is due to a 2649-bp genomic DNA deletion spanning the first and second exons of *CsGL1* non-allelic with *gl-2*.	Zhao et al., 2015	2017
99	***mj***		*Resistance to Meloidogyne javanica*	The resistant to the root knot nematode, *Meloidogyne javanica* in LJ90430 (*C. sativus* var. *hardwickii*) is conditioned by a single recessive gene *mj*.	Walters et al., 1996; Walters and Wehner, 1997	2001
100	***Mod-F1***		*Subgynoecious-1*	In cucumber line S-2-98, incomplete dominance; enhances intensity of femaleness; high ratio of female to male flowers with continuous female flower nodes at high node positions. The subgynoecious sex expression in S-2-98 is determined by three QTL, *sg3.1*, *sg6.1*, and *sg6.2* with *sg3.1* having the largest effect.	Chen et al., 2011	2017
101	***mod-F2***		*Subgynoecious-2*	In cucumber line 97-17, recessive, enhances intensity of femaleness, high ratio of female to male flowers with continuous female flower nodes at high node positions	Chen et al., 2011; Bu et al. 2016	2017
102	***mp***	pf^{+}, pf^{d}, pf^{p}	*Multiple pistillate flower*	Several pistillate flowers per node, recessive to single pistillate flower per node. *mp* from MSU 604G and MSU 598G.	Nandgaonkar and Baker, 1981; Fujieda et al., 1982	1982
103	***Mp-2***		*Multiple pistillate flower-2*	*Multi-pistillate-2*. Several pistillate flowers per node. Single dominant gene with several minor modifiers. *Mp-2* from MSU 3091-1.	Thaxton, 1974	1990
104	***mpy***	*mpi*	*Male pygmy*	Dwarf plant with only staminate flowers in 'Gnome 1', a selection of 'Rochford's Improved'	Pyzhenkov and Kosareva, 1981	1993
105	***ms-1***	-	*Male sterility-1*	Staminate flowers abort before anthesis; partially female-sterile. *ms-1* from selections of 'Black Diamond' and 'A & C'.	Shifriss, 1950; Robinson and Mishanec, 1965; Whelan, 1972a	1976
106	***ms-2***	-	*Male sterility-2*	Male-sterile; pollen abortion occurs after first mitotic division of the pollen grain nucleus. *ms-2* from a mutant of 'Burpless Hybrid'.	Whelan, 1973	1976
107	***ms-2$^{(PS)}$***	-	*male sterile-2 pollen sterile*	Male-sterile; allelic to *ms-2*, but not to *ap. ms-2$^{(PS)}$* from a mutant of Sunseeds 23B-X26.	Zhang et al., 1994	1990
108	***mwm***		*Resistance to MWMV*	A single recessive gene controls resisatnce to Moroccan watermelon mosaic virus in TMG-1 and Dina-1.	Kabelka and Grumet, 1997	2001
109	***n***		*Negative geotropic peduncle response*	Pistillate flowers grow upright; *n* from 'Lemon'; *N* produces the pendant flower position of most cultivars.	Odland and Groff, 1963b	1976
110	***nlb***		*Non-lateral branch*	Cucumber line 419 has no lateral branches, which is controlled a recessive gene nlb mapped in chromosome 1	Jiang et al., 2008; Ren et al., 2013	2017

111	***nlc***		*Necrotic lesions on cotyledons*	An EMS-induced mutant from Poinsett 76 cucumber; spontaneous necrotic spots appear on cotyledons. We propose gene symbol '*nlc*' for this mutant.	Fraenkel et al., 2014	2017
112	***ns***	*f, s-2, s-3*	*Numerous spines*	Spine number on fruits is controlled by a single gene; many spines on WI 2757 is recessive to few spines in SMR 18.	Poole, 1944; Hutchins, 1940; Piece and Wehner 1990; Fanourakis and Simon 1987	1990
113	***nsl***		*Non-serrated leaf*	An EMS-induced mutant from Poinsett 76 cucumber; leaf edge appears smooth. We propose gene symbol '*nsl*' for this mutant.	Fraenkel et al., 2014	2017
114	***o***	*y*	*Orange-yellow corolla*	Pale yellow corolla, recessive, but observed only in single instance.	Tkachenko, 1935	1976
115	***opp***		*Opposite leaf arrangement*	A single recessive gene linked with *m* and *cn*; incomplete penetrance; difficult to score.	Robinson, 1987d	1990
116	***or***		*Orange flesh*	Orange flesh in mature fruits of Xishuangbanna cucumber is recessive to white; the *or* locus on chromosome 3 encodes a β-carotene hydroxylase gene.	Bo et al., 2011; Qi et al., 2013	2017
117	***ots***		*Opposite tendrils on stem*	EMS induced mutation from a North China type cucumber line "Shannong No 5", tendrils at opposite positions	Wang et al., 2014a	2017
118	***Pc***		*Parthenocarpic fruit set*	Pike and Peterson (1969) suggested an incompletely dominant gene, *Pc*, affected by numerous modifiers, was responsible for parthenocarpic fruit set in 'Spotvrie'. Molecular mapping studies support quantitative nature of parthenocarpic fruit setting.	Pike and Peterson, 1969; Sun et al., 2006	1976
119	***pe***		*Palisade epidermis*	Epidermal cells arranged perpendicular to the fruit surface; *pe* from WI 2757.	Fanourakis and Simon, 1987	1990
120	***pf***		*Plural pistillate flower*	Plural pistillate flowering controlled by 3 alleles with single pistillate being incompletely dominant over multiple pistillate pf^{+} for single pistillate, pf^{d} for double pistillate and pf^{m} for multiple pistillates.	Fujieda et al., 1982	1990
121	***pl***		*Pale lethal*	Monogenic, recessive, lethal, cotyledons paler than normal; recognized 2d after emergence; seedling died after 6-7d; *pl f*rom a mutant of 'Burpless Hybrid'.	Whelan and Chubey, 1973	1976
122	***Pm1.1***		*Powdery mildew resistance*	From a North China type cucumber line Jin5-508, a dominantly inherited PM resistance major-effect QTL, *Pm1.1* was identified that was located in a 41.1 kb region of cucumber Chromosome 1 harboring two tandemly arrayed cysteine rich receptor like protein kinase genes.	Xu et al. 2016	2017
123	***pm5.1***	*CsMLO-1, CsMLO8, pm-h*	*Powdery mildew resistance*	Ni et al. (2015) fine mapped a powdery mildew resistance major QTL, *pm5.1*, that belong to the *mlo*-type disease resistance. This QTL seems to co-localize with *pm-h*.	Ni et al., 2015	2017
124	***pm-h***	*s, pm*	*Hypocotyl resistance to powdery mildew*	Powdery mildew (PM) resistance in cucumber is quantitative in nature. Shanmugasundarum et al. (1971b) proposed a gene for hypocotyl resistance (*pm-h*) that played the major role in whole plant PM resistance; located in chromosome 5; may be the same as *pm5.1*.	Shanmugasundarum et al., 1971b; de Ruiter et al., 2008; He et al., 2013	1990

125	***prsv^{02245}***		*Resistance to PRSV*	PRSV resistance in cucumber line 02245 is controlled by a single recessive gene, *prsv$^{0224;}$* mapped in cucumber chromosome 6, linked with but not the same same as ZYMV locus.	Tian et al. 2015	2017
126	***prsv-1***	*wmv1-1*	*Resistance to PRSV-1*	Resistance in cucumber line 'Surinam' against PRSV-W was inherited as a recessive allele at a single locus (Wang et al. 1984).	Wang et al., 1984	1993
127	***Prsv-2***		*Resistance to PRSV-2*	PRSV-W resistance in TMG-1 is controlled by a dominant locus (*Prsv-2*); PRSV-W resistance loci in Surinam (*prsv-1*) and TMG1 (*Prsv-2*) were allelic.	Wai and Grumet, 1995 ; Wai et al., 1997; (Park et al., 2000	2001
128	***psl***	*pl*	*Resistance to Pseudomonas syringae pv. lachrymans*	Non-halo type resistance to angular leaf spot (ALS, *Pseudomonas syringae* pv. *Lachrymans*) (Syn. *Pseudomonas lachryman*) was governed by a single recessive gene *psl.*	Dessert et al., 1982	1997
129	***Psm***		*Paternal sorting of mitochondria*	The single dominant gene *Psm* from MSC16 cucumber controls sorting of wild-type mitochondrial DNA from paternal parent.	Havey et al., 2004; Calderon et al., 2012	2005
130	***qARN6.1***		*Adventitious root number*	The waterlogging tolerant line Zaoer-N produces more hypocotyl-derived adventitious roots (AR) under waterlogging stress. The AR number (ARN) in Zaoer is controlled by 3 QTL, *ARN3.1, ARN5.1,* and *ARN6.1* with ARN6.1 as the major-effect QTL.	Xu et al. 2016	2017
131	***qCVYV***		*Resistance o CVYV*	A major-effect QTL for resistance to cucumber vein yellowing virus, which also confers a general resistance against tobamoviruses including the cucumber green mottle mosaic virus (CGMMV) and cucumber fruit mottle mosaic virus (CFMMV).	Faber et al., 2014	2017
132	***qCYSDV5.1***		*Resistance to CYSDV*	A major-effect QTL for CYSDV resistance from PI 250147; mapped in chromosome 5.	de Router et al., 2008	2017
133	***qFoc6.1***		*Resistance to Fusarium oxysporum f. sp. cucumerinum*	One of two linked QTLs (*qFoc6.1, qFoc6.2*) in cucumber line URS 189 for resistance against *Fusarium* stem and root rot *Fusarium oxysporum* f. sp. *radicis cucumerinum*.	de Milliano et al., 2012	2017
134	***qFoc6.2***		*Resistance to Fusarium oxysporum f. sp. cucumerinum*	One of two linked QTLs (*qFoc6.1, qFoc6.2*) in cucumber line URS 189 for resistance against *Fusarium* stem and root rot *Fusarium oxysporum* f. sp. *radicis cucumerinum*.	de Milliano et al., 2012	2017
135	***qFt1.1***	*qDa1.1, qfft1.1*	*Flowering time*	From a population derived from WI7200 and the semi-wild Xishuangbana cucumber accession WI7167, this is one of three QTL identified for male and female flowering time.	Qu et al. 2014; Bo et al. 2015, Pan et al. unpublished data	2017
136	***qFt5.1***		*Flowering time*	From a population derived from WI7200 and the semi-wild Xishuangbana cucumber accession WI7167, this is one of three QTL identified for male and female flowering time.	Qu et al. 2014; Pan et al. unpublished data	2017

137	***qFt6.1***		*Flowering time*	From a population derived from CC3 and the semi-wild Xishuangbana cucumber accession SWCC8, this is a QTL for female flowering time.	Bo et al. 2015	2017
138	***qFt6.2***		*Flowering time*	From a population derived from WI7200 and the semi-wild Xishuangbana cucumber accession WI7167, this is one of three QTL identified for male and female flowering time.	Pan et al. unpublished data	2017
139	***qGsb1.1***		*Gummy stem blight resistance*	*Cucumis hystrix*-derived resistance to GSB (*Didymella bryonia*), one of the three GSB resistance QTL (*qGsb1.1*, *qGsb4.1*, and *qGsb6.1*)	Lou et al., 2013	2017
140	***qGsb4.1***		*Gummy stem blight resistance*	*Cucumis hystrix*-derived resisatnce to GSB (*Didymella bryonia*), one of the three GSB resisatnce QTLs (*qGsb1.1*, *qGsb4.1*, and *qGsb6.1*)	Lou et al., 2013	2017
141	***qGsb6.1***		*Gummy stem blight resistance*	*Cucumis hystrix*-derived resisatnce to GSB (*Didymella bryonia*), one of the three GSB resisatnce QTLs (*qGsb1.1*, *qGsb4.1*, and *qGsb6.1*)	Lou et al., 2013	2017
142	***qMYSV1.1***	*Swf-1*	*Melon yellow spot virus resistanc*	Major-effect QTLs for resistance to Melon yellow spot virus (MYSV) FuCu05P-1 strain in cucumber line 27028930	Sugiyama et al. 2015	2017
143	***qMYSV3.1***	*Swf-2*	*Melon yellow spot virus resistanc*	Major-effect QTLs for resistance to Melon yellow spot virus (MYSV) FuCu05P-1 strain in cucumber line 27028930	Sugiyama et al. 2015	2017
144	***qMYSV4.1***	*Swf-3*	*Melon yellow spot virus resistanc*	Minor-effect QTLs for resistance to Melon yellow spot virus (MYSV) FuCu05P-1 strain in susceptible cucumber line 'Tokiwa'	Sugiyama et al. 2015	2017
145	***qMYSV7.1***	*Swf-4*	*Melon yellow spot virus resistanc*	Minor-effect QTLs for resistance to Melon yellow spot virus (MYSV) FuCu05P-1 strain in cucumber line 27028930	Sugiyama et al. 2015	2017
146	***R***		*Red fruit color*	Li et al. (2013) classified mature fruit colors into two groups: yellow (orange, red, brown), and white (white, creamy, light green, green); yellow controlled by *R* is dominant to white (*rr*); *B* gene for black spine is pleiotropic that also controls orange/yellow fruit color.	Wellington, 1913; Hutchins, 1940; Li et al., 2013	1976
147	***rc***		*Revolute cotyledon*	Cotyledons are short, narrow, and cupped downwards; enlarged perianth. *rc* from 'Burpless Hybrid' mutant.	Whelan et al., 1975	1976
148	***rc-2***	-	*Revolute cotyledon-2*	Recessive gene for revolute cotyledons; *rc-2* from NCG-0093 (short petiole mutant)	Wehner et al., 1998b	2001
149	***res***		*Reduced ethylene sensitivity*	Single recessive gene from chemically induced mutagenesis; co-dominance in heterozygotes; reduced sensitivity to ethylene.	Dirks et al., 2013	2017
150	***ro***		*Rosette*	A mutant with reduced plant height, shorter internodes, more obtuse leaf lobing; muskmelon-like leaves; *ro* from 'Megurk', the result of a cross involving a mix of cucumber and muskmelon pollen.	de Ruiter et al., 1980	1982
151	***Sa***		*Salt tolerance*	Increased tolerance to high salt levels in PI 177361 is conditioned by a dominant gene, *Sa*.	Jones, 1984	1990
152	***sc***	*cm*	*Stunted cotyledon*	Small, concavely curved cotyledons; stunted plants with cupped leaves; abnormal flowers. *Sc* and *sc* from Wis. 9594 and 9597, respectively.	Shanmugasundarum et al., 1972	1976

153	***scp***		*Super compact*	EMS-induced mutant with drastically reduced main stem length and no lateral branches; controlled by a recessive gene, *scp*.	Niemirowicz-Szczytt et al., 1996	1990
154	***scp-1***		*Super compact-1*	A dwarf mutant C257 was discovered from EMS mutagenesis of the North China cucumber line CCMC; the mutant exhibited a super compact (SCP) phenotype with drastically reduced internode length (<5 cm) and reduced number of internodes, no tendrils, more round shaped leaf with wrinkled surface and dark green color. The cytochrome P450 gene *CsCYP85A1* is a putative candidate for *Scp-1*	Wang et al. 2017	2017
155	***scp-2***		*Super compact-2*	Spontaneous dwarf mutant AM204M with super compact phenotype identified in PI 618937. A mutation in the *CsDET2* gene leads to a systemic brassinosteriod deficiency and super compact phenotype in AM204M	Li Zheng, unpublished data	2017
156	***Sd***		*Resistance to sulfur dioxide air pollution*	A single dominant gene, Sd, in the National Pickling is responsible for resistance to acute exposure of sulfur dioxide.	Bressan et al., 1981	1990
157	***sf***		*Small flower*	EMS induced mutation from a North China type cucumber line "Shannong No 5", smaller flower size (both male and female) than wild type.	Wang et al. 2014	2017
158	***sfr***		*Short fruit*	EMS induced mutation from a North China type cucumber line "Shannong No 5"; shorted fruit than wild type controlled by a single recessive gene.	Wang et al., 2014	2017
159	***sh1***		*Short hypocotyl*	The semi-wild Xishuangbanna cucumber accession SWCC8 has shorter hypocotyl compared with regular cucumebr; low doage UVB-insensistve hypocotyl elongation; (regular cucumebrs are sensistive); mapped in chromosome 3; encodes a human SMARCA3-like chromatin remodeling factor.	Bo et al., 2015a; 2016	2017
160	***shl***		*Shrunken leaf*	Irradiation induced mutation from 'Nishiki Suyo'; first leaf shrunken, but later leaves progressively become more normal.	Iida and Amano, 1991	1993
161	***Si***		*short internode*	The EMS-induced dwarf mutant exhibited shorter internode, smaller fruits, and wrinkled leaves as compared with its wild-type line 406, which is shown to be due to a mutation in an F-box gene	Lin et al. 2016	2017
162	***sp***		*Short petiole-1*	Very short petioles of first true leaf, leaf blade smoothly narrows to the petiole; later leaves have petioles shorter than wild type; opposite arrangement of the first leaves due to short internode.	den Nijs and Boukema, 1985	1990
163	***sp-2***		*Short petiole-2*	From mutagenesis of 'Borszczagowski'; 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 *sp*.	Rucinska et al., 1992a	1993
164	***ss***	*s, s-1*	*small spines (ss):*	Small spine size on fruits of WI 2757 is recessive to large spines on SMR 18.	Poole, 1944; Hutchins, 1940; Piece and Wehner 1990; Fanourakis and Simon 1987	1990
165	***T***		*Tall plant*	Tall incompletely dominant to short.	Hutchins, 1940	1976

166	***tbh***	*Csgl1*	*Tiny branched hair*	Spontaneous mutant from North China cucumber line R1407, glabrous foliage and fruits; no visible trichomes under light microscope.	Chen et al., 2014	2017
167	***td***		*Tendrilless*	Tendrils lacking; associated with misshapen ovaries and brittle leaves. *Td* from 'Southern Pickler'; *td* from a mutant of 'Southern Pickler'.	Rowe and Bowers, 1965	1976
168	***td-1***		*tendrilless-1*	No tendrils on B007 mutant plant, dwarf, trichome-free, identified from an EMS mutagenesis population from a North China type cucumber line CCMC	Li YH, personal communication	2017
169	***te***		*Tender skin of fruit*	Tender fruit skin vs tough is recessively inherited; linked with tough and warty fruits.	Strong, 1931; Poole, 1944; Fanourakis and Simon, 1987	2017
170	***ten***		*Tendrilless*	Tendril-less spontaneous mutation from CG9192, a landrace from the semi-wild Xishuangbanna cucumber (*C. sativus* var. *xishuangbannesis*) of subtropical Southwest China. The mutant plant forms branches instead of tendrils. The affected gene *TEN* encodes a TCP transcription factor	Wang et al., 2015	2017
171	***tf***		*Twin fused fruit*	Spontaneous mutant from cucumber line B5263; single recessive; two separate pistallate flowers with partially joined ovaries on a single peduncle at a node develop into twin fused fruit; only observed on gynoecious plants	Klosinka et al., 2006	2010
172	***Tr***		*Trimonoecious*	Plants with staminate, bisexual and pistillate flowers; bisexual flowers form superior ovaries, single dominant major gene; independent of F and m genes	Kubicki, 1969d	1976
173	***tr-1***		*Trimonoecious-1*	The line 'GW' is trimonoecious with elongated fruits from hermaphrodite flowers; hermaphrodite flowers usually turn into female flowers in higher nodes; expression affected by temperature	Fujieda and Fujita, 1978	2017
174	***tril***	*CsGl3*	*Trichome-less*	Mutant that was completely free from trichomes on all aerial organs, which is true even under an SEM suggesting the *Tril* gene may function in trichome cell fate determination.	Wang et al. 2016b	2017
175	***Tu***		*Tuberculated fruit*	Tuberculated, warty fruit is dominant to smooth (glabrous fruit); encodes a transcription factor with a single C2H2 zinc finger domain.	Wellington, 1913; Strong, 1931; Yang et al., 2014	1976
176	***u***	*M*	*Uniform immature fruit color*	Immature fruit has uniform color; mottled is dominant to uniform	Andeweg, 1956; Fanourakis and Simon, 1987; Yang et al., 2014	1976
177	***ul***		*Umbrella leaf*	Under certain temperature and relative humidity, new leaves expand unevenly with leaf margin growing less than leaf blade resulting in downward or upward; curled leaves reminiscent of an umbrella.	den Nijs and de Ponti, 1983	1990
178	***v***		*Virescent leaf*	Yellow leaves change to green.	Tkachenko, 1935; Poole, 1944	1976
179	***v-1***		*Virescent leaf-1*	Yellow cotyledons change to green; first 3-4 true leaves start with yellow then turn to green; from 9110Gt; mapped in chromosome 6 with the candidate gene *CsaCNGCs* encoding a cyclic-nucleotide-gated ion channel protein.	Miao et al., 2011a; 2016	2017

180	***vvi***		*Variegated virescence*	Yellow cotyledons turn green in 7-10d; true leaves start with pale yellow that become strongly variegated in a green and white pattern; hypocotyl, stem and petioles white to light green; corolla lighter yellow than normal; plant grows slower and smaller in size.	Abul-Hayja and Williams, 1976	1976
181	***w***		*White immature fruit color*	White immature skin color is recessive to the normal green. The *w* allele encodes a candidate gene for the '*two-component response regulator-like*' (*APRR2*) protein (Liu et al., 2015, 2016).	Cochran, 1938; Dong et al., 2012	1976
182	***wf***		*white flesh*	Intense white flesh color is recessive to dingy white; acts with *yf* to produce F_2 of 12 white (*WfWf YfYf* or *wfwf YfYf*): 3 yellow (*WfWf yfyf*) : 1 orange (*wfwf yfyf*). *Wf* from EG and G6, each being dingy white (*WfWf YfYf*): *wf* from 'NPI ' which is orange (*wfwf yfyf*)	Kooistra, 1971	1990
183	***wi***		*Wilty leaf*	Irradiation induced mutation from 'Nishiki Suyo'; rim of leaves wilted	Iida and Amano, 1991	1993
184	***Wmv***		*Resistance to watermelon mosaic virus*	A dominant gene, *Wmv* in the cultivar 'Kyoto 3 Feet', controls resistantace to strain 2 of WMV.	Cohen et al., 1971	1976
185	***wmv^{0224}***		*Resistance to watermelon mosaic virus*	WMV resistance in the cucumber inbred line '02245' is controlled by a single recessive locus, *wmv^{02245}* on mapped to Chromosome 6.	Tain et al. 2016	2017
186	***wmv-2***		*Resistance to watermelon mosaic virus*	There are two independent factors governing WMV resistance in TMG-1 : *wmv-2* expressed at the cotyledon stage and throughout the plant; *wmv-3* (recessive) and *Wmv-4* (dominant) with epistatic interactions expressed only in true leaves; *Wmv-4* was from susceptible WI2757.	Wai et al., 1997	2001
187	***wmv-3***		*Resistance to watermelon mosaic virus*	There are two independent factors governing WMV resistance in TMG-1 : *wmv-2* expressed at the cotyledon stage and throughout the plant; *wmv-3* (recessive) and *Wmv-4* (dominant) with epistatic interactions expressed only in true leaves; *Wmv-4* was from susceptible WI2757.	Wai et al., 1997	2001
188	***Wmv-4***		*Resistance to watermelon mosaic virus*	There are two independent factors governing WMV resistance in TMG-1 : *wmv-2* expressed at the cotyledon stage and throughout the plant; *wmv-3* (recessive) and *Wmv-4* (dominant) with epistatic interactions expressed only in true leaves; *Wmv-4* was from susceptible WI2757.	Wai et al., 1997	2001
189	***wy***		*Wavy rimmed cotyledons*	Irradiation induced mutation from 'Nishiki Suyo'; center of cotyledons occasionally white and rims green, later becoming wavy	Iida and Amano, 1991	1993
190	***yc-1***		*Yellow cotyledon-1*	Yellow seedling develops green color one week after germination; *yc-1* from a mutant of Ohio MR 25.	Aalders, 1959	1976
191	***yc-2***		*Yellow cotyledon-2*	Pale-yellow cotyledons becoming normal green when exposed to light of normal intensity; *yc-2* from a mutant of 'Burpless Hybrid'; *yc-1* and *yc-2* are two different loci.	Whelan and Chubey, 1973; Whelan et al., 1975	1976

192	***yf***	*v*	*Yellow flesh*	The mature fruit of cucumber line PI 200815 exhibits yellow flesh, which is recessive to white flesh; mapped on chromosome 7.	Kooistra, 1971; Lu et al., 2015	1976
193	***yg***	*gr*	*Yellow green immature fruit color*	*Yellow green* is recessive to *dark green* and epistatic with light green; *yg* from 'Lemon'.	Youngner, 1952	1976
194	***yp***		*Yellow plant*	Plant is light yellow green throughout life with slow growth and small plant size. A mutant (C528) with similar phenotype was recovered from EMS mutagenesis population from a North China type cucumber CCMC. The chlorophyll-deficient golden leaf mutation in C528 is due to a single nucleotide substitution in *CsChlI* for magnesium chelatase I subunit.	Abul-Hayja and Williams, 1976; LI 2015a; Gao et al., 2016	1976, 2017
195	***ys***		*Yellow stem*	Chemically induced mutant from 'Borszczagowski'; yellow cotyledons that gradually turns creamy; creamy stems, leaf petioles and leaf veins; shorter hypocotyl, internode and vine length.	Rucinska et al., 1991	1993
196	***zyf***		*Resistance to ZYFV*	A single recessive gene in TMG-1 and Dina-1 conditions resistance to zucchini yellow fleck virus.	Gilbert-Albertini et al., 1995; Kabelka and Grumet, 1997	2017
197	***zym$^{A192-18}$***		*Resistance to ZYMV*	Resistance to zucchini yellow moscai virus (ZYMV) in A192-18 cucumber line is conferred by single gene, *zym$^{A192-18}$*, putatively encodes a vacuolar protein sorting-associated protein 4-like (VPS4-like) protein. The *zym$^{A192-18}$* locus is physically close to *zym^{Dina}*	Amano et al., 2014	2017
198	***zym^{Dina}***		*Resistance to ZYMV*	Resistance to zucchini yellow moscai virus (ZYMV) in Dina-1 is conferred by single gene, *zym^{Dina}*, which is allelic to *zym^{TMG}*.	Provvidenti 1987; Abul-Hayja and Al-Shawan 1991; Kabelka et al. 1997	2001
199	***zym^{TMG}***		*Resistance to ZYMV*	Resistance to zucchini yellow moscai virus (ZYMV) in TMG-1 is conferred by single gene, *zym^{TMG}*, which is allelic to *zym^{Dina}*.	Provvidenti 1987; Abul-Hayja and Al-Shawan 1991; Kabelka et al. 1997	2001

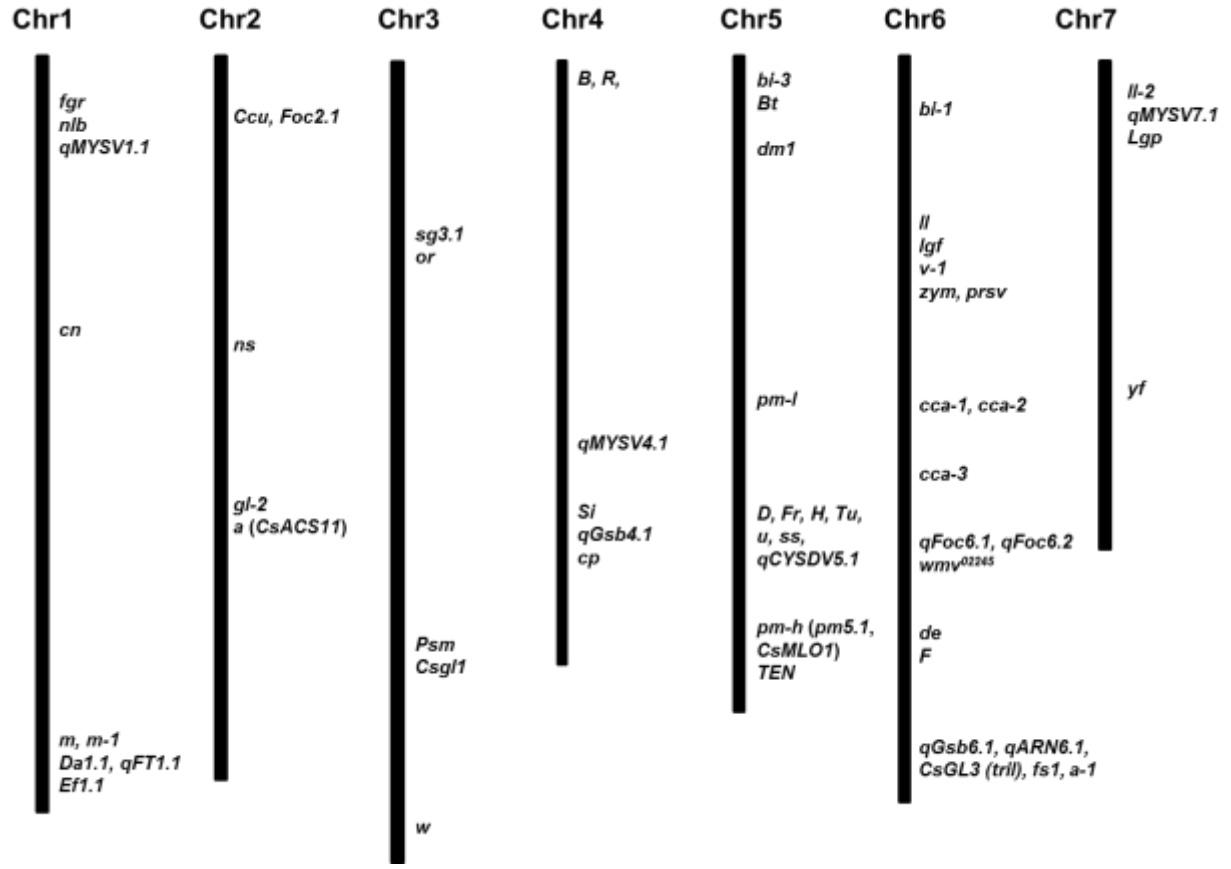

Figure 1. Chromosomal locations of mapped cucumber genes. The relative locations of genes on each chromosome are approximations based on molecular markers in original publications.