

## Review Article

### Marker assisted selection (MAS) and its improvement in vegetable crop

#### 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* spp. against chilli leaf spot thanks to marker-assisted gene pyramiding. Major QTLs associated to SSR marker CAMS451 on chromosome 1 (from *Capsicum* accession LS2341) and marker ID10-194305124 on chromosome 10 (from *C. annum* 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.

#### 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 (Singh and Lebeda, 2007). 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 (FAOSTAT, 2020). 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" (Singh, 2007). Cutting-edge breeding methods including Marker-Assisted Recurrent Selection (MARS) (Charmetet et al., 1999), Marker-Assisted Backcrossing (MABC) (Collard and Mackill, 2008), and Marker-Assisted Selection (MAS) (Collard and Mackill, 2008), based on the complexity of the genetics and breeding of the species, and Sequencing Selection (GS) (Heffner et al., 2009) are in varying phases of development for diverse vegetable crops. Linkage mapping (Tanksley, 1993); genome-wide association analysis

(GWAS) (Thornsberry et al., 2001); embedded association mapping (NAM) (Tian et al., 2011); and multi-parent advanced era inter-cross (MAGIC) populations (Cavanagh et al., 2008) 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 (Simko, 2015). 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 (Wani et al., 2023).

## **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 (Foolad and Panthee, 2012). 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 (Valpuesta, 2002). 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 (Vinson et al., 1998), even though they are often not thought to have a high nutritional value. This is mostly due to the amount of it is consumed (USDA, 2012). The main substance that gives the red color of the fruit is lycopene, which is mainly found in tomatoes. Important antioxidants lycopene and  $\beta$ -carotene, which are also present in tomato fruit, have been linked to a decreased risk of developing certain tumors when consumed (Johnson, 2002).

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 tomato 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 (Bauchet and Causse, 2012; Foolad and Panthee, 2012). 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 (F<sub>2</sub> and BC<sub>1</sub>), 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 (Foolad et al., 2007). Butler (1968) 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 (Tanksley, 1993).

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 (Lukyanenko, 1991). 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:

“Fusariumoxysporum-caused Fusarium wilt, Verticillium wilt, Cladosporiumfulvum, 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)” [84]. According to Foolad and Panthee (2012) and Causse and Grandillo (2016), 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.

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 (Wani et al., 2023). Tomato shelf life is reportedly increased by an SNP marker (Maxwell et al., 2022).

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 Jakhwa *et al.*, 2024).

Despite being one of the first crop plants to be bred using genetic markers and maps (Tanksley, 1983), 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 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 (Foolad and Panthee, 2012). 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.

**Table 1: Major tomato genes and QTLs used in marker-assisted breeding for resistance against fungal, bacterial, viral, and nematode diseases [84]:**

Disease (pathogen)	Gene/QTL	Chr.	MAS assay	Citation
Fusarium wilt (Fusariumoxysporum)	I	11	CAPS	Catanzariti <i>et al.</i> , 2017
Fusarium wilt (Fusariumoxysporum)	I-2	11	SCAR	Simons <i>et al.</i> , 1998
Fusarium wilt (Fusariumoxysporum)	I-3	7	CAPS/SCAR	Catanzariti <i>et al.</i> , 2015
Verticillium wilt (Verticilliumalbo-atrum)	Ve1	9	ARMS-PCR	Kawchuket <i>et al.</i> , 2001
Verticillium wilt (Verticilliumalbo-atrum)	Ve2	9	ARMS-PCR	Kawchuket <i>et al.</i> , 2001
Leaf mold (Cladosporiumfulvum)	Cf-2	6	SSR	Dixon <i>et al.</i> , 1996; Grushetskaya <i>et al.</i> , 2007
Leaf mold (Cladosporiumfulvum)	Cf-4	1	SNP/InDel	Thomas <i>et al.</i> , 1997
Leaf mold (Cladosporiumfulvum)	Cf-5	6	SSR	Dixon <i>et al.</i> , 1996; Grushetskaya <i>et al.</i> , 2007
Leaf mold (Cladosporiumfulvum)	Cf-9	1	SNP/InDel	Jones <i>et al.</i> , 1994
Late blight (Phytophthorainfestans)	Ph-1	7	Unknown	Clayberg <i>et al.</i> , 1965
Late blight (Phytophthorainfestans)	Ph-2	10	CAPS	Moreau <i>et al.</i> , 1998

Late blight (Phytophthora infestans)	Ph-3	9	CAPS	Robbins <i>et al.</i> , 2010
Late blight (Phytophthora infestans)	Ph-5	10	Unknown	Merk <i>et al.</i> , 2012
Bacterial spot (Xanthomonas Race T1-T4)	Rx4	11	InDel	Pei <i>et al.</i> , 2012
Bacterial spot (Xanthomonas Race T1-T4)	RxopJ4	6	CAPS	Sharlachet <i>et al.</i> , 2013
Tomato mosaic virus (ToMV)	Tm-1	2	SCAR	Ishibashi <i>et al.</i> , 2007
Tomato spotted wilt virus (TSWV)	Sw-5	9	SCAR/CAPS/RAPD	Foolad and Panthee, 2012;
Tomato shelf life	Sh4	6	SNP	Maxwell <i>et al.</i> , 2022

### 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 (Perry *et al.*, 2007)—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 (FAOSTAT, 2022). 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 (Cheng *et al.*, 2019; Nimmakayala *et al.*, 2016). 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 (Siddique et al., 2019). 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 (Kim et al., 2019). 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 (Yeamet et al., 2005). 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 (Moury et al., 2000; Hoang et al., 2013; Holdsworth and Mazourek, 2015). *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. (2010) Vallejos *et al.* Major QTLs connected to SSR marker CAMS451 (Mimura et al., 2009) 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 (Hong et al., 2020). 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 (Hong et al., 2020).

### **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 (FAOSTAT, 2023). 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 Mennella et al. (2012) and Plazas et al. (2013), 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 (*α*-solanargine and *α*-solasoinine) 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 (Friedman, 2015). 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 (Cericola et al., 2013). 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<sub>2</sub> population of 58 individuals from a cross between *Solanum melongena* and *S. linneanum* (Doganlaret *et al.*, 2002). “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” (Frary *et al.*, 2014). “An enhanced genetic map was developed by increasing both the number of individuals (108) and markers” (Doganlaret *et al.*, 2002).

“Another genetic map was developed using an interspecific F<sub>2</sub> population of 48 individuals from a cross between *S. melongena* and *S. linneanum* (also known as *S. sodomium*), which located two QTLs for Verticillium wilt” (Sunseriet *et al.*, 2003). “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” (Gramazio *et al.*, 2019).

“The first intraspecific genetic linkage map for eggplant was published in 2001, based on 168 F<sub>2</sub> individuals and 181 RAPD and AFLP markers, which helped identify QTLs for fruit shape, stem, and calyx pigmentation” (Nunome *et al.*, 2001). “The Rfo-sal locus from *S. aethiopicum* makes “305E40” resistant to *Fusariumoxysporum*. Another intraspecific map, published in 2010, used 238 molecular markers and 141 F<sub>2</sub> individuals from a cross between 67/3 and 305E40” (Barchi *et al.*, 2010). “A significant dominant resistance gene, ERs1, was discovered in an F<sub>6</sub> RIL population that resulted from a cross between a susceptible line (“MM738”) and a *Ralstoniasolanacearum*-resistant line (“AG91-25”)” (Lebeauet *et al.*, 2013). “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” (Salgonet *et al.*, 2017). “Two more intraspecific maps were developed from F<sub>2</sub> 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” (Fukuoka *et al.*, 2012). “Cop8.1 was further confirmed in a RIL population” (Miyatake *et al.*, 2012). 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 (PI) gene locus on chromosome 6, responsible for the absence of prickles, was developed using an F<sub>2</sub> population from a cross between the non-prickly cultivar “Togenashi-senryo-nigo” and the prickly line “LS1934.” A 5-kb deletion within the PI locus was identified, with primers developed for marker-assisted selection of this trait” (Miyatake *et al.*, 2020).

“The advent of NGS technologies has enabled the creation of high-density genetic linkage maps and the identification of candidate genes. In the F<sub>2</sub> 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” (Barchi *et al.*, 2011). “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 *Fusariumoxysporum* and *V. dahlia*” (Toppino *et al.*, 2016; Barchi *et al.*, 2019).

## 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 (FAOSTAT, 2023). 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 (Sebastian et al., 2010). *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. *xishuangbannanensis*), 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  $\beta$ -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 (Sebastian et al., 2010). Cucumber spread eastward to China approximately 2,000 years ago and westward to Europe between 1,500 and 700 years ago (Paris et al., 2012). 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) (Wehner, 1989). Modern breeding has further intensified this diversity, creating specialized market classes designed for large-scale production in diverse environments (Weng, 2021). 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 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 (Weng, 2016). These factors have contributed to a notable increase in cucumber-related publications.

The most recent *Cucumber Gene Catalogue* (Weng and Wehner, 2017) 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 Wang et al. (2019a), 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 gynoeious trait (the production of predominantly female flowers), which is vital in cucumber breeding. By identifying markers associated with the gynoeious 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 (Dhal et al., 2023). 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 (Feng et al., 2020). 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.

**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	<i>Pseudomonas syringae</i> pv. <i>Lachryma</i>	CsGy5G003280	Magnesium dechelataase	Gy14, WI2757	5	2,149,251	SNP08	Weng et al., 2020
Anthrax nose	<i>Colletotrichum lag</i> <i>enarium</i>	CsGy5G003280	Magnesium dechelataase	Gy14, WI2757	5	2,149,251	SNP08	Pan et al., 2017
Downy mildew	<i>Pseudoperonospora racubensis</i>	dm CsGy5G003280	Magnesium dechelataase	Gy14, WI2757	5	2,149,251	SNP08	Weng et al., 2020
Downy mildew	<i>Pseudoperonospora racubensis</i>	dm5.2	n.a	WI7120	5	23,380,844	CsDM4-055	Wang et al., 2018c
Downy mildew	<i>Pseudoperonospora racubensis</i>	dm5.3	CsGy5G026540	IL52	5	30,434,472	SNP6	Zhang et al., 2020
Downy mildew	<i>Pseudoperonospora racubensis</i>	dm4.1.1	CsGy4G017560	PI197088	4	22,673,270	551 bp deletion	Berg et al., 2021
Downy mildew	<i>Pseudoperonospora racubensis</i>	dm4.1.3	CsGy4G019790	PI197088	4	26,526,343	Retrotransposon insertion	Berg et al., 2021
Fusarium wilt	<i>Fusarium oxysporum</i> f. sp. <i>cucumerinum</i>	Foc	n.a	9110Gt	2	3,276,171	SSR17631	Zhang et al., 2020

Fusarium wilt	<i>Fusarium oxysporum</i> f. sp. <i>cucumerinum</i>	fw2.1	n.a	Superina 2	n.a	n.a	n.a	Dong <i>et al.</i> , 2019
Powdery mildew	<i>Podosphaera fuscata</i>	pm5.3	CsGy5G026660	S1003, PI 197088	5	30,524,541	N7F-N14R	Berg <i>et al.</i> , 2021
Powdery mildew	<i>Podosphaera fuscata</i>	pm5.3	CsGy5G026540	IL52	5	30,434,472	SNP6	Zhang <i>et al.</i> , 2020
Powdery mildew	<i>Podosphaera fuscata</i>	pm5.2	CsGy5G015660	PM-R	5	21,851,875	CAPS_CsGy5G015660	Zhang <i>et al.</i> , 2020
Scab	<i>Cladosporium cucumerinum</i>	ccu	n.a	9110Gt	2	3,276,171	SSR17631	Kang <i>et al.</i> , 2011
CMV	<i>Cucumber mosaic virus</i>	cmv6.1	n.a	02245	6	7,688,887	SSR9-56	Shi <i>et al.</i> , 2018
CVYV	<i>Cucumber vein yellowing virus</i>	CsCvy-1	CsaV3_5G011200	CE0749	5	7,212,250	Not tested	Pujol <i>et al.</i> , 2019

## **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.

## **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.

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- 2.
- 3.

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