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Marker Assisted Selection (MAS) and It's Application in Vegetable Crop Improvement

Varun Shekhar [a++*], Vijay Bahadur [a#] and Lalita Lal [a++]

[a] *Department of Horticulture, Naini Agricultural Institute, SHUATS, Prayagraj-211007, Uttar Pradesh, India.*

Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Vegetable crop breeding has changed dramatically since the early 1980s due to technological breakthroughs, especially high-throughput sequencing and molecular marker technologies, which have made it possible to sequence many plant genomes, create dense genetic maps, and identify important genes and QTLs linked to traits like yield and disease resistance.These instruments have expedited genetic research and breeding programs in crops including tomato, pepper, eggplant, and cucumber, establishing marker-assisted selection (MAS) as a crucial component of contemporary breeding. The use of these technologies has improved crop characteristics significantly and is still influencing the development of vegetable crops in the future. For instance, in the majority of private and public tomato breeding projects, major-gene disease resistance traits like verticillium wilt and anthracnose are selected for using PCR-based markers such as SCAR and CAPS.Bs5 and Bs6 have broad-spectrum resistance against *Xanthomonas s*pp. against chilli leaf spot thanks to marker-assisted gene pyramiding. Major QTLs associated to SSR marker CAMS451

[++] *Ph.D Scholar;*
[#] *Professor;*
**Corresponding author: E-mail: varunshekhar65@gmail.com;*

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on chromosome 1 (from Capsicum accession LS2341) and marker ID10-194305124 on chromosome 10 (from *C. annuum* BVRC1) have been mapped for resistance to Ralstonia bacterial wilt.Constantly searching crop germplasm for new resistance genes or alleles is essential to diversify the gene pool and stop resistance from breaking down. By using marker-assisted selection (MAS), it is possible to combine genes for resistance to different pathogens or several sources of resistance to the same pathogen to create novel cultivars.

Keywords: Gene pyramiding; hybrids; marker assisted selection; QTLs.

1. INTRODUCTION

Vegetables are a broad group of crop species that are essential to the diets of people all around the world. These species include fruits, flowers, roots, stems, leaves, and seeds. They are rich in vitamins, minerals, and dietary fiber and can be eaten raw or cooked. They are generally low in fats and carbohydrates [66].The precise meaning of a "vegetable" depends on several classifications, including culinary and botanical perspectives. Many vegetables, such as spinach, eggplants, cucumbers, lettuce, peppers, and tomatoes, are most abundant in Asia. Europe, on the other hand, exports the most chicory [20]. Asia continues to be the world's leading producer of cucumbers, spinach, eggplants, and chili peppers when it comes to per capita production. In terms of tomato, lettuce, and sweet pepper production, North America is in the lead, whereas Europe is the major producer of chicory. In addition to these crops, a wide variety of other vegetables are very well-liked throughout the world. Nonetheless, cucumber, eggplant, tomato, and pepper are the main topics of this review.

Traditional breeding methods are typically expensive, labor-intensive, and slow. On the other hand, novel techniques, instruments, and approaches that can improve plant breeding programs have been created as a result of recent developments in genetics and genomics. Molecular markers, genetic linkage maps, marker assays, and whole-genome sequences have been created and published for various crop species, including several vegetable species [65]. Cutting-edge breeding methods including Marker-Assisted Recurrent Selection (MARS) [13], Marker-Assisted Backcrossing (MABC) [15], and Marker-Assisted Selection (MAS) [15], based on the complexity of the genetics and breeding of the species, and Sequencing Selection (GS) [29] are in varying phases of development for diverse vegetable crops. Linkage mapping [68]; genome-wide association analysis (GWAS) [72]; embedded association mapping (NAM) [73]; and multi-parent advanced era inter-cross (MAGIC) populations [9] are some of the methods for finding and mapping genes and Quantitative Trait Loci (QTLs) that have been developed.

While initially focused mostly on key cereal crops like maize, rice, and wheat, these innovative genetic and genomic tools and methodologies are gradually finding their way into vegetable genetics and breeding [63]. In order to give current information on genomic resources that are accessible, the application of genetic and genomic tools and techniques in breeding programs, and the primary areas of future study anticipated for each crop, the current review focuses on vegetable crops. Vegetable crops' nutritional qualities and health advantages are influencing customer tastes more and more. Many quantitative trait loci (QTLs) or genes associated with molecular markers have been found for several commercially important tomato features.According to theory, using this marker data to aid in marker-assisted breeding could improve tomatoes' qualitative characteristics. The time and expense involved in breeding attempts to improve solanaceous vegetable quality attributes can be significantly reduced through the integration of traditional breeding techniques with cutting-edge instruments like molecular markers [79].

2. TOMATO

By economic measures and consumption values, the cultivated tomato (*Solanum lycopersicum* L.), a diploid plant (2n = 2x = 24 chromosomes), is one of the most significant vegetable crops in the world.Global tomato production for processing and fresh consumption reached just over 189.1 million metric tonnes in 2021, up 2% from the 184.8 million mT grown in 2020 and 4% from the average (182.7 million mT) of the preceding three years (2018–2020), according to data gathered and updated by FAOSTAT in December 2022. More tomato cultivars than any other vegetable crop are sold

globally [22]. Tomatoes are a tropical plant that are grown practically anywhere in the world. Leading producers of tomatoes are China (33.8%), India (10.6%), the United States (6.9%), Turkey (3.6%), and Egypt (3.6%). In addition to being a staple food, tomatoes are also highly consumed in a variety of dishes, such fresh fruit, sauces, soups, and processed foods like canned tomatoes and ketchup.

In many nations, like the US, tomatoes are a vital element of the diet [77]. Tomatoes are the top fruit and vegetable among all others in terms of important dietary sources of vitamins A and C, minerals, and phenolic antioxidants [78], even though they are often not thought to have a high nutritional value. This is mostly due to the amount of it is consumed [75]. The main substance that gives the red color of the fruit is lycopene, which is mainly found in tomatoes. Important antioxidants lycopene and β-carotene, which are also present in tomato fruit, have been linked to a decreased risk of developing certain tumors when consumed [35].

Tomato breeding started in the 1930s when attempts were made to enhance the tomato's general horticultural qualities. Tomatoes have undergone substantial genetic variability in terms of fruit shape, size, color, and taste as well as plant type, size, and growth habit. Presently, the majority of tomato cultivars available are divided into two categories: tomatoes for the fresh market (FM) and tomatoes for processing (PROC). The majority of fresh market tomatoes are sold and consumed raw. These include huge beefsteak/slicer, plum/roma, campari, cherry, and grape varieties. To prepare canned goods, processing tomatoes are often peeled, cubed, juiced, or sauced. Although the unifying goal of breeding PROC and FM tomatoes is to achieve increased yield per unit area for all tomato kinds, the breeding objectives for these two t.

omato varieties differ greatly. Both kinds share these specific top breeding priorities:

1. Resistance/tolerance to various biotic stresses (e.g., diseases and insects)
2. Resistance/tolerance to various abiotic stresses (e.g., salt, cold, and drought)
3. Adaptability to the changing climate
4. Maturity and plant type for specific environments and production systems

Tomato crops are important to the world's food supply, and these breeding goals seek to increase their yield and quality.Through the use of wild tomato accessions as germplasm resources for crop improvement, breeding efforts were made to make up for the restricted genetic diversity within the farmed tomato species. The identification and introgression of desirable genes and QTLs, as well as genetic mapping, have all benefited greatly from these wild accessions. These genetic features include enhanced fruit quality and nutritional qualities, resistance to disease and insects, and tolerance to abiotic stress [2,22]. Breeders have mostly used interspecific crosses between elite tomato breeding lines and accessions within related wild species to identify and map novel genes and QTLs. Mapping populations, such as early filial and backcross populations (F2 and BC1), backcross inbred lines (BILs), recombinant inbred lines (RILs), and near-isogenic lines (NILs), have been developed as a result of these crosses. Genetic maps are created using these populations [22,5] created the first genetic linkage map of tomatoes using 153 physiological and morphological markers, which revealed all 12 tomato linkage groups (LGs). In 1986, Bernatzky and Tanksley released the first tomato molecular linkage map, which combined 94 RFLP markers with 18 isozymes.The first "high-density" genetic map of tomatoes, which included 1,030 molecular markers (mainly RFLPs), was published in 1992 [68].

Genes and QTLs linked to numerous agriculturally significant features have been identified, mapped, and characterized through the application of molecular markers and genetic maps of tomatoes. These features include plant type, maturity, yield, and qualities connected to flowers and fruits, as well as resilience and tolerance to biotic and abiotic challenges. More than 200 bacterial, viral, fungal, and nematode illnesses can affect grown tomatoes [40]. Host plant resistance has thus been the main goal of numerous tomato breeding plans around the world. Through these studies, resistance genes, or QTLs, for a variety of diseases, including the following, have been found, genetically identified, and used:

Fusarium oxysporum-caused *Fusarium wilt*, *Verticillium wilt*, *Cladosporium fulvum*, Tomato leaf mold, Late blight, Bacterial speck, *Pseudomonas syringae*, *Bacterial spot*, *Xanthomonas* strain T1–T4, and Tomato mosaic virus (ToMV); Root-knot nematode (RKN; Meloidogyne spp.); Tomato Yellow Leaf Curling Virus (TYLCV); Tomato Spotted Wilt Virus

(TSWV). According [22,8], more than 20 resistance genes for various worm, bacterial, viral, and fungal diseases have been identified and/or cloned in tomato. These successes have accelerated the process of creating tomato cultivars resistant to disease, that will help develop more sustainable tomato production systems. Since then, other molecular markers linked to novel genes or QTLs for a variety of tomato real estate have been discovered. Through more accurate and effective breeding techniques, improved tomato varieties can be evolved. This continuing research helps us better understand the genetic basis of crucial tomato features [4,11,27,28,37].

Now, most of the markers used in tomato genetic mapping and breeding are based on PCR methods. These include SNPs, insertion-deletion (InDel) markers, sequence characterized amplified regions (SCAR), cleaved amplified polymorphic sequences (CAPS), amplified fragment length polymorphism (AFLP), random amplified polymorphic DNA (RAPD), and simple sequence repeats (SSR or microsatellites). A few requirements need to be met for these genetic markers to work well in breeding applications. By examining the banding patterns of related genetic markers, marker-assisted selection (MAS) entails the indirect selection of a desired plant phenotype [79]. Tomato shelf life is reportedly increased by an SNP marker [41].

Numerous applications of marker-assisted selection (MAS) exist in the breeding of vegetables. The tomato leaf curl virus, a severely devastating disease that is common on the plains of northern and eastern throughout the cold season is notable. Six resistant genes (Ty1, Ty2, Ty3, Ty4, Ty5 and Ty6) have shown to be associated with this feature. The Ty3 gene has been successfully inserted into the genetic make-up of popular varieties of Pusa Ruby, Pusa Rohini and Pusa-120 [34].

Despite being one of the first crop plants to be bred using genetic markers and maps [68], nearly all tomato breeding projects depended primarily on phenotypic selection (PS) until the early 1980s. There is growing interest in employing markers to help improve tomato crops now that more breeder-friendly and high-throughput genetic markers, such as SNPs and PCR-based markers, have been discovered. Although most significant disease resistance features in tomatoes have markers, not all of the reported markers have been validated or are easily transferable to tomato breeding, according to a review of the literature. However, most tomato breeding efforts use marker-assisted selection (MAS) for gene stacking and

Table 1. Major tomato genes and QTLs used in marker-assisted breeding for resistance against fungal, bacterial, viral, and nematode diseases

Disease (pathogen)	Gene/QTL	Chr.	MAS assay	Citation
Fusarium wilt (*Fusarium oxysporum*)	I	11	CAPS	[6]
Fusarium wilt (*Fusarium oxysporum*)	I-2	11	SCAR	[63]
Fusarium wilt (*Fusarium oxysporum*)	I-3	7	CAPS/SCAR	[7]
Verticillium wilt (*Verticillium albo-atrum*)	Ve1	9	ARMS-PCR	[38]
Verticillium wilt (*Verticillium albo-atrum*)	Ve2	9	ARMS-PCR	[38]
Leaf mold (*Cladosporium fulvum*)	Cf-2	6	SSR	[17]
Leaf mold (*Cladosporium fulvum*)	Cf-4	1	SNP/InDel	[71]
Leaf mold (*Cladosporium fulvum*)	Cf-5	6	SSR	[17]
Leaf mold (*Cladosporium fulvum*)	Cf-9	1	SNP/InDel	[36]
Late blight (*Phytophthora infestans*)	Ph-1	7	Unknown	[14]
Late blight (*Phytophthora infestans*)	Ph-2	10	CAPS	[47]
Late blight (*Phytophthora infestans*)	Ph-3	9	CAPS	[57]
Late blight (*Phytophthora infestans*)	Ph-5	10	Unknown	[43]
Bacterial spot (*Xanthomonas* Race T1-T4)	Rx4	11	InDel	[53]
Bacterial spot (*Xanthomonas* Race T1-T4)	RxopJ4	6	CAPS	[60]
Tomato mosaic virus (ToMV)	Tm-1	2	SCAR	[33]
Tomato spotted wilt virus (TSWV)	Sw-5	9	SCAR/CAPS/RAPD	[22]
Tomato shelf life	Sh4	6	SNP	[41]

integration, particularly when breeding cultivars for various disease resistance features. To select for many of the major-gene disease resistance traits, for instance, most private and public tomato breeding projects use PCR-based markers such as SCAR and CAPS. A summary of specific marker data can be found elsewhere [22]. Genetic markers are also frequently employed for a number of other objectives, such as determining the purity of hybrids and screening breeding populations for traits related to plant species and fruit quality. But when breeding for complicated traits—including polygenic disease resistance (such bacterial canker and early blight), abiotic stress tolerance, yield, and numerous fruit quality traits—markers are rarely used [46,64,69,70].

3. PEPPER

Pepper, a member of the Solanaceae family's genus Capsicum, is a widely grown vegetable and spice crop. The 35 species of the genus Capsicum—which is thought to have originated in Bolivia [54] include the five commercially significant cultivated species Capsicum annuum L., C. frutescens L., C. baccatum L., C. chinense Jacq., and C. pubescens Ruiz & Pav. While many wild species have 26 chromosomes, all capsicum species are diploids, often having 24 chromosomes (2n = 2x = 24). The morphological and yield-related traits that pepper displays a wide range of diversity in include plant architecture, flowering time, fruit size, shape, and color, phytochemical contents, and tolerance or resistance to biotic and abiotic stimuli. Whereas bell peppers may be grown in nearly any type of soil, loamy, well-drained soil that retains moisture is ideal. While plant growth and fruit development require temperatures between 18 and 30°C, pepper seed germination requires a temperature between 25 and 30°C. 63.44 million metric tons of pepper were produced globally in 2021 on 4.6 million hectares of land [20] Pepper is utilized in a variety of applications in the food, pharmaceutical, and cosmetics industries in addition to being a vegetable.Pepper is rich in vitamins (A, C, and E), minerals (potassium and magnesium), and phytochemicals such as carotenoids and capsaicinoids, which contribute to its nutritional and medicinal properties. Capsaicin, the compound responsible for the pungency in peppers, has been extensively studied for its health benefits, including its role in pain relief, weight loss, and cancer prevention. The breeding history of pepper involves significant efforts to improve yield, quality, and resistance to various stresses. Traditional breeding methods, such as selection and hybridization, have been complemented by modern techniques, including molecular breeding and genetic engineering. Marker-assisted selection (MAS) and genome-wide association studies (GWAS) have accelerated the identification and utilization of genes and quantitative trait loci (QTLs) associated with important traits in pepper breeding programs. Pepper breeding objectives include improving fruit quality (size, shape, colour, and taste), increasing yield, and enhancing resistance to diseases (e.g., bacterial spot, Phytophthora blight, and powdery mildew) and pests (e.g., aphids and thrips). Additionally, breeding efforts focus on developing varieties with improved tolerance to abiotic stresses such as drought, salinity, and temperature extremes.

In the last twenty years, the main goal of pepper breeding has been to genetically enhance sweet and spicy peppers by adding resistance to pests and diseases. The development of high-throughput genotyping techniques and next-generation sequencing (NGS) has sped up the process of identifying single nucleotide polymorphism (SNP) markers in Capsicum species. There are published high-density genetic linkage maps for a number of populations, primarily F2 or doubled haploid (DH), and high-throughput sequencing makes it easy to identify sequence variants such as SNPs and insertions/deletions (Indels). Numerous platforms can be effectively used for genotyping [67,49]. Among the several NGS methods, genotyping by sequencing (GBS) is a quick and easy method that has been applied in genome-wide association studies (GWAS) and biparental QTL mapping [62]. Over the past 20 years, molecular marker technology has demonstrated the most advancement and practicality. Researchers working with Capsicum currently have access to many marker databases based on different marker types, such as RFLPs, RAPDs, AFLPs, SCARs, SSRs, CAPS, and high-resolution melting-PCR (HRM-PCR), in addition to high-throughput genotyping systems. Using publically available genome sequences has reduced the cost of developing markers [12]. SNPs are widely distributed across the genome, and their low cost of identification makes them useful for GWAS, QTL mapping, and target region identification. It also makes high-resolution QTL mapping and marker-assisted selection (MAS) possible.

For MAS, a number of trait-linked markers have been created and are used in pepper breeding initiatives. Examples include pvr1, pvr11, pvr12, and pvr2 genes created for the capsanthin pigment found in chillies as allele-specific CAPS markers [83]. Additionally, for MAS, markers that are strongly associated with resistance to major pepper diseases, like those brought on by Phytophthora capsici, pepper mottle virus (PePMoV), tomato spotted wilt virus (TSWV), and anthracnose, have been developed [48,32,31]. Bs1, Bs2, and Bs3 resistant genes have been inserted into a number of commercial pepper cultivars. Bs5 and Bs6 have broad-spectrum resistance against Xanthomonas species that cause bacterial leaf spot thanks to marker-assisted gene pyramiding [76]. Major QTLs connected to SSR marker CAMS451 [44] for resistance to Ralstonia bacterial wilt have been mapped to chromosome 1 (from Capsicum accession LS2341) and chromosome 10 (from C. annuum BVRC1), linked to marker ID10-194305124.

Using 351 accessions from the pepper core collection as a training population, genomic selection (GS) for fruit-related variables in pepper was recently studied [30]. Effective GS was tested under a variety of circumstances, including the quantity of markers and various genomic prediction models. A recombinant inbred line (RIL) population was used to evaluate the genomic selection models, and the results showed reasonable prediction accuracies of 0.34, 0.48, 0.32, and 0.50 for fruit form, weight, length, and width, respectively. This study illustrated how GS may be used as a method to enhance fruit-related attributes. While the first work yielded moderate prediction accuracy, integration of larger-scale genomics, GWAS, and phenomics platforms is anticipated to yield even higher genetic prediction accuracy [32].

4. EGGPLANT (BRINJAL)

After potatoes and tomatoes, eggplant (*Solanum melongena* L.), sometimes referred to as brinjal or aubergine, is the third most commonly grown Solanaceous vegetable. It is a member of the Solanaceae family. China, India, and Iran are the world's top producers of eggplant, while the Mediterranean region's top producers are Egypt, Turkey, and Italy. Annually, the world produces over 58.69 million metric tons of eggplant, valued at more than US$12.45 billion [23]. Eggplant fruit is considered healthful since it is low in calories and contains a high concentration of vitamins, minerals, and bioactive components like the skin's anthocyanins and the flesh's chlorogenic acid (CGA). According to [42] and [55], the fruit's developmental stage, storage conditions, and environmental factors can all have an impact on the CGA content, which can differ amongst cultivars. After cutting, the fruit flesh turns brown, which is caused by polyphenol oxidases oxidizing CGA. While steroidal glycoalkaloids (a-solamargine and a-solasonine) and saponins are also anti-nutritional substances found in eggplant, there is no set maximum healthy dose of these compounds. These substances may be beneficial to health, as they have the ability to stop the growth of cancer cells both in vivo and in vitro [24]. Different ideas propose distinct beginnings for the eggplant. For example, eggplant comes from the Old World, while tomato and potato are native to Central and South America. While there may have been another domestication center in the Philippines, it is generally accepted that eggplant was separately domesticated from S. insanum in the Indian subcontinent and China [10]. Eggplant reached the Mediterranean Basin and subsequently the Americas by the seventh century, having first migrated eastward to Japan and then westward to Southeast Asia and Africa.

The first RFLP-based genetic map for eggplant was created using an F_2 population of 58 individuals from a cross between *Solanum melongena* and *S. linneanum* [18]. This map was later refined by adding 110 COSII markers previously mapped in tomato, allowing for the identification of QTLs related to morphological traits such as leaf lobing, leaf prickles, and prickle anthocyanin [25]. An enhanced genetic map was developed by increasing both the number of individuals (108) and markers [18].

Another genetic map was developed using an interspecific F2 population of 48 individuals from a cross between S. melongena and *S. linneanum* (also known as *S. sodomeum*), which located two QTLs for Verticillium wilt [59]. A subsequent map was constructed from 91 BC1 individuals from a cross between S. melongena and S. incanum, including 242 markers (COSII, SSRs, AFLPs, CAPS, and SNPs), covering 1,085 cM. This map helped identify six candidate genes involved in chlorogenic acid biosynthesis, five polyphenol oxidase genes, and genes affecting fruit shape (OVATE, SISUN1) and prickliness [26].

The first intraspecific genetic linkage map for eggplant was published in 2001, based on 168 F2 individuals and 181 RAPD and AFLP markers, which helped identify QTLs for fruit shape, stem, and calyx pigmentation [50]. The Rfo-sa1 locus from S. aethiopicum makes "305E40" resistant to Fusarium oxysporum. Another intraspecific map, published in 2010, used 238 molecular markers and 141 F2 individuals from a cross between "67/3" and "305E40" [1]. A significant dominant resistance gene, ERs1, was discovered in an F6 RIL population that resulted from a cross between a susceptible line ("MM738") and a Ralstonia solanacearum-resistant line ("AG91-25") [39]. In order to find one significant phylotype-specific QTL and two broad-spectrum QTLs for RS resistance, this map was later updated with additional markers [58]. Two more intraspecific maps were developed from F2 populations derived from crosses between non-parthenocarpic lines “LS1934” and “Nakate-Shinkuro” and a parthenocarpic line “AE-P03”. These maps were integrated and compared with the tomato genome using 326 common markers, leading to the identification of QTLs for parthenocarpy, including Cop3.1 and Cop8.1 on chromosomes 3 and 8, respectively [25]. Cop8.1 was further confirmed in a RIL population [45]. However, many of these genetic maps had large QTL regions, making precise introgression via marker-assisted selection challenging due to potential linkage drag.

Recently, a fine map of the semi-dominant Prickle (Pl) gene locus on chromosome 6, responsible for the absence of prickles, was developed using an F2 population from a cross between the no-prickly cultivar “Togenashi-senryo-nigo” and the prickly line “LS1934.” A 5-kb deletion within the Pl locus was identified, with primers developed for marker-assisted selection of this trait [45].

The advent of NGS technologies has enabled the creation of high-density genetic linkage maps and the identification of candidate genes. In the F2 population from the cross “305E40” x “67/3,” RAD sequencing identified 10,000 SNPs and 1,000 InDels, with over 2,000 SNPs useful for genotyping via a GoldenGate assay [3]. This led to the development of the first post-NGS genetic map for eggplant, featuring 415 SNP markers across the 12 eggplant chromosomes. This map was subsequently used to locate QTLs for traits such as anthocyanin content, fruit yield, morphological traits, and response to diseases like *Fusarium oxysporum* and *V. dahliae* [74,1].

5. CUCUMBER

Cucumber (*Cucumis sativus* L., 2n = 2x = 14), a member of the Cucurbitaceae family, is globally significant as a widely cultivated and consumed vegetable. In 2018, cucumbers were grown on 1.98 million hectares, producing 92.42 million metric tons, with China, Iran, Russia, Turkey, and the U.S. as leading producers [20]. The genus *Cucumis* consists of 50 species, including melon (*C. melo* L., 2n = 2x = 24) and *C. hystrix* (2n = 2x = 24), the latter being the closest relative to cucumber, diverging 10 to 5 million years ago [59]. *C. hystrix* is a secondary gene pool species for cucumber breeding, as it can interbreed with cucumber.The cucumber's primary gene pool includes four botanical varieties: the cultivated cucumber (*C. sativus* var. *sativus*), the wild cucumber (*C. sativus* var. *hardwickii*), the semi-wild Xishuangbanna cucumber (*C. sativus* var. *xishuangbannanesis*), and the Sikkim cucumber (*C. sativus* L. var. *sikkimensis*). The wild cucumber is the progenitor of modern cucumbers, while the Xishuangbanna variety, native to Southwest China, features traits like large fruit and orange flesh due to high β-carotene. The Sikkim cucumber, found in India and Nepal, is adapted to local conditions with characteristics such as black spines and brown, netted fruit.

India, recognized as the center of cucumber diversity, has cultivated the crop for at least 3,000 years [59]. Cucumber spread eastward to China approximately 2,000 years ago and westward to Europe between 1,500 and 700 years ago [52]. This expansion, along with natural and human selection, has resulted in a variety of ecotypes or landraces adapted to different climates, farming systems, and consumer preferences.Cucumbers from different regions display notable morphological diversity, with variations in fruit size, skin color, texture, firmness, crispness, and taste, due to selection for either fresh consumption or processing (pickling) [82]. Modern breeding has further intensified this diversity, creating specialized market classes designed for large-scale production in diverse environments [81]. However, this commercial breeding has also led to genetic erosion, narrowing the genetic base of each market type.Despite the large number of cucumber accessions stored in gene banks worldwide, molecular marker analyses suggest

Table 2. Major Genes and QTLs for Disease Resistance Traits in Cucumber

Diseases	Pathogens	Gene/QTL	Candidate Gene	Resistance Source	Chr	Position	Diagnostic Markers	References
Angular leaf spot	*Pseudomonas syringae*pv. *Lachryma*	CsGy5G003280	Magnesium dechelatase	Gy14, WI2757	5	2,149,251	SNP08	[81]
Anthracnose	*Colletotrichum lagenarium*	CsGy5G003280	Magnesium dechelatase	Gy14, WI2757	5	2,149,251	SNP08	[51]
Downy mildew	*Pseudoperonospora cubensis*	dm CsGy5G003280	Magnesium dechelatase	Gy14, WI2757	5	2,149,251	SNP08	[82]
Downy mildew	*Pseudoperonospora cubensis*	dm5.2	n.a	WI7120	5	23,380,844	CsDM4-055	[81]
Downy mildew	*Pseudoperonospora cubensis*	dm5.3	CsGy5G026540	IL52	5	30,434,472	SNP6	[76]
Downy mildew	*Pseudoperonospora cubensis*	dm4.1.1	CsGy4G017560	PI 197088	4	22,673,270	551 bp deletion	[3]
Downy mildew	*Pseudoperonospora cubensis*	dm4.1.3	CsGy4G019790	PI 197088	4	26,526,343	Retrotransposon insertion	[3]
Fusarium wilt	*Fusarium oxysporum* f. sp. *cucumerinum*	Foc	n.a	9110Gt	2	3,276,171	SSR17631	[82]
Fusarium wilt	*Fusarium oxysporum* f. sp. *cucumerinum*	fw2.1	n.a	Superina 2	n.a	n.a	n.a	[19]
Powdery mildew	*Podosphaera fusca*	pm5.3	CsGy5G026660	S1003, PI 197088	5	30,524,541	N7F-N14R	[3]
Powdery mildew	*Podosphaera fusca*	pm5.3	CsGy5G026540	IL52	5	30,434,472	SNP6	[82]
Powdery mildew	*Podosphaera fusca*	pm5.2	CsGy5G015660	PM-R	5	21,851,875	CAPS_CsGy5G015660	[82]
Scab	*Cladosporium cucumerinum*	Ccu	n.a	9110Gt	2	3,276,171	SSR17631	[12]
CMV	*Cucumber mosaic virus*	cmv6.1	n.a	02245	6	7,688,887	SSR9-56	[61]
CVYV	*Cucumber vein yellowing virus*	CsCvy-1	CsaV3_5G011200	CE0749	5	7,212,250	Not tested	[56]

that only a small fraction of the genetic diversity from the crop's center of origin is reflected in landraces or commercial cultivars. This highlights the importance of gene banks as vital reservoirs of genetic variation for the future of cucumber breeding.

The availability of draft genome sequences and cost-effective high-throughput sequencing and genotyping technologies has significantly advanced molecular mapping and quantitative trait loci (QTL) analysis in cucumber. Cucumber's small genome size, which has not undergone recent whole-genome duplication, along with its annual growth habit and short life cycle (2-3 months from seed to seed), provides a strong foundation for genetic research [80]. These factors have contributed to a notable increase in cucumber-related publications.

The most recent *Cucumber Gene Catalogue* [82] lists 199 genes or major-effect QTLs, with 70 added since the release of the first draft genome in 2009. In contrast, the 2010 gene catalog included only a few cucumber genes with known chromosomal locations, and just one known candidate gene, the femaleness (*F*) locus, which is responsible for 1-aminocyclopropane-1-carboxylate synthase involved in ethylene biosynthesis.Recent reviews, such as that by [81], have cataloged 81 major genes and QTLs that have been cloned or fine-mapped, including their chromosomal locations, allelic variants, and linked markers for marker-assisted selection (MAS) in breeding programs. Additionally, they identified 322 QTLs for 42 quantitative traits, including 109 related to pathogen resistance. This wealth of genetic knowledge is crucial for enhancing cucumber breeding strategies.

The compact genome of cucumber offers significant advantages for researchers using molecular breeding methods to develop new cultivars. One key aspect of this is mapping the gynoecious trait (the production of predominantly female flowers), which is vital in cucumber breeding. By identifying markers associated with the gynoecious locus, breeders can use marker-assisted backcross breeding to transfer this trait to desirable cucumber genotypes, thereby accelerating the breeding process.

However, cucumber has relatively limited genetic diversity and low levels of polymorphism [16]. This presents challenges but also emphasizes the importance of developing molecular markers for key horticultural traits. These markers are crucial for marker-assisted selection (MAS), particularly in breeding cucumber varieties with multiple disease resistances, as many of these resistance traits are controlled by multiple recessive QTLs [21]. MAS is especially valuable for international vegetable seed companies, which commonly employ this approach in their cucumber breeding programs to efficiently develop improved varieties with enhanced disease resistance and other beneficial traits.

6. CONCLUSIONS

Since the early 1980s, advancements in technology have significantly revolutionized vegetable crop breeding, particularly through the introduction of high-throughput sequencing and molecular marker technologies. These developments have facilitated the sequencing of numerous plant genomes, the creation of comprehensive genetic maps, and the identification of essential genes and quantitative trait loci (QTLs) linked to important characteristics such as disease resistance and yield. In crops like tomato, pepper, eggplant, and cucumber, these innovations have expedited genetic research and breeding initiatives, making marker-assisted selection (MAS) a fundamental component of contemporary breeding practices. The implementation of these technologies has resulted in notable enhancements in crop traits and continues to influence the future of vegetable crop improvement. For instance, SCAR, CAPS, and other PCR-based markers are widely utilized in both private and public tomato breeding programs for selecting major-gene disease resistance traits, including anthracnose and verticillium wilt. The marker-assisted gene pyramiding of genes has provided broad-spectrum resistance against diseases in crops. To enhance genetic diversity and mitigate the risk of resistance breakdown, it is essential to continue exploring crop germplasm for new resistance genes or alleles. By combining multiple sources of resistance to the same pathogen or genes that confer resistance to various pathogens, new cultivars can be developed through marker-assisted selection (MAS). The cost of developing markers has decreased due to the availability of public genome sequences, making it more affordable to identify SNPs across the genome. This cost-effectiveness supports their application in QTL mapping, genome-wide association studies (GWAS), and targeting specific regions, thereby enabling high-resolution mapping of QTLs and facilitating marker-assisted selection (MAS). The

advent of NGS technologies has enabled the creation of high-density genetic linkage maps and the identification of candidate genes.

7. FUTURE PROSPECTS

The advancement of genomic and genetic resources is transforming crops genetic research and breeding practices, although several challenges persist. The latest genome assembly currently covers only 60% of the crop's genome, and a more comprehensive assembly with improved coverage and annotation is needed. While there is a growing pool of genomic data, analysing this data and establishing meaningful sequence-trait associations remains a significant challenge. Although many genes and QTLs related to important horticultural traits have been identified, many have yet to be validated across different genetic backgrounds or environments. To diversify the gene pool and prevent resistance breakdown, ongoing exploration of crops germplasm for novel resistance genes or alleles is crucial. Multiple sources of resistance to the same pathogen, or genes for resistance to various pathogens, can be combined in new cultivars through marker-assisted selection (MAS). Currently, only a small number of genes and QTLs have been cloned in crops, and their functions are not well understood. Additionally, the absence of a reliable and efficient genetic transformation system hampers efforts to study gene function and perform gene editing for crops improvement.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

REFERENCES

1. Barchi L, Acquadro A, Alonso D, Aprea G, Bassolino L, Demurtas O, Ferrante P, Gramazio P, Mini P, Portis E, Scaglione D, Toppino L, Vilanova S, D´ıez MJ, Rotino GL, Lanteri S, Prohens J, Giuliano G. Single primer enrichment technology (SPET) for high-throughput genotyping in tomato and eggplant germplasm. Front. Plant Sci. 2019;10:1005.
DOI: 10.3389/fpls. 2019.01005
2. Bauchet G, Causse M. Genetic diversity in tomato (*Solanum lycopersicum*) and its wild relatives. In Genetic Diversity in Plants. C¸ali¸skan M, Ed. InTech: Rijeka. 2012;133–162.
3. Berg JA, Hermans FWK, Beenders F, Abedinpour H, Vriezen WH, Visser RGF, Bai Y, Schouten HJ. The amino acid permease (AAP) genes CsAAP2A and SlAAP5A/B are required for oomy- cete susceptibility in cucumber and tomato. Mol. Plant Pathol. 2021;22:658–672.
DOI: 10.1111/mpp.13052
4. Bernatzky R, Tanksley SD. Towards a saturated linkage map in tomato based on isozymes and random cDNA sequences. Genetics. 1986;112:887–898.
DOI: 10. 1093/genetics/112.4.887
5. Butler L. Linkage summary. Rep. Tomato Genet. Coop. 1968;18:4–6.
6. Catanzariti AM, Do HTT, Bru P, De Sain M, Thatcher LF, Rep M, Jones DA. The tomato I gene for Fusarium wilt resistance encodes an atypical leucine-rich repeat receptor-like protein whose function is nevertheless dependent on SOBIR1 and SERK3/BAK1. Plant J. 2017;89:1195–1209.
7. Catanzariti AM, Lim GT, Jones DA. The tomato I-3 gene: A novel gene for resistance to Fusarium wilt disease. New Phytol. 2015;207:106–118.
DOI: 10.1111/nph. 13348
8. Causse M, Grandillo S. Gene mapping in tomato. In The Tomato Genome; Causse M, Giovannoni J, Bouzayen M, Zouine M, Eds. Springer. 2016;23–37.
9. Cavanagh C, Morell M, Mackay I, Powell W. From mutations to MAGIC: Resources for gene discovery, validation and delivery in crop plants. Curr. Opin. Plant Biol. 2008;11:215–221.
DOI: 10.1016/j.pbi.2008.01.002
10. Cericola F, Portis E, Toppino L, Barchi L, Acciarri N, Ciriaci T, Sala T, Rotino GL, Lanteri S. The population structure and diversity of eggplant from Asia and the Mediterranean basin. Plos One. 2013;8:e73702.
DOI: 10.1371/journal.pone.0073702
11. Changkwian A, Venkatesh J, Lee JH, Han JW, Kwon JK, Siddique MI, Solomon AM, Choi GJ,

12. Kim E, Seo Y, Kim YH, Kang BC. Physical localization of the root-knot nematode (Meloidogyne incognita) resistance locus Me7 in Pepper (*Capsicum annuum*). Front. Plant Sci. 2019;10:886.
DOI: 10. 3389/fpls.2019.00886
13. Charmet G, Robert N, Perretant MR, Gay G, Sourdille P, Groos C, Bernard S, Bernard M. Marker-assisted recurrent selection for cumulative additive and interactive QTLs in recomninant inbred lines. Theor. Appl. Genet. 1999;99:143–1148.
14. Clayberg CD, Butler L, Rick CM, Robinson RW. Report of tomato genes of Rep. Tomato Genet. Coop. 1965;15:7–21.
15. Collard BCY, Mackill DJ. Marker-assisted selection: An approach for precision plant breeding in the twenty-first century. Philos. Trans. R. Soc. Lond. B Biol. Sci. 2008;363:557–572.
DOI: 10.1098/rstb.2007.2170.
16. Dhall RK, Kaur H, Manchanda P, Eshanee. Genetics and marker-assisted breeding for sex expression in cucumber. Frontiers in Genetics. 2023;14:1180083.
17. Dixon MS, Jones DA, Keddie JS, Thomas CM, Harrison K, Jones JDG. The tomato Cf-2 disease resistance locus comprises two functional genes encoding leucine-rich repeat proteins. Cell. 1996;84:451–459.
DOI: 10.1016/S0092-8674(00)81290-8
18. Doganlar S, Frary A, Daunay MC, Lester RN, Tanksley SD. A comparative genetic linkage map of eggplant (*Solanum melongena*) and its implications for genome evolution in the Solanaceae. Genetics. 2002;161:1697–1711.
DOI: 10.1093/genetics/161.4.1697
19. Dong S, Wang W, Bo K, Miao H, Song S, Wei S, Zhang SP, Gu X. Quantitative trait loci mapping and candidate gene analysis of low temperature tolerance in cucumber seedlings. Front. Plant Sci. 2019;10:1620.
DOI: 10.3389/fpls.2019.01620
20. FAOSTAT. Crops data for 2018; 2020.
Available:http://faostat3.fao.org Fazari, A., Palloix, A., Wang, L., Yan Hua, M., Sage-Palloix,
21. Feng S, Zhang J, Mu Z, Wang Y, Wen C, Wu T, Yu C, Li Z, Wang H. Recent progress on the molecular breeding of *Cucumis sativus L*. in China. Theor. Appl. Genet. 2020;133:1777–1790.
22. Foolad MR, Panthee DR. Marker-assisted selection in tomato breeding. Crit. Rev. Plant Sci. 2012;31:93–123.
23. Foolad MR, Zhang L, Subbiah P. Genetics of drought tolerance during seed germination in tomato: Inheritance and QTL mapping. Genome. 2007;46:536–545.
DOI: 10.1139/g03-035
24. Friedman M. Chemistry and anticarcinogenic mechanisms of glycoalkaloids produced by eggplants, potatoes, and tomatoes. J. Agric. Food Chem. 2015;63:3323–3337.
25. Fukuoka H, Miyatake K, Nunome T, Negoro S, Shirasawa K, Isobe S, Asamizu E, Yamaguchi H, Ohyama A. Development of gene-based markers and construction of an integrated linkage map in egg- plant by using Solanum orthologous (SOL) gene sets. Theor. Appl. Genet. 2012;125: 47–56.
26. Gramazio P, Yan H, Hasing T, Vilanova S, Prohens J, Bombarely A. Whole-genome resequencing of seven eggplant (*Solanum melongena*) and one wild relative (S. incanum) accessions provides new insights and breeding tools for eggplant enhancement. Front. Plant Sci. 2019; 10:1220.
DOI: 10.3389/fpls.2019.01220
27. Grushetskaya ZE, Lemesh VA, Poliksenova VD, Khotyleva LV. Mapping of the Cf-6 Tomato leaf mould resistance locus using SSR markers. Russ. J. Genet. 2007;43:1266–1270.
DOI: 10.1134/S1022795407110099
28. Hao N, Han DG, Huang K, Du YL, Yang JJ, Zhan J, Wen CL, Wu T. Genome-based breeding approaches in major vegetable crops. Theor. Appl. Genet. 2020;133:1739–1752.
DOI: 10.1007/s00122-019- 03477-z
29. Heffner EL, Sorrells ME, Jannink JL. Genomic selection for crop improvement. Crop Sci. 2009;49:1–12.
30. Hoang NH, Yang HB, Kang BC. Identification and inheritance of a new source of resistance against Tomato spotted wilt virus (TSWV) in Capsicum. Sci. Hortic. 2013;161:8–14.
31. Holdsworth WL, Mazourek M. Development of user-friendly markers for the pvr1 and Bs3 disease resistance genes in pepper. Mol. Breed. 2015;35:28.
32. Hong JP, Ro N, Lee HY, Kim GW, Kwon JK, Yamamoto E, Kang BC. Genomic selection for prediction of fruit-related traits in pepper (*Capsicum spp*.). Front. Plant Sci. 2020;11:1575.

DOI: 10.3389/fpls.2020. 570871
33. Ishibashi K, Masuda K, Naito S, Meshi T, Ishikawa M. An inhibitor of viral RNA replication is encoded by a plant resistance gene. Proc. Natl. Acad. Sci. U.S.A. 2007;104:13833–13838.
34. Jakhwal R, Kumar V, Kapoor N, Singh G. Role of marker-assisted technology in vegetable crop improvement. In Proceedings of the International Conference on Next-Generation Agriculture for Sustainable Environment and One Health (NASEH-2024). 2024;4:62-70.
35. Johnson EJ. The role of carotenoids in human health. Nutr. Clin. Care. 2002;5:56–65.
DOI: 10.1046/j.1523- 5408.2002.00004.x
36. Jones DA, Thomas CM, Hammond-Kosack KE, Balint-Kurti PJ, Jones JDG. Isolation of the tomato Cf-9 gene for resistance to Cladosporium fulvum by transposon tagging. Science. 1994;266: 789–793.
DOI: 10. 1126/science.7973631
37. Kang WH, Hoang NH, Yang HB, Kwon JK, Jo SH, Seo JK, Kim KH, Choi D, Kang BC. Molecular mapping and characterization of a single dominant gene controlling CMV resistance in peppers (*Capsicum annuum L.).* Theor. Appl. Genet. 2011;120:1587–1596.
DOI: 10.1007/s00122-010-1278-9
38. Kawchuk LM, Hachey J, Lynch DR, Kulcsar F, Van Rooijen G, Waterer DR, Robertson A, Kokko E, Byers R, Howard RJ, Fischer R, Prufer D. Tomato Ve disease resistance genes encode cell surface- like receptors. Proc. Natl. Acad. Sci. U.S.A. 2001;98:6511–6515.
DOI: 10.1073/pnas.091114198
39. Lebeau A, Gouy M, Daunay MC, Wicker E, Chiroleu F, Prior P, Frary A, Dintinger J. Genetic mapping of a major dominant gene for resistance to Ralstonia solanacearum in eggplant. Theor. Appl. Genet. 2013;126:143–158.
DOI: 10.1007/s00122-012-1969-5
40. Lukyanenko AN. Genetic improvement of tomato: Disease resistance in tomato. Monographs ontheoretical and applied genetics. Springer Berlin, Heidelberg, Germany. 1991;14.
41. Maxwell DP, Kwabenaosei M, Danquah A, Danquah EY, Blay E, MassoudI M. Marker Assisted Backcrossing of alcobaca gene into two elite Tomato breeding lines. Fronter in Horticulture. 2022;6(1):1-10.
42. Mennella G, Lo Scalzo R, Fibiani M, D'Alessandro A, Francese G, Toppino L, Acciarri N, De Almeida AE, Rotino GL. Chemical and bioactive quality traits during fruit ripening in eggplant (S. *melongena L*.) and allied species. J. Agric. Food Chem. 2012;60:11821–11831.
43. Merk HL, Ashrafi H, Foolad MR. Selective genotyping to identify late blight resistance genes in an accession of the tomato wild species Solanum Pimpinellifolium. Euphytica. 2012;187:63–75.
DOI: 10.1007/s10681-012-
44. Mimura Y, Kageyama T, Minamiyama Y, Hirai M. QTL analysis for resistance to Ralstonia solanacearum in Capsicum accession 'LS2341'. J. Japan. Soc. Hort. Sci. 2009;78:307–313.
DOI: 10.2503/jjshs1.78.307
45. Miyatake K, Saito T, Negoro S, Yamaguchi H, Nunome T, Ohyama A, Fukuoka H. Development of selective markers linked to a major QTL for parthenocarpy in eggplant (*Solanum melongena L*.). Theor. Appl. Genet. 2012;124:1403–1413.
46. Miyatake K, Saito T, Nunome T, Yamaguchi H, Negoro S, Ohyama A, Wu J, Katayose Y, Fukuoka H. Fine mapping of a major locus representing the lack of prickles in eggplant revealed the availability of a 0.5-kb insertion/deletion for marker-assisted selection. Breed. Sci. 2020;70:438–448.
47. Moreau P, Thoquet P, Olivier J, Laterrot H, Grimsley N. Genetic mapping of Ph-2, a single locus controlling partial resistance to Phytophthora infestans in tomato. MPMI. 1998;11:259–269.
48. Moury B, Pflieger S, Blattes A, Lefebvre V, Palloix A. A CAPS marker to assist selection of tomato spotted wilt virus (TSWV) resistance in pepper. Genome. 2000;43:137–142.
49. Nimmakayala P, Abburi VL, Saminathan T, Alaparthi SB, Almeida A, Davenport B, Nadimi M, Davidson J, Tonapi K, Yadav L, Malkaram S, Vajja G, Hankins G, Harris R, Park M, Choi D, Stommel J, Reddy UK. Genome-wide diversity and association mapping for capsaicinoids and fruit weight in *Capsicum annuum L*. Sci. Rep. 2016;6:38081.
DOI: 10.1038/ srep38081
50. Nunome T, Ishiguro K, Yoshida T, Hirai M. Mapping of fruit shape and Color

development traits in eggplant (*Solanum melongena L*.) based on RAPD and AFLP markers. Breed. Sci. 2001;51:19–26.

51. Pan YP, Liang XJ, Gao ML, Meng HW, Liu HQ, Weng Y, Cheng ZH. Round fruit shape in WI7239 cucumber is controlled by two interacting quantitative trait loci with one putatively encoding a tomato SUN homolog. Theor. Appl. Genet. 2017;130:573–586.
52. Paris HS, Daunay MC, Janick J. Occidental diffusion of cucumber (*Cucumis sativus*) 500-1300 CE: two routes to Europe. Ann. Bot. 2012;109:117–126.
53. Pei C, Wang H, Zhang J, Wang Y, Francis DM, Yang W. Fine mapping and analysis of a candidate gene in tomato accession PI128216 conferring hypersensitive resistance to bacterial spot race T3. Theor. Appl. Genet. 2012;124:533–542.
DOI: 10.1007/s00122-011-1726-1
54. Perry L, Dickau R, Zarrillo S, Holst I, Pearsall DM, Piperno DR, Berman MJ, Cooke RG, Rademake K, Ranere AJ, Raymond JS, Sandweiss DH, Scaramelli F, Tarble K, Zeidler JA. Starch fossils and the domestication and dispersal of chili peppers (*Capsicum spp. L*.) in the Americas. Science. 2007;315:986–988.
55. Plazas M, Andu´jar I, Vilanova S, Hurtado M, Gramazio P, Herraiz FJ, Prohens J. Breeding for chlorogenic acid content in eggplant: Interest and prospects. Not. Bot. Hort. Agrobot. Cluj. 2013;41:26–35.
56. Pujol M, Alexiou KG, Fontaine AS, Mayor P, Miras M, Jahrmann T, Garcia-Mas J, Aranda MA. Mapping cucumber vein yellowing virus resistance in cucumber (*Cucumis sativus L.)* by using BSA seq analysis. Front. Plant Sci. 2019;10:1583.
57. Robbins MD, Masud MAT, Panthee DR, Gardner RG, Francis D, Stevens MA. Markerassisted selection for coupling phase resistance to tomato spotted wilt virus and Phytophthora infestans (late blight) in tomato. Hort Science. 2010;45:1424–1428.
58. Salgon S, Jourda C, Sauvage C, Daunay MC, Reynaud B, Wicker E, Dintinger J. Eggplant resistance to the Ralstonia solanacearum species complex involves both broad-spectrum and strain-specific quantitative trait loci. Front. Plant Sci. 2017;8:828.
DOI: 10.3389/fpls.2017.00828
59. Sebastian P, Schaefer H, Telford IRH, Renner SS. Cucumber (*Cucumis sativus*) and melon (C. melo) have numerous wild relatives in Asia and Australia, and the sister species of melon is from Australia. Proc. Natl. Acad. Sci. U.S.A. 2010;107:14269–14273.
DOI: 10.1073/ pnas.1005338107
60. Sharlach M, Dahlbeck D, Liu L, Chiu J, Jimenez- Gomez JM, Kimura S, Koenig D, Maloof JN, Sinha N, Minsavage GV, Jones JB, Stall RE, Staskawicz BJ. Fine genetic mapping of RXopJ4, a bacterial spot disease resistance locus from *Solanum pennellii* LA716. Theor. Appl. Genet. 2013;126:601–609.
61. Shi L, Yang YH, Xie Q, Miao H, Bo KL, Song ZC, Wang Y, Xie BY, Zhang SP, Gu XF. Inheritance and QTL mapping of cucumber mosaic virus resistance in cucumber (*Cucumis sativus L*.). Plos One. 2018;13:e0200571.
62. Siddique MI, Lee HY, Ro NY, Han K, Venkatesh J, Solomon AM, Patil AS, Changkwian A, Kwon JK, Kang BC. Identifying candidate genes for Phytophthora capsici resistance in pepper (*Capsicum annuum*) via genotyping-by-sequencing-based QTL map- ping and genome-wide association study. Sci. Rep. 2019;9:9962.
63. Simko I. Analysis of bibliometric indicators to deter- mine citation bias. Palgrave Commun. 2015;1:15011.
64. Simons G, Groenendijk J, Wijbrandi J, Reijans M, Groenen J, Diergaarde P, Van Der Lee T, Bleeker M, Onstenk J, De Both M, Haring M, Mes J, Cornelissen B, Zabeau M, Vos P. Dissection of the fusarium I2 gene cluster in tomato reveals six homologs and one active gene copy. Plant Cell. 1998;10:1055–1068.
65. Singh RJ. Genetic resources, chromosome engineering, and crop improvement. Volume 3 – Vegetable Crops. CRC Press, Boca Raton, FL, USA; 2007.
66. Singh RJ, Lebeda A. Landmark research in vegetable crops. In Genetic Resources, Chromosome Engineering, and Crop Improvement. Volume 3 – Vegetable Crops. Singh, R. J., Ed. CRC Press: Boca Raton, FL. 2007;1–15.
67. Cheng S, Muchugi A, Jamnadass R, Shapiro HY, Van Deynze A, Yang H, Wang J, Xu X, Odeny DA, Liu X. Draft genome sequence of Solanum aethiopicum provides insights into disease resistance,

drought tolerance, and the evolution of the genome. Giga Science. 2019;8:giz115.
68. Tanksley SD. Molecular markers in plant breeding. Plant Mol. Biol. Rep. 1983;1:3–8.
DOI: 10.1007/BF02680255
69. Tanksley SD. Mapping polygenes. Annu. Rev. Genet. 1993;27:205–233.
70. Tanksley SD. Linkage relationships and chromosomal locations of enzyme-coding genes in pepper, Capsicum annuum. Chromosoma. 1984;89:352–360.
71. Thomas CM, Jones DA, Parniske M, Harrison K, Kurti PJB, Hatzixanthis K, Jones JDG. Characterization of the tomato Cf-4 gene for resistance to Cladosporium fulvumIdentifies sequences that determine recognitional specificity in Cf-4 and Cf-9. Plant Cell. 1997;9:2209–2224.
72. Thornsberry JM, Goodman MM, Doebley J, Kresovich S, Nielsen D, Buckler ES. Dwarf8 polymorphisms associate with variation in flowering time. Nat. Genet. 2001;28:286–289.
73. Tian F, Bradbury PJ, Brown PJ, Hung H, Sun Q, Flint-Garcia S, Rocheford TR, McMullen MD, Holland JB, Buckler ES. Genome-wide association study of leaf architecture in the maize nested association mapping population. Nat. Genet. 2011;43:159–162.
74. Toppino L, Barchi L, Lo Scalzo R, Palazzolo E, Francese G, Fibiani M, D'Alessandro A, Papa V, Laudicina VA, Sabatino L, Pulcini L, Sala T, Acciarri N, Portis E, Lanteri S, Mennella G, Rotino GL. Mapping quantitative trait loci affecting biochemical and morphological fruit properties in eggplant (*Solanum melongena L.*). Front. Plant Sci. 2016;7:256.
DOI: 10.3389/fpls.2016.00256
75. USDA. National Nutrient Database for Standard Reference; 2012.
Available:http://ndb.nal.usda.gov
76. Vallejos CE, Jones V, Stall RE, Jones JB, Minsavage GV, Schultz DC, Rodrigues R, Olsen LE, Mazourek M. Characterization of two recessive genes controlling resistance to all races of bacterial spot in peppers. Theor. Appl. Genet. 2010;121: 37–46.
77. Valpuesta V. Fruit and Vegetable Biotechnology. Woodhead Publishing, UK; 2002.
78. Vinson J, Hao Y, Su X, Zubik L. Phenol antioxidant quantity and quality in foods: Vegetables. J. Agric. Food Chem. 1998;46:3630–3634.
79. Wan P, Kolur SM, Goudara R. Marker assisted selection approach for improvement of quality traits in tomato. Just Agriculture Journal. 2023;3(9):152-157.
80. Weng Y. The cucumber genome. In Genetics and Genomics of Cucurbitaceae, Plant Genetics and Genomics: Crops and Models; Grumet R, Garcia-Mas J. Eds. Springer. 2016;183–198.
81. Weng Y. Cucumis sativus: Chromosome evolution, domestication, and genetic diversity: Implications for cucumber breeding. Plant Breed. Rev. 2021;49:77–111.
82. Weng Y, Wehner TC. Cucumber gene catalogue. Cucurbit Genet. Coop. 2017;34–35.
Available:https://www.ars.usda.gov/southeast-area/charleston-sc/vegetable-research/docs/cgc
83. Yeam I, Kang BC, Lindeman W, Frantz JD, Faber N, Jahn MM. Allele-specific CAPS markers based on point mutations in resistance alleles at the pvr1 locus encoding eIF4E in Capsicum. Theor. Appl. Genet. 2005;112:178–186.

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