Review Article

Marker assisted selection (MAS) and it's improvement in vegetable crop

ABSTRACT

Technological advancements since the early 1980s have transformed vegetable crop breeding, particularly with the advent of high-throughput sequencing and molecular marker technologies. These innovations have enabled the sequencing of numerous plant genomes, development of dense genetic maps, and identification of key genes and QTLs associated with traits like disease resistance and yield. In vegetables such as tomato, pepper, eggplant, and cucumber, these tools have accelerated genetic research and breeding programs, making marker-assisted selection (MAS) and genomic selection (GS) integral to modern breeding. The application of these technologies has led to significant improvements in crop traits and continues to shape the future of vegetable crop development.

Keywords: *Marker Assisted Selection, hybrids, genomicSelection, QTLs.*

INTRODUCTION

Vegetables are a diverse group of crop species whose stems, leaves, fruits, flowers, roots, or seeds are vital components of the human diet worldwide. They can be consumed raw or cooked and are typically low in carbohydrates and fats while being rich in vitamins, minerals, and dietary fibre (Singh and Lebeda, 2007). The exact definition of a "vegetable" can vary, as it depends on different classifications, such as botanical and culinary perspectives. Asia is the largest producer of many vegetables, including spinach, eggplants, cucumbers, lettuce, peppers, and tomatoes. In contrast, Europe leads in the production of chicory (FAOSTAT, 2020). When considering per capita production, Asia remains the main producer of chili peppers, spinach, eggplants, and cucumbers. North America leads in producing tomatoes, lettuce, and sweet peppers, while Europe is the largest producer of chicory. Besides these crops, many other vegetables are highly popular in different regions of the world. However, this review focuses on tomato, pepper, eggplant and cucumber.

Traditional breeding approaches are generally slow, labour-intensive, and costly. However, recent progress in genetics and genomics has led to the development of novel tools, techniques, and approaches that can enhance plant breeding programs. For many crop species, including several vegetables, molecular markers, genetic linkage maps, marker assays, and whole-genome sequences have been developed and published (Singh, 2007). Advanced breeding techniques such as Marker-Assisted Selection (MAS) (Collard and Mackill, 2008), Marker-Assisted Backcrossing (MABC) (Collard and Mackill, 2008), Marker-Assisted Recurrent Selection (MARS) (Charmet*et al.*, 1999), and Genomic Selection (GS) (Heffner *et al.*, 2009) are in various stages of development for

different vegetable crops, depending on available resources and the complexity of the species' genetics and breeding.

Several approaches for detecting and mapping genes and Quantitative Trait Loci (QTLs) have been developed, including Linkage Mapping (Tanksley, 1993); Genome-Wide Association Mapping (GWAS) (Thornsberry *et al.*, 2001); Nested Association Mapping (NAM) (Tian *et al.*, 2011); Multi-Parent Advanced Generation Inter-Cross (MAGIC) Populations (Cavanagh *et al.*, 2008).

Although these novel genetic and genomic tools and techniques were initially applied primarily to major cereal crops such as maize, rice, and wheat (Simko, 2015), they are gradually being adopted in vegetable genetics and breeding. The current review focuses on vegetable crops to provide up-to-date information on available genomic resources, the use of genetic and genomic tools and techniques in breeding programs, and the major anticipated areas of future research for each crop.

Tomato

The cultivated tomato (*Solanum lycopersicum* L.), a diploid species (2n = 2x = 24 chromosomes), is one of the world's most important vegetable crops by economic standards and consumption values. In 2018, tomato production worldwide reached nearly 182 million metric tons, with a gross production value of US$ 47.7 billion, making it second only to potato (*S. tuberosum* L.) among all vegetable crops (FAOSTAT, 2020). There are more varieties of tomato sold worldwide than any other vegetable crop (Foolad and Panthee, 2012). Although a tropical species, tomato is grown in almost every corner of the world. The top tomato-producing countries include: China (33.8%); India (10.6%); United States (6.9%); Turkey (3.6%); Egypt (3.6%). Tomato is also an essential dietary component, widely consumed in various forms such as fresh fruit, sauces, soups, and processed products like ketchup and canned tomatoes.

The tomato is an essential dietary component in many countries, including the United States (Valpuesta, 2002). Although tomato fruit is generally not considered high in nutritional value, it ranks first among all fruits and vegetables as a major dietary source of vitamins A and C, minerals (Rick, 1980), and phenolic antioxidants (Vinson *et al.*, 1998) in the U.S. This is mainly due to its large consumption volume (USDA, 2012). Lycopene, a key carotenoid predominantly found in tomatoes, provides the red colour in the fruit. Both lycopene and β-carotene (also found in tomato fruit) are important antioxidants, and their consumption has been correlated with lower risks of certain cancers (Johnson, 2002). The breeding history of tomatoes dates back to the 1930s when efforts to improve the overall horticultural characteristics of the tomato began. Substantial diversity

has been bred into tomatoes in terms of plant type, size and growth habit, and fruit shape, size, colour, and taste. The majority of tomato cultivars on the market are currently separated into two types: fresh market (FM) and processing (PROC) tomatoes. Fresh market tomatoes, including large beefsteak/slicer, plum/roma, campari, cherry, and grape types, are mainly sold and consumed fresh. Processing tomatoes are usually peeled, cubed, juiced, or sauced to make canned products. Breeding objectives for FM and PROC tomatoes are vastly different, though they share the common goal of achieving higher yield per unit area for all tomato types. Other major breeding priorities common to both types include:

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

These breeding goals aim to improve both the quality and productivity of tomato crops, ensuring their continued importance in the global food supply.To compensate for the limited genetic diversity within cultivated tomato species, breeding programs have utilized wild tomato accessions as germplasm resources for crop improvement. These wild accessions have been essential for genetic mapping and the identification and introgression of desirable genes and QTLs. These genetic factors include disease and insect resistance, abiotic stress tolerance, and improved fruit quality and nutritional values (Bauchet and Causse, 2012; Foolad and Panthee, 2012). To identify and map new genes and QTLs, breeders have primarily used interspecific crosses between elite tomato breeding lines and accessions within related wild species. These crosses have led to the development of mapping populations, including early filial and backcross populations (e.g., F2 and BC1), backcross inbred lines (BILs), recombinant inbred lines (RILs), and near-isogenic lines (NILs). These populations are used to construct genetic maps (Foolad*et al.*, 2007). The first genetic linkage map of tomato was constructed in 1968 with 153 morphological and physiological markers, revealing all 12 tomato linkage groups (LGs) (Butler, 1968). The first molecular linkage map of tomato was published in 1986, using a combination of 18 isozymes and 94 RFLP markers (Bernatzky and Tanksley, 1986). In 1992, the first "high-density" genetic map of tomato was published, comprising 1,030 molecular markers, mostly RFLPs (Tanksley 1993).

Molecular markers and genetic maps of tomatoes have been extensively used for the identification, mapping, and characterization of genes and QTLs associated with many agriculturally important traits. These traits include resistance and tolerance to biotic and abiotic stresses, flower- and fruit-related characteristics, plant type, maturity, and yield. The cultivated

tomato is vulnerable to over 200 fungal, bacterial, viral, and nematode diseases (Lukyanenko, 1991). As a result, host plant resistance has been a primary focus of many tomatoes breeding programs globally. These efforts have led to the identification, genetic mapping, and utilization of resistance genes or QTLs for numerous diseases, including:

Fusarium wilt (caused by Fusarium oxysporum); Verticillium wilt (Verticillium albo-atrum); Tomato leaf mold (*Cladosporium fulvum*); Late blight (*Phytophthora infestans*); Bacterial speck (*Pseudomonas syringae*); Bacterial spot (*Xanthomonas race T1-T4*); Tomato mosaic virus (ToMV); Tomato yellow leaf curling virus (TYLCV); Tomato spotted wilt virus (TSWV); Root-knot nematode (RKN; *Meloidogyne* spp.) To date, more than 20 resistance genes for these fungal, bacterial, viral, and nematode diseases have been mapped and/or cloned in tomato (Table 1) (Foolad and Panthee, 2012; Causse and Grandillo, 2016). These achievements have significantly advanced the development of disease-resistant tomato varieties, contributing to more sustainable tomato production systems. In a previous review, most of the genes and QTLs identified and genetically mapped on tomato chromosomes for various traits up until 2012 were tabulated (Foolad and Panthee, 2012). Since then, additional molecular markers associated with new genes or QTLs for many traits in tomatoes have been reported. This ongoing research continues to enhance our understanding of the genetic basis of important traits in tomatoes, facilitating the development of improved tomato varieties through more precise and efficient breeding strategies.

Although tomato was among the first crop plants for which genetic markers and maps were utilized for breeding purposes (Tanksley, 1983), until the early 1980s, almost all tomato breeding programs relied mainly on phenotypic selection (PS). With the discovery of high-throughput and more breeder-friendly genetic markers, including PCR-based markers and SNPs, there has been increased interest in using markers to facilitate tomato crop improvement. A review of the literature indicates that although markers have been identified for most important disease resistance traits in tomato, not all reported markers have been verified or are readily applicable in tomato breeding. However, marker-assisted selection (MAS) is frequently employed in most tomato breeding programs for gene incorporation and stacking, especially when breeding cultivars for multiple disease resistance traits. For example, SCAR, CAPS, and other PCR-based markers are commonly used in most private and public tomato breeding programs when selecting for many of the major-gene disease resistance traits. Specific marker information has been summarized elsewhere (FooladandPanthee, 2012). Genetic markers are also routinely used for various other purposes, including testing hybrid purity and screening breeding populations for plant types and fruit quality characteristics. However, markers are not typically employed when breeding for complex traits,

such as polygenic disease-resistant traits (e.g., bacterial canker and early blight), abiotic stress tolerance, yield, and many fruit quality characteristics.

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	Catanzariti *et al.*, 2017
Fusarium wilt (Fusarium oxysporum)	I-2	11	SCAR	Simons *et al.*, 1998
Fusarium wilt (Fusarium oxysporum)	I-3	7	CAPS/SCAR	Catanzariti *et al.*, 2015
Verticillium wilt (Verticillium albo-atrum)	Ve1	9	ARMS-PCR	Kawchuk*et al.*, 2001
Verticillium wilt (Verticillium albo-atrum)	Ve2	9	ARMS-PCR	Kawchuk*et al.*, 2001
Leaf mold (Cladosporium fulvum)	Cf-2	6	SSR	Dixon *et al.*, 1996; Grushetskaya*et al.*, 2007
Leaf mold (Cladosporium fulvum)	Cf-4	1	SNP/InDel	Thomas *et al.*, 1997
Leaf mold (Cladosporium fulvum)	Cf-5	6	SSR	Dixon *et al.*, 1996; Grushetskaya*et al.*, 2007
Leaf mold (Cladosporium fulvum)	Cf-9	1	SNP/InDel	Jones *et al.*, 1994
Late blight (Phytophthora infestans)	Ph-1	7	Unknown	Clayberg *et al.*, 1965
Late blight (Phytophthora infestans)	Ph-2	10	CAPS	Moreau *et al.*, 1998
Late blight (Phytophthora infestans)	Ph-3	9	CAPS	Robbins *et al.*, 2010
Late blight (Phytophthora infestans)	Ph-5	10	Unknown	Merk *et al.*, 2012
Bacterial spot (Xanthomonas Race T1-T4)	Rx4	11	InDel	Pei *et al.*, 2012
Bacterial spot (Xanthomonas Race T1-T4)	RxopJ4	6	CAPS	Sharlach*et al.*, 2013
Tomato mosaic virus (ToMV)	Tm-1	2	SCAR	Ishibashi *et al.*, 2007
Tomato spotted wilt virus (TSWV)	Sw-5	9	SCAR/CAPS/RAPD	Foolad and Panthee, 2012;

Pepper

Pepper, belonging to the genus Capsicum of the family Solanaceae, is an important vegetable and spice crop worldwide. Believed to have originated in Bolivia (Perry *et al.*, 2007), the genus Capsicum comprises 35 species, including the five economically important cultivated species *Capsicum annuum L., C. frutescens L., C. baccatum L., C. chinense Jacq., and C. pubescens* Ruiz & Pav. Capsicum species are all diploids, generally having 24 chromosomes (2n = 2x = 24), whereas many wild species carry 26 chromosomes. Pepper exhibits diverse variation in morphological and yield-related characteristics, including plant architecture, flowering time, fruit

size, shape, color, phytochemical contents, and resistance/tolerance to biotic and abiotic stresses. Pepper can grow in almost all soil types, but well-drained, moisture-retaining loamy soil is most desirable. The optimum temperature for pepper seed germination is 25—30°C, whereas that for plant growth and fruit development ranges from 18 to 30°C. In 2018, worldwide pepper production was 59.5 million metric tons on a total area of 4.6 million hectares (FAOSTAT, 2020). Apart from being used as a vegetable, pepper has a wide range of uses in the food, pharmaceutical, and cosmetics industries. 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.

Over the past two decades, pepper breeding has primarily focused on the genetic improvement of both hot and sweet peppers by incorporating pest and disease resistance. Recent advancements in next-generation sequencing (NGS) and high-throughput genotyping approaches have significantly accelerated the discovery of single nucleotide polymorphism (SNP) markers in Capsicum spp. High-density genetic linkage maps for various populations, mostly F2 or doubled haploid (DH), have been published, and sequence variations, including SNPs and insertions/deletions (Indels), can be readily identified using high-throughput sequencing. Genotyping can be efficiently performed using several platforms (Cheng *et al.*, 2019; Nimmakayala*et al.*, 2016). Among many NGS technologies, genotyping by sequencing (GBS) is a simple, rapid approach that has been used in biparental QTL mapping and genome-wide association studies (GWAS) (Siddique *et al.*, 2019). Molecular marker technology has shown the most significant development and utility over the last two decades. Multiple marker datasets based on various marker types, including RFLPs, RAPDs, AFLPs, SCARs, SSRs, CAPS, and high-resolution melting-PCR (HRM-PCR), are now available for Capsicum researchers, along with high-throughput genotyping platforms. The development of markers has become less expensive with the use of publicly available genome sequences (Kim *et*

al., 2019). The low cost of identifying SNPs distributed throughout the genome allows their use for QTL mapping, GWAS, or pinpointing a target region, facilitating high-resolution mapping of QTLs and conducting marker-assisted selection (MAS).

Several trait-linked markers have been developed for MAS and are utilized in pepper breeding programs. Examples include allele-specific CAPS markers for pvr1, pvr11, pvr12, and pvr2 genes (Yeam*et al.*, 2005). Markers closely linked to resistance to important diseases in pepper, such as those caused by Phytophthora capsici, pepper mottle virus (PePMoV), tomato spotted wilt virus (TSWV), and anthracnose, have also been developed for MAS (Moury *et al.*, 2000; Hoang *et al.*, 2013; Holdsworth and Mazourek, 2015). Resistance genes Bs1, Bs2, and Bs3 have been introgressed into several commercial pepper cultivars. Marker-assisted gene pyramiding of Bs5 and Bs6 has conferred broad-spectrum resistance against Xanthomonas spp. (Vallejos *et al.*, 2010). Major QTLs for resistance to Ralstonia bacterial wilt have been mapped to chromosome 1 (from Capsicum accession LS2341), linked to SSR marker CAMS451 (Mimura *et al.*, 2009), and chromosome 10 (from C. annuum BVRC1), linked to marker ID10-194305124.

Recently, genomic selection (GS) was investigated for fruit-related traits in pepper using 351 accessions from the pepper core collection as a training population (Hong *et al.*, 2020). Various conditions were tested for effective GS, including different genomic prediction models and the number of markers. Genomic selection models were tested using a recombinant inbred line (RIL) population and produced moderate prediction accuracies of 0.34, 0.48, 0.32, and 0.50 for fruit shape, weight, length, and width, respectively. This study demonstrated the potential use of GS as a tool for improving fruit-related characteristics. Although moderate prediction accuracies were obtained in the initial study, further improvements in the accuracy of genomic prediction are expected by integrating larger-scale genomics, GWAS, and phenomics platforms (Hong *et al.*, 2020).

Eggplant (Brinjal)

Eggplant (*Solanum melongena* L.), also known as brinjal or aubergine, is a member of the Solanaceae family and ranks as the third most widely cultivated Solanaceous vegetable, following potato and tomato. Leading producers of eggplant include China, India, and Iran, with Egypt, Turkey, and Italy being prominent producers in the Mediterranean region. The global production of eggplant reaches approximately 54 million metric tons annually, with a market value exceeding US$10 billion (FAOSTAT, 2020). Eggplant fruit is low in calories and is valued for its health benefits due to its rich content of vitamins, minerals, and bioactive compounds, such as anthocyanins in the skin and chlorogenic acid (CGA) in the flesh. The CGA content can vary among cultivars and is influenced by factors like the fruit's developmental stage, storage conditions, and environmental factors (Mennella *et al.*, 2012; Plazas *et al.*, 2013). The browning of

the fruit flesh after cutting is attributed to the oxidation of CGA by polyphenol oxidases. Although eggplant also contains anti-nutritional compounds such as saponins and steroidal glycoalkaloids (a-solamargine and a-solasonine), there are no established guidelines for maximum healthy levels of glycoalkaloids. These compounds may potentially have health benefits, including inhibiting cancer cell growth in vitro and in vivo (Friedman, 2015). Various theories suggest different origins for eggplant. Unlike tomato and potato, which are native to Central and South America, eggplant originates from the Old World. It is widely believed that eggplant was independently domesticated from *S. insanum* in the Indian subcontinent and China, with a possible additional domestication center in the Philippines (Cericola *et al.*, 2013). By the eighth century, eggplant had spread eastward to Japan, then westward to Southeast Asia and Africa, eventually reaching the Mediterranean Basin and later the Americas.

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* (Doganlar*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 (Doganlar*et al.*, 2002).

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 (Sunseri *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 F2 individuals and 181 RAPD and AFLP markers, which helped identify QTLs for fruit shape, stem, and calyx pigmentation (Nunome*et al.*, 2001). Another intraspecific map, published in 2010, utilized 238 molecular markers and 141 F2 individuals from a cross between “305E40” (resistant to Fusarium oxysporum due to the Rfo-sa1 locus from *S. aethiopicum*) and “67/3” (Barchi *et al.*, 2010). An F6 RIL population derived from a cross between a Ralstonia solanacearum-resistant line (“AG91-25”) and a susceptible line (“MM738”) identified a major dominant resistance gene, ERs1 (Lebeau*et al.*, 2013). This map was later expanded with additional markers to identify one major phylotype-specific QTL and two broad-spectrum QTLs for RS resistance (Salgon*et al.*, 2017).

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 (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 (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 (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 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 (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 *Fusarium oxysporum* and *V. dahliae* (Toppino*et al.*, 2016; Barchi *et al.*, 2019).

Cucumber

Cucumber (*Cucumis sativus* L., 2n = 2x = 14), a member of the Cucurbitaceae family, is one of the most widely cultivated and consumed vegetables globally. In 2018, it was harvested from 1.98 million hectares, yielding a total of 75.22 million metric tons. The top producers of cucumbers are China, Iran, Russia, Turkey, and the U.S. (FAOSTAT, 2020). The genus *Cucumis* includes 50 species, such as melon (*C. melo* L., 2n = 2x = 24) and the cucumber's sister species *C. hystrix* (2n = 2x = 24), which diverged from the cucumber lineage 10 and 5 million years ago, respectively (Sebastian *et al.*, 2010). *C. hystrix* is the only species in this genus that can interbreed with cucumber and is considered a secondary gene pool for cucumber breeding.

The primary gene pool of cucumber includes four cross-compatible 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, found widely in South and Southeast Asia, is the progenitor of modern cucumbers. The semi-wild Xishuangbanna cucumber, native to Southwest China and nearby areas, has unique traits like very large fruit, orange flesh due to high b-carotene, late flowering, and strong seed dormancy in some accessions, likely due to diversifying

selection post-domestication. The Sikkim cucumber, found mainly in India and Nepal, is known for its black spine, brown fruit with fine netting, and a large hollow in mature fruit. It is considered an ecotype of the cultivated cucumber selected for local adaptation.

India is recognized as the centre of cucumber diversity, where it has been cultivated for at least 3,000 years (Sebastian *et al.*, 2010). Cucumber spread eastward to China around 2,000 years ago and westward to Europe between 1,500 and 700 years ago (Paris *et al.*, 2012). This spread, combined with natural and human selection, has led to many ecotypes or landraces adapted to different climates, production systems, and consumer preferences. Cucumbers from various regions exhibit significant morphological diversity in fruit size, skin colour, texture, firmness, crispness, and taste, resulting from selection for fresh consumption or processing (pickles) (Wehner, 1989). Modern breeding has intensified these divisions, creating several market classes suited to large-scale production in diverse environments (Weng, 2021). However, commercial breeding has also led to genetic erosion, narrowing the genetic base of each market type. Gene banks around the world preserve hundreds of cucumber accessions, but molecular marker analyses show that only a small fraction of the genetic diversity from the centre of origin is represented in landraces or commercial cultivars from other regions. This indicates that gene bank collections remain a crucial source of genetic variation for future cucumber breeding.

The availability of draft genome sequences, along with cost-effective high-throughput sequencing and genotyping technologies, has significantly accelerated molecular mapping and QTL analysis in cucumber. The small genome size of cucumber, which has not undergone recent whole-genome duplication, combined with its annual growth habit and short life cycle (2-3 months from seed to seed), offers considerable advantages for genetic research (Weng, 2016). This progress is evident in the rapid increase in cucumber-related publications.

For instance, 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. Prior to this, the 2010 gene catalog documented only a few cucumber genes with known chromosomal locations and just one known candidate gene, the femaleness (F) locus, which codes for the 1-aminocyclopropane-1-carboxylate synthase involved in ethylene biosynthesis. Recently, Wang *et al.* (2019a) reviewed mutants, genes, and QTLs in cucumber, detailing 81 major genes and QTLs that have been cloned or fine-mapped, including chromosomal locations, allelic variants, and linked markers for marker-assisted selection (MAS) in breeding. They also identified 322 QTLs for 42 quantitative traits, including 109 related to pathogen resistance.

The development of numerous molecular markers for important horticultural traits facilitates MAS in cucumber breeding (Feng *et al.*, 2020). MAS and QTL pyramiding are crucial for breeding

cucumber varieties with multiple disease resistances, as these traits are often controlled by multiple recessive QTLs. This approach is especially valuable for international vegetable seed companies, which commonly use MAS in their cucumber breeding programs.

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.

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	Weng *et al.*, 2020
Anthracnose	*Colletotrichum lagenarium*	CsGy5G003280	Magnesium dechelatase	Gy14, WI2757	5	2,149,251	SNP08	Pan *et al.*, 2017
Downy mildew	*Pseudoperonospora racubensis*	dm CsGy5G003280	Magnesium dechelatase	Gy14, WI2757	5	2,149,251	SNP08	Weng *et al.*, 2020
Downy mildew	*Pseudoperonospora racubensis*	dm5.2	n.a	WI7120	5	23,380,844	CsDM4-055	Wang *et al.*, 2018c
Downy mildew	*Pseudoperonospora racubensis*	dm5.3	CsGy5G026540	IL52	5	30,434,472	SNP6	Zhang *et al.*, 2020
Downy mildew	*Pseudoperonospora racubensis*	dm4.1.1	CsGy4G017560	PI 197088	4	22,673,270	551 bp deletion	Berg *et al.*, 2021
Downy mildew	*Pseudoperonospora racubensis*	dm4.1.3	CsGy4G019790	PI 197088	4	26,526,343	Retrotransposon insertion	Berg *et al.*, 2021
Fusarium wilt	*Fusarium oxysporum* f. sp. *cucumerinum*	Foc	n.a	9110Gt	2	3,276,171	SSR17631	Zhang *et al.*, 2020
Fusarium wilt	*Fusarium oxysporum* f. sp. *cucumerinum*	fw2.1	n.a	Superina 2	n.a	n.a	n.a	Dong *et al.*, 2019
Powdery mildew	*Podosphaerafusca*	pm5.3	CsGy5G026660	S1003, PI 197088	5	30,524,541	N7F-N14R	Berg *et al.*, 2021

Powdery mildew	*Podosphaerafusca*	pm5.3	CsGy5G026540	IL52	5	30,434,472	SNP6	Zhang *et al.*, 2020
Powdery mildew	*Podosphaerafusca*	pm5.2	CsGy5G015660	PM-R	5	21,851,875	CAPS_CsGy5G015660	Zhang *et al.*, 2020
Scab	*Cladosporium cucumerinum*	Ccu	n.a	9110Gt	2	3,276,171	SSR17631	Kang *et al.*, 2011
CMV	*Cucumber mosaic virus*	cmv6.1	n.a	02245	6	7,688,887	SSR9-56	Shi *et al.*, 2018
CVYV	*Cucumber vein yellowing virus*	CsCvy-1	CsaV3_5G011200	CE0749	5	7,212,250	Not tested	Pujol *et al.*, 2019

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