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REVIEW ARTICLE

Cucumber: Breeding and Genomics

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Abstract

Cucumber (*Cucumis sativus* L.) is one of the most important vegetable crops grown worldwide for immature fruits. Several improved varieties with a number of economically important traits were developed through conventional breeding. The availability of draft genome sequences has facilitated the wide application of genomics tools in cucumber improvement in last two decades. *C. sativus* var. *hardwickii* widely distributed in the northern foothills of the Himalayas is the progenitor of the present-day cultivated cucumbers. A large number of commercially cultivated varieties and hybrids were developed through conventional breeding approaches. In hybrid breeding, gynoecious sex expression has been used widely for the development of more productive hybrids economically. Genetic inheritance and molecular characterization were done for a large number of traits including agro-morphological, quality, biotic and abiotic stress tolerance. Besides, candidate genes were also identified for the number of traits and later on validated through transformation and knock-out. Sex expression has been studied widely in this crop and cucumber serves as the model crop to study sex expression. A number of genes for sex expression and other economically important traits were characterized and cloned. Development of cucumber inbreds with multiple disease resistance, better quality and tolerance to abiotic stress tolerance are the major focus in future cucumber improvement programme.

Keywords: Cucumber, Breeding methods, Sex expression, Stress tolerance, QTL, Candidate genes.

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Introduction

Cucumber (*Cucumis sativus* L.) is the most important vegetable crop in the family Cucurbitaceae and is cultivated worldwide and it is one of the oldest cultivated vegetable crops. For over 5,000 years, this crop has held historical significance, featuring a diploid chromosome number of 2n = 2X = 14. Due to its relatively smaller estimated genome size (367 Mbp), it has become a focal point in genomic research for cucurbitaceous vegetable crops (Dey *et al.* 2022). India is recognized as the primary center of origin for cucumber, with the wild cucumber (*Cucumis sativus var. hardwickii* R.) believed to be the progenitor of modern cultivated types, known for its extremely bitter fruits due to high cucurbitacins and a distinctive multiple branching nature, unlike cultivated cucumber genotypes. Notably, seedlings exhibit an epigeal growth habit, and the species displays crown fruit inhibition. The wild forms of cucumbers are widely dispersed in the southern foothills of the Himalayas, showcasing significant diversity in fruit shape, size, and color (Horejsi and Staub 2000).

Cucumber, a thermophilic and frost-susceptible summer season vegetable crop, thrives in diverse climatic conditions ranging from tropical and subtropical to temperate regions worldwide (Bacci *et al.* 2006). Primarily cultivated for its tender and edible fruits, cucumber holds a prominent place in culinary applications, being a favored ingredient in salads, pickles, desserts, and cooked dishes. The nutritional composition of cucumber includes 96.3% water content, 0.1 g of fat, 0.4 g of proteins, 0.3 g of minerals, and 7 mg of vitamin C per 100 g. Among cucurbits, cucumber stands out in terms of production, export, nutritional value, and consumer preference. Its tender fruits, consumed raw in salads, cooked as vegetables, or pickled in their immature stage, contribute to its popularity (Sumathi *et al.* 2008).

Typically, white-fleshed, common cucumber varieties exhibit lower carotenoid levels, while orange-fleshed genotypes boast higher carotenoid concentrations (Ranjan *et al.* 2019). Bitterness in cucumbers, primarily attributed to Cucurbitacin C (*CuC*), is regulated by genes such as Bitter (*Bi)* and Bitter fruit (*Bt*) (Shang *et al.* 2020). The hard skin of cucumbers is rich in essential minerals like calcium, potassium, and magnesium. Known for its cooling effect, cucumbers are often recommended for individuals dealing with jaundice and related conditions, and they are effective in preventing constipation. Cucumber seeds contain oil beneficial for brain development and overall well-being, making them a component in Ayurvedic preparations (Robinson and Decker-Walters, 1997). Additionally, the entire fruit finds applications in the cosmetic and soap industries.

In India, it is grown in an area of 1.13 lakh hectares with an annual production of 1.638 million tonnes (NHB 2021-22). China ranks first in cucumber production contributing around 77 percent of the world's cucumber production, followed by Russia, Turkey and Iran, whereas India stands at the 27th place (FAO 2017). In 2019, global cucumber production amounted to approximately 87.805 million tons. Notably, China claimed the top position as the leading producer with 70.3 million tonnes, followed by Turkey, which produced 1.92 million tonnes. The Russian Federation and Ukraine also contributed significantly to the production, yielding 1.62 million and 1.03 million tonnes, respectively (Table 1).

Table 1: Top 10 cucumber-producing states in india

Rank	*State*	*Production in tonnes*	*State's contribution (%)*
1.	West Bengal	326,820 tonnes	20.32%
2.	Madhya Pradesh	237,330 tonnes	14.76%
3.	Haryana	182,960 tonnes	11.38%
4.	Karnataka	130,360 tonnes	8.11%
5	Punjab	108,710 tonnes	6.76%
6	Uttar Pradesh	103,740 tonnes	6.45%
7	Assam	90,230 tonnes	5.61%
8	Andhra Pradesh	66,170 tonnes	4.11%
9	Maharashtra	62,480 tonnes	3.88%
10	Orissa	54,630 tonnes	3.40%
India's total contribution (2021-22)		1,608,290 tonnes	84.78%

(https://numerical.co.in/numerons/collection/6404cdd6757099577072a0ba)

Cucumber has a robust taproot system, extending up to 1 meter in length. As a monoecious crop, it features unisexual flowers occurring in leaf axils. Female flowers, both solitary and clustered, are found in gynoecious parthenocarpic hybrids, while male flowers are predominantly clustered (Robinson and Decker-Walters 1997). Gynoecious and parthenocarpic (gy + Pc) cucumbers are widely favored for protected cultivation due to their ability to yield higher. Gynoecious-based inbreds play a crucial role in hybrid seed production, contributing to increased seed yield (Behera *et al.* 2011).

Cucurbits exhibit a broad spectrum of sex forms, ranging from primitive hermaphrodites to advanced gynoecious forms, with sex expression being intricately regulated by environmental, genetic, and physiological-hormonal factors. The plant's main stem undergoes three phases of flowering: the male phase, mixed male-female phase, and predominately female phase. The F, m, a, gy, and h genes primarily determine cucumber sex expression, with 'Shogoin' (PI 220860) being a notable cultivar with gynoecious lines.

Breeding behavior of cucumber

Cucumber is a naturally cross-pollinated crop and have a considerable heterozygous balance. Frequent cross-pollination tends to create and maintain a tremendous amount of genetic variability mainly because of high degree of heterozygosity in the population. Thus, the role of the dominance gene is potential so the development of hybrid in this crop will be rewarding. Despite being a cross-pollinated crop, cucumber displays genomic characteristics similar to self-pollinated crops. Historical inherent selfing has led to the loss of lethal alleles, with the basic sex form being hermaphrodite. Geitonogamy, where female flowers are pollinated by male flowers from the same plants, is common. This intrinsic selfing has resulted in the absence of inbreeding depression (Peterson *et al.* 1978). In order to promote cross-pollination, cucumber has evolved different sex type of plants. For proper utilization of the available germplasm, it is very important to understand the different sex types of the cucumber. The majority of cucumber accessions are monoecious, however other sex form are also present in this crop including gynoecious, androecious, andromonoecious and hermaphroditic plants. Owing such large variation for sex type, cucumber is used as a model plant for sex determination studies. Researchers have deciphered the inheritance pattern and genetics underlying these sex types, several mutants have been identified and many genes/QTLs have been mapped. Sex determination in cucumber is mainly governed by three genes *F, M* and *A* (Kubicki 1969; Li *et al.* 2012). According to three gene model, *MMffAA* will produce monoecious plant (both male and female in one plant but at different position), *MMFFAA/MMFFaa* will produce gynocious plant (only female flowers), *MMffaa/mmffaa* exhibit androecious plant (only male flowers), *mmffAA* will produce andromonoecious plant (bisexual flowers and male flowers), *mmFFAA/ mmFFaa* will produce hermaphroditic plants (both male and female in one flower) (Mibus and Tatlioglu, 2004). Femaleness is governed by F*/f* gene; dominant *F* allele suppresses expression of *A/a* gene, although the recessive *a* allele exhibits androecious in *ff* genotypes (Kubicki 1969). Bisexual flower expression is governed by *M/m* (Tan *et al.* 2015). Sex determination in cucumber appears to be under more complicated genetic control than three gene model. Many factors like modifier or additional genetic control are feasible; moreover temperature, day length etc. can also stimulate sex expression in cucumber. Chen *et al.* (2011) identified two modifier gene *Mod-F1* and *mod-F2* independent of *F* and *M* loci, enhances intensity of femaleness. One intensifier for *F* gene (*In-F*) which enhances pistillate flowers and single dominant gene *Tr,* independent of *F* and *m* genes governing trimonoecious sex expression (staminate, bisexual and pistillate flowers) were identified (Kubicki 1969). In conclusion, understanding the different models of sex determination in cucumber plants is important for efficient cultivation and breeding (Tables 2, 3 and 4).

Based on the above studies, the sex expression of different genotypes is as follows

Respective sex forms	Genotype
Completely male	mmffaa/M_ffaa
Monoecious with mostly male flowers	M_ff
Female	M_F_
Hermaphroditic	mmF_
Andromonoecious	mmff

Genes involved in floral biology with their function and molecular mechanism

- *F* (female): Plants bearing the dominant F allele exhibit female traits (dominant femininity, dF). The expression of this gene is modulated by other sex genes and environmental factors, termed 'soft femininity.' Homozygous lines for the dominant F allele are consistently female. The F locus has been cloned and identified as an additional copy of the CsACS1G gene, which encodes 1-aminocyclopropane-1-carboxylic acid synthase (ACS).
- *m* (andromonoecious): This recessive allele influences the formation of bisexual flowers. The M locus has also been cloned, and identified as the CsACS2 gene, another member of the ACS family. The m allele carries a mutation at a conserved site (Gly33Cys), resulting in reduced enzymatic activity.
- *a* (androecious): Homozygotes with the aa genotype exhibit an intensification of male features. This gene is hypostatic to the F gene and may be related to CsACS11.
- *gy* (gynoecious): The recessive gy allele is responsible for more stable femininity compared to that conferred by the F gene (recessive femininity, rF; hard femininity). The *gy* gene, often abbreviated as g, is commonly associated with the gene indirectly influencing sex and could be correlated with CsWIP.
- *h* (andromonoecious-2): This allele results in the production of bisexual flowers with normal ovaries.
- *In-F* (intensifier of female sex expression): It enhances the action of the F gene.
- *Tr* (trimonoecious): This gene regulates the formation of female, male, and bisexual flowers, with the ratio influenced by environmental factors.

Breeding methods

Genetic improvements of cucumbers have been done by several breeding methods based on breeding objectives. High yielding with better quality fruit and resistance to biotic and abiotic stress is the chief objective in the cucumber breeding program. The most commonly used breeding methods for cucumber improvement are selection, backcross breeding, heterosis breeding, and population improvement approaches. Besides conventional breeding marker-assisted selection (MAS) is one of the popular methods used for cucumber breeding for different market type. Choices of breeding methods are based on the mode of pollination, a pattern of inheritance (qualitative/ quantitative), the amount of variability present in the population, life cycle of the plant and breeding objectives.

Selection

Selection is a method of plant breeding in which only the individuals with the desired traits are selected for breeding. In other words, the selection is a simple method where plants are chosen based on their overall appearance and performance. This method involves allowing the selected cucumber plants to naturally cross-pollinate, either through insects or wind. The resulting seeds will produce plants with a combination of traits from the parent plants. In the next generation, we have to choose the best-performing plants from a population and using them as parent plants for the next generation. Two basic requirements for selection to work on are the presence of variability in the population and that variability should be heritable. Effective selection could be made only if the selected variation is heritable. Selection does not create any variation it only utilizes the already available variation in the population. This method is often used for selecting plants that are resistant to certain diseases or pests, or that have a high yield. Sheetal having high yield, good keeping quality and early type developed from BSKKV, Dapoli, Khira 90 and Khira 75 are high yielding under temperate conditions, released by YSPUH&F, Solan, Pusa Long Green is an early maturing long fruited variety developed by IARI, New Delhi these are the example of varieties of cucumber developed by selection.

Hybridization

Hybridization is a method where plants are crossed to create new varieties with a combination of desirable traits. As cucumber is basically monoecious and cross-pollinated in nature, this allows harnessing the heterosis vigor. Use of gynoecious line for hybrid production in cucumber is the most common method. Gynoecious inbreed lines are used as female parent and monoecious inbreeds are used as male parent. Gynoecious lines are maintained by spraying of $AgNO_3$ which induces male flowers for self-pollination in these lines. The first cucumber hybrid of India, Pusa Sanyog is developed by using gynoecious inbreed line in 1971. Hybridization followed by pedigree selection can be used for the development of new varieties of cucumber that have specific traits, such as high resistance to disease or high yield. Some of the popular varieties like Phule Shubhangi and Himangi were developed by hybridization between Poinsette × Kalyanpur Ageti followed by selection.

Breeding for protected cultivation

The surge in urbanization, deforestation, subdivision of ancestral properties into smaller plots, indiscriminate use of inorganic fertilizers, and the conversion of cultivated land to uncultivated areas have driven a heightened adoption of protected cultivation or greenhouse cultivation. This technology involves cultivating cucumber in a controlled environment where factors like temperature, humidity, light, soil, water, and fertilizers are meticulously manipulated to achieve maximum yields. The controlled environment enables a consistent supply of produce, even during off-seasons. The preferred choice for protected cultivation is parthenocarpic gynoecious-based cucumber hybrids, which involve the pyramiding of Pc + Gy genes. While the cultivation of parthenocarpic cucumbers in greenhouses with partial environmental control has gained traction over the last decade in our country, there has been limited effort in developing varieties and hybrids specifically tailored for protected environments (Malhotra and Singh 2019). Consequently, there arose a necessity to create and identify parthenocarpic gynoecious hybrids and cultivars well-suited for protected cultivation across various seasons and regions in the country.

Parthenocarpic and Gynoecious cucumber

The cultivation of parthenocarpic and gynoecious (Pc + Gy) based cucumber hybrids is predominantly favored in protected conditions due to their ability to yield higher production and quality crops. Pollination plays a crucial role in cucumber production, with one or more pollen grains required per seed development, and approximately 10 to 20 bee visits necessary per flower to ensure proper fruit shape and size. Thus, it is crucial to introduce hives into the field when around 25% of the plants are initiating the flowering stage. Insufficient seed development may lead to issues such as fruit abortion, misshapen, curved, or short fruit, and poor fruit set. While parthenocarpic cucumber genotypes can produce fruit without pollination, normal seed formation occurs when successful pollination with viable pollen grains takes place.

Parthenocarpic cucumber varieties offer several benefits over conventional seeded varieties. They can sequentially set fruits without experiencing first-fruit inhibition (Sun *et al.* 2006). The combination of parthenocarpy with a stable gynoecious habit is crucial, as fruits formed after fertilization of parthenocarpic plants may become misshapen, lack economic value, and result in productivity loss if female flowers receive viable pollen.

Inheritance of parthenocarpy in cucumber

The conflicting evidence regarding the inheritance of parthenocarpy in cucumbers was reported by authors (Cao *et al.* 1997). Some reports suggested control by a single partially dominant gene (P), while others indicated the involvement of three independent major genes with additive and epistatic effects. Additionally, there were reports suggesting inheritance patterns typical of quantitative traits. In some other models, it is characterized as incompletely recessive, governed by two additive-dominant-epistatic major genes, and involved additive-dominant polygenes (Yan *et al.* 2008). In summary, the inheritance of parthenocarpy in cucumbers is governed by an incomplete dominant gene, denoted as *Pc*.

Stages in development of cucumber hybrids

- Gathering parthenocarpic and gynoecious genotypes.
- Preserving parthenocarpic lines through tissue culture and assessing their expression of parthenocarpy.
- Stimulating the formation of male flowers in parthenocarpic lines through hormonal regulation, specifically using silver thiosulphate (STS).
- Creating inbred lines and isolating parthenocarpic lines with enhanced quality in subsequent generations.
- Formulating crosses that involve both parthenocarpic and gynoecious lines.
- Assessing the performance of F_1 hybrids within a polyhouse environment.

Ideotype breeding in cucumber for protected cultivation

- Node to a first female flower
- Days to a first female flower

- Multi-pistillate flowering habit
- Parthenocarpic and gynoecious-based hybrids for protected cultivation
- Short internodal length
- Higher female: male sex ratio.
- More flesh thicknesses.
- Dark green color without spines.
- Proper fruit shape and length as per local preference without crooked neck.
- Less or negligible cucurbitacin content.
- Earliness and Uniformity of fruiting.
- Highest heterosis for horticultural traits
- Resistance to biotic (ToLNDV, Downy mildew, Powdery mildew, white fly resistant) and abiotic stress (Heat and frost tolerance).
- Stable gynoecious lines at high temperatures and suitable for tropical and subtropical regions of India.

Sex expression of the cucumber

Cucumber, an annual monoecious herb, produces staminate flowers in clusters, while pistillate ones are generally solitary and feature an inferior/epigynous ovary. Over the course of domestication, cucumber has undergone significant changes, resulting in the development of new forms such as exclusively female plants (gynoecious), species bearing only male flowers (lemon cucumber), bush-type forms with determinant main stem growth, and individuals with shortened internodes or a glabrous appearance. Cucumber sex expression typically follows a three-phase pattern: a male phase featuring only staminate flowers, a mixed phase, and a continuous-female phase.

Role of growth regulators on sex expression

Table 2: Agronomic and yield-related gene/QTLs mapped in the cucumber

S No.	*Trait*	*Genetics*	*Gene/QTL*	*Cloning of gene if any*	*Referencesw*
1	Fruit length	Recessive	*fl*	-	Pierce and Wehner, 1990
2	Short fruit	Recessive and Monogenic	*sfr*	-	Wang *et al.* 2014
3	Long fruit	Recessive	*lfr*	-	
4	Fragrance	Recessive and Monogenic	*fgr*	cloned	Pramnoi *et al.* 2013
5	Parthenocarpy	Incomplete dominant	*Pc*	-	Pike and Peterson, 1969; Sun *et al.* 2006
6	Tender fruit skin	Recessive	*te*	-	Strong 1931; Poole 1944
7	Tuberculated fruit	Dominant and monogenic	*Tu*	cloned	Strong 1931; Zhang *et al.* 2010
8	Bitter free fruits	Two recessive gene	*bi, bi-3*	cloned	Zhang *et al.* 2013
9	Bitter fruit	Dominant	*Bt*	cloned	Shang *et al.* 2014
10	Orange flesh	Recessive and Monogenic	*ore*	cloned	Bo *et al.* 2012
11	Early flowering	Polygenic	*Ef1.1*	cloned	Lu *et al*. 2014
12	Delayed flowering	Recessive and monogenic	*df*	-	Walters *et al.* 2001
13	Femaleness	partially dominant	*F*	cloned	Zhang *et al.* 2015; Win *et al.* 2015
14	Gynoecious	Recessive	*gy*	-	Kubicki 1974, Hu *et al.* 2017
15	Andromonoecious	Recessive	*m*	-	Tkachenko 1935
16	Androecy	Recessive and Monogenic	*a-1*	cloned	Chen *et al.* 2016
17	Male sterility -1	Recessive	*ms-1*	-	Shifriss 1950, Whelan 1972
18	Male sterility -2	Recessive	*ms-2*	-	Whelan 1972
19	Male sterility -3	Recessive	*ms-3*	cloned	Han *et al.* 2018, Wang *et al.* 2020
20	Determinate	Recessive and Monogenic	*de*	cloned	Weng *et al.* 2010
21	Compact	Recessive and Monogenic	*cp*	cloned	Chen *et al.* 2022
22	Pre-harvest sprouting	Polygenic	*qPHS4.1, qPHS5.1*	-	Cao *et al.* 2021

Table 3: Genetic inheritance, identification of QTLs and candidate genes associated with biotic stresses in cucumber

Trait	*Inheritance*	*Resistance source*	*Candidate gene*	*References*
Scab (*Cladosporium cucumerinum*)	Single dominant gene; *Ccu* linked with *Foc*	-	*Ccu*	Abul-Hayja *et al.* 1978
Bacterial wilt (BW) (*Erwinia tracheiphila*)	Single dominant gene; *Bw* linked with m	-	*Bw*	-
Downy mildew (*Pseudoperonospora cubensis*)	Single recessive gene	PI 197087	*dm*-1	Barnes and Epps (1954)
	Three recessive genes	Aojihai	s1, s2 and s3	Shimizu *et al.* (1963)
	At least three major genes exhibiting partial dominance	Sadao Rischu		Pershin *et al.* (1988)
	A single recessive gene	Poinsett/PI 197087	*p/dm*-1	Horejsi *et al.* (2000)
	A single recessive gene	Ashley/PI 197087	*dm-1*	Fanourakis and Simon (1987)
	An epistatic interaction between a dominant susceptible gene and a recessive resistance gene	Palmetto and Yomaki		El-Hafaz *et al.* (1990)
	Two recessive genes	PI 197088		Angelov (2000)
	Single recessive gene	Poinsett		Angelov (2000)
	Resistance was controlled by three recessive genes, where *dm-3* and either *dm-1* or *dm-2* had to be homozygous recessive for maximum resistance	-	*dm-1, dm-2 and dm-3*	Doruchowski and Lakowska-Ryk (1992)
	One or two incompletely dominant genes	J-13/ Wisconsin 2843/PI 197087	-	Petrov *et al.* (2000)
	At least three genes for resistance to downy mildew	PI 197088	-	Criswell (2008)
Downy mildew (*Pseudoperonospora cubensis*)	Number of genes controlling DM resistance and one of them seems to be allelic to dm-1	Ames 2354 (a selection from SC50)	-	Kozik *et al.* (2013)
Downy mildew (*Pseudoperonospora cubensis*)	Five QTLs	129, S94, K8	-	Ding *et al.* (2007)
Downy mildew (*Pseudoperonospora cubensis*)	Three QTLs	*C. hystrix* introgression line IL52	-	Pang *et al.* (2013)
Downy mildew (*Pseudoperonospora cubensis*)	Three QTLs	PI 197088	-	Caldwell *et al.* (2011)
Downy mildew (*Pseudoperonospora cubensis*)	Ten QTLs	CS-PMR1		Yoshioka *et al.* (2014)
Downy mildew (*Pseudoperonospora cubensis*)	Three QTLs	PI 197085		Szczechura *et al.* (2015)
Downy mildew (*Pseudoperonospora cubensis*)	Five QTLs	WI7120 (PI 330628)		Wang *et al.* (2016)
Downy mildew (*Pseudoperonospora cubensis*)	Ten QTLs	PI 197088		Wang *et al.* (2018)
Downy Mildew (DM)	QTLs	WI7120 (PI330628)	*dm,2.1, dm_4.1, dm_6.1, dm_5.1*	Wang *et al.* 2016

Powdery mildew (PM)	Csa1M064780 and Csa1M064790 (cysteine rich receptor-like protein kinase) F2 Population studied (Ch-1)	Jin5–508	pm_1.1	Xu *et al.* 2015b
Powdery mildew (PM)	CsMLO1 (MLO-like gene) Linkage gr-5	S1003	Pm_5.1 (UW06502-UW065094)	Nie *et al.* 2015
Fusarium Wilt (FW)	7 NBS-LRR predicted type. Linkage group- 2 RIL population studies,	9110Gt	Foc_2.1 (SSR17631)	Zhang *et al.* 2014
Fusarium Wilt (FW)	Linkage group- 2 F2 population studies,	Rijiecheng	*fw_2.1*	Dong *et al.* 2019
Gummy Stem Blight (GSB)	Linkage group- 5 RIL population studies,	PI183967	gsb_5.1 (SSR15321-SSR07711)	Liu *et al.* 2017
Gummy Stem Blight (GSB)	14 for disease resistance and 1 (Csa6G062270) for leucine rich repeat region within gsb-s_6.2 RILs (F9), Linkage group-1	PI183967	gsb-s_1.1	Zhang *et al.* 2017
Target leaf spot (TLS)	Indel16874230 and Indel16953846 linked to cca-3. F2:3 populations used. Linkage group-6	D31	CsGy6G019440.1 (CC–NB-ARC type resistance homolog)	Wen *et al.* 2015
Anthracnose	RILs. Linkage group; 5	150 Gy-14	*Cla*	Pan *et al.* 2018
Angular leaf spot (ALS)	CsGy5G003280.1 (staygreen) RILs. Linkage group; 5	Gy14	CsSGR (staygreen) psl/psl_5.1 (IS_16,325,300-UW085415); psl_5.2 (16,327,616-IS_16,326,693)	Slomnica *et al.* 2018
CMV	*cmv6.1* (SSR9–56 and SSR11–177) RILs. Linkage group; 6	Inbred line 2245	*Csa6M133680* (bZIP domain-containing transcriptional activator)	Shi *et al.* 2018
ZYMV	QTL: zymA192–18 (SSR07248 and SSR13884) F2:3, Linkage group; 6	A192–18	*CsVPS4* (Vacuolar protein sorting-associated protein 4 like)	Amano *et al.* 2013
Meloidogyne incognita (Root-knot nematode	QTL: qRKN1–1 (C01B2) RILs. Linkage group; 1	IL10–1 (Cucumis × hytivus)	4 genes on chr. 5, of which Csa5M608240n and Csa5M610420, encoding a leucine-rich repeat family	Cheng *et al.* 2019
Insect-pest Striped and spotted cucumber beetle	*bi-1* (SSR0004- SSR02309). *bi-3* (SSR00116–SSR05321) Linkage group; 6	9910Gt	*Csa008595* (terpene synthase)	Zhang *et al.* 2013

The use of growth regulators significantly influences sex expression and flowering in various cucurbits. Plant hormones, particularly ethylene and auxin, play a crucial role in regulating the male-to-female flower ratio in cucumber plants. Ethylene and auxin promote the formation of female flowers, while gibberellins encourage the development of male flowers. Ethylene, a major player in inducing female flowers, suppresses gibberellin, a hormone associated

Table 4: Genetic inheritance, identification of QTLs and candidate genes associated with abiotic stresses in cucumber

Trait	*Inheritance*	*Resistance source*	*Candidate gene*	*References*
Heat, salt stress and biotic stress resistance	Polygenic	*C. sativus.* L	*CsERF1*, *CsERF3* and *CsCHS2*	Ahmad *et al.* 2023
Sulfur dioxide air pollution conditioned	Single dominant gene	National Pickling and Chipper	Sd	Bressan *et al.* 1981
High salt levels	Single dominant gene	PI 177,361	Sa	Jones *et al.* 1984
Seedling chilling resistance	Single dominant gene	line NC-76 (PI 246,930) K	Ch	Kozik and wehner, 2008
Low temperature	qLTG1.1 (IndelLTG33–IndelLTG31) RILs. Linkage group; 1	65G	*Csa1M408720* (encodes the DELLA protein) within qLTG1.1 region	Song *et al.* 2018
Salinity	SSR20710, SSR16667, SSR13312 markers identified. F2:3. Linkage group; 3	11411S		Kere *et al.* 2017
High temperature	qHT3.1, qHT3.2, qHT3.3, RIL. Linkage group; 3	65G	9 genes within qHT3.2	Dong *et al.* 2020
Water-logging	ARN3.1 (UW084507–SSR02051). F2:3. Linkage group; 3	Zaoer-N	Csa6G503880 (ethylene activated signal pathways).	Xu *et al.* 2017
Low temperature	Recombinant inbred line (RIL) derived from the tolerant variety Coolgreen and the sensitive inbred line 7088D.	Coolgreen (tolerant)	*QTL qLTG1.2* and *qLTG2.1* exhibited major on ch 1 and 2	Yagcioglu *et al.* 2019
Low-temperature tolerance	Recombinant inbred lines (RILs) derived from a cross between 65G (low-temperature-tolerant) and 02245 (low-temperature-sensitive)	65G (low-temperature-tolerant)	The results showed that qLTG1.1 and qLTG4.1 play an important role in low-temperature tolerance during seed germination.	Song *et al.* 2018
Heat stress tolerance	DGC-103, WBC-39-1, WBC-13 and DC-83 have been identified as high heat tolerant,	DGC-103, WBC-39-1, WBC-13 and DC-83	High chlorophyll retention, stable membrane stability index, higher retention of water content in plants, stability in net photosynthesis, good stomatal conductance and transpiration rate and maintaining less canopy temperatures in tolerant genotypes are the key physiological mechanisms in cucumber	Hongal *et al.* 2023

with male flower production. The internal ethylene level influences the expression of sex phenotypes, with gynoecious lines exhibiting two to threefold higher ethylene levels than monoecious or andromonoecious ones. Gibberellic acid (GA_3) acts as an ethylene biosynthesis blocker, hindering ethylene production, while silver nitrate ($AgNO_3$) acts as an ethylene action blocker, promoting male flower production.

Cucumber Genome

Currently, genome sequences have been deciphered for three distinct cucumber genotypes: Chinese Long 9930 (Huang *et al.* 2009a), Gy14 (Cavagnaro *et al.* 2010), and B10 (Wóycicki *et al.* 2011). The B10 sequence, covering 94% of the cucumber genome, stands as the most comprehensive draft version to date (Osipowski *et al.* 2016). The cucumber genome, characterized by the absence of recent whole-genome duplication and few tandem duplications, accounts for its relatively small number of genes. Notably, five of the cucumber's seven chromosomes originated from fusions of ten ancestral chromosomes after divergence from *Cucumis melo* (Yang *et al.* 2022). The cucumber genome serves as a crucial resource for the development of elite cultivars and facilitates the exploration of evolutionary and functional aspects of the plant vascular system. The construction of a genetic map, utilizing 77 recombinant inbred lines from the intersubspecific cross between Gy14 (a North American processing market–type cucumber cultivar) and PI183967 (an accession of *C. sativus var. hardwickii* from India), spans

Table 5 : Application of CRISPR-Cas9-based editing in cucumber

Target gene	*Improved/mutant trait*	*References*
eIF4E	Immunity to Cucumber vein yellowing virus (Ipomovirus) infection Resistance to the potyviruses Zucchini yellow mosaic virus Resistance to the Papaya ring spot mosaic virus-W.	Chandrasekaran *et al.* 2016
CsWIP1	Gynoecious phenotype	Hu *et al.* 2017
Homologs of *ERECTA CsaV3_4G036080*	Compact plant architecture mutant	Xin *et al.* 2022
CsAKT1	salt tolerance	Peng *et al.* 2022
CsaMLO8	Powdery mildew resistance	Shnaider *et al.* 2022

581 cM and incorporates 1,885 markers, including 995 microsatellite markers.

Molecular mapping of important traits

For a better understanding of the pattern of inheritance and genetic mechanism behind the essential traits of cucumber, several mutants have been identified and many genes or QTLs have been cloned or tagged by molecular markers. Genes/QTLs identified for some of the important agronomic and yield-related traits are discussed below:

Besides, the agronomic traits, a large number of biotic and abiotic stresses are studied in cucumber using the germplasm from different parts of the world. After identification of the potential source of resistance, the underlying genetic inheritance, molecular mapping, and identification of possible candidate genes were identified for a number of diseases caused by fungi, bacteria and viruses. The details of the abiotic and abiotic stress tolerance are presented in Tables 2 and 3.

Progress and prospects of genome editing

Genome editing is a powerful tool that permits the induction of desirable alleles directly into the plants without the extensive process of backcrossing required by conventional breeding methods. Also, genome editing does not essentially involve transgenic segments, which makes it more acceptable method as it can bypass the strict regulatory policies made for transgenic breeding methods (Jones 2015). Genome editing tools include zinc-finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs), meganucleases and clustered regularly interspaced short palindromic repeats (CRISPR/Cas9). Among these tools, CRISPR/Cas9 is most commonly and powerful tool used in various crops to improve plant traits and for understanding gene function (Zhang et al. 2021). As CRISPR/Cas9 is an RNA-based approach, it can be more easily and efficiently modified than protein-based methods. In cucumber, CRISPR/Cas9 has been used by some workers for genome editing studies in cucumber (Table 2).

Successful application of CRISPR-Cas9 for the first time in cucumber was conferred by Chandrasekaran *et al.* (2016) for virus resistance. In cucumber, when the recessive *eIF4E* (eukaryotic translation initiation factor 4E) gene was interrupted using Cas9/sgRNA constructs, broad virus resistance generated against cucumber vein yellowing virus (Ipomovirus), potyviruses Zucchini yellow and Papaya ring spot mosaic virus-W (Chandrasekaran *et al.* 2016). Gynoecious cucumber lines are commercially valuable due to their use in heterosis breeding and higher yield. Mutagenesis of *CsWIP1* is generated by CRISPR-Cas9 tools to produce *Cswip1* T_0 mutants that exhibit gynoecious cucumber phenotype, bearing only female flowers (Hu *et al.* 2017). Compact plant architecture mutant generated by CRISPR/Cas9-mediated mutagenesis in cucumber targets *CsaV3_4G036080* homologs of the *ERECTA* gene family encodes plant internode length in Arabidopsis (Xin *et al.* 2022). One of the limiting factors for growth and development in cucumbers is salinity. CRISPR/Cas9 technique verifies that *CsAKT1* is a key gene behind the PNC (poly acrylic acid coated nanoceria)-improved cucumber salt tolerance in cucumber (Peng *et al.* 2022). Powdery mildew is one of the devastating diseases of Cucurbitaceae family. Two transgene-free *Csamlo8* CRISPR mutant lines (*Csamlo-cr-1* and *Csamlo-cr-2*) showing high resistance to PM were isolated from susceptible cucumber cultivar 'Ilan' using CRISPR/Cas9-mediated mutagenesis (Shnaider *et al.* 2022). Genome editing especially by CRISPR-Cas9 is a cost-effective, highly efficient method due to its targeted approach. However, some improvement is recommended to optimize and enhance the efficiency of genome this technology. This includes optimizing the technology in a selection of target genes and type of mutation to avoid off-target effects. Furthermore, most of the traits are quantitatively inherited hence edition in a single gene may not be sufficient to achieve desirable results. In addition to these challenges, sgRNA and GC amount, and expression level of Cas9 also influence the successful transformation of desired genotype (Azameti and Dauda 2021) (Table 5).

Conclusion

The increased challenges and rapid advancement in breeding techniques has helped in achieving resistance for biotic and tolerance to abiotic stresses in cucumbers. The availability of genome sequences and mapping of several genes/QTLs related to diseases and agronomic trait followed by introgression has helped in achieving rapid genetic gains. Based on the available reports and progress made till date, it was evident that the identification of potential donor for a number of emerging problems and their detailed characterization using the advanced OMICS-based tools are required to sustain cucumber production in the future.

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सारांश

खीरा (*कुकुमिस सैटिवस* एल.), अपरिपक्व फलों के लिए दुनिया भर में उगाई जाने वाली सबसे महत्वपूर्ण सब्जी फसलों में से एक है। पारंपरिक प्रजनन के माध्यम से, कई उन्नत किस्में विकसित की गईं है, जो आर्थिक रूप से महत्वपूर्ण है। ड्राफ्ट जीनोम अनुक्रम की उपलब्धता ने पिछले दो दशकों में खीरा सुधार में जीनोमिक्स टूल के व्यापक अनुप्रयोग की सुविधा प्रदान की है। *सी. सैटिवस वर. हार्डविकी,* उत्तरी हिमालय की तलहटी में व्यापक रूप से वितरित, वर्तमान समय में खेती की जाने वाली खीरे का पूर्वज है। पारंपरिक प्रजनन के माध्यम से बड़ी संख्या में व्यावसायिक रूप से खेती की जाने वाली किस्मों और संकरों को विकसित किया गया है। संकर प्रजनन में, अधिक से अधिक उत्पादक संकरों के विकास के लिए गाइनोशियस अभिव्यक्ति का व्यापक रूप से उपयोग किया गया है। कृषि-रूपात्मक, गुणवत्ता, जैविक और अजैविक तनाव सहिष्णुता सहित बड़ी संख्या में लक्षणों के लिए आनुवंशिक वंशानुक्रम और आणविक लक्षण वर्णन किया गया है। इसके अलावा, कई गुणों के लिए उम्मीदवार जीन भी पहचाने गए है और बाद में प्रपांतरण और नॉक-आउट के माध्यम से मान्य किया गया। इस फसल में यौन-अभिव्यक्ति का व्यापक रूप से अध्ययन किया गया है, और खीरा यौन अभिव्यक्ति का अध्ययन करने के लिए मॉडल फसल है। यौन अभिव्यक्ति और अन्य आर्थिक रूप से महत्वपूर्ण गुणों के लिए कई जीनों का मापन और क्लोनिंग की गई है। भविष्य में खीरा सुधार कार्यक्रम में मुख्य फोकस बहु रोग प्रतिरोधक क्षमता, बेहतर गुणवत्ता और अजैविक तनाव सहनशीलता वाली खीरे की नस्लों का विकास करना है।