

BIOTECHNOLOGY-DRIVEN BREEDING OF SOLANACEOUS VEGETABLE CROPS: ADVANCES IN IN VITRO CULTURE AND MARKER-ASSISTED SELECTION

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ABSTRACT

Solanaceous crops like tomato, brinjal, chilli and potato are vital for global food security. Traditional breeding methods face limitations, including being time-consuming, labour-intensive, and constrained by limited genetic diversity. In vitro and marker-assisted breeding techniques offer solutions to overcome these challenges. In vitro breeding includes embryo rescue, which helps in interspecific hybridization, and anther and microspore culture, which accelerates the production of homozygous plants. Protoplast fusion allows combining genetic material from incompatible species, while in vitro mutagenesis creates genetic variations through induced mutations. These techniques enable the use of wild relatives as sources of desirable traits, especially disease resistance. Marker-assisted breeding uses DNA markers linked to specific traits, enabling precise selection without the influence of environmental factors. Advances in genomics, particularly single nucleotide polymorphisms (SNPs), have enhanced marker-assisted selection, improving resistance to biotic and abiotic stresses, yield potential, and nutritional qualities. Specifically, in vitro techniques combined with marker-assisted breeding have shown synergistic effects. For instance, embryo rescue has been used to create hybrids between cultivated tomatoes and wild relatives with disease resistance genes. Anther culture facilitates rapid development of doubled haploid lines in eggplants. Protoplast fusion has enabled the transfer of disease resistance from wild species to cultivated eggplants. In vitro mutagenesis has induced drought tolerance in tomatoes. Marker-assisted selection is used to select disease resistance genes in tomatoes and to pyramid multiple resistance genes against late blight in potatoes. Marker-assisted backcrossing efficiently transfers specific genes while retaining the genetic background of the cultivated variety. Genomic selection uses genome-wide markers to predict the breeding value of individuals for complex traits like fruit quality in tomatoes and tuber yield in potatoes, enhancing genetic gain. These integrated approaches accelerate the development of improved solanaceous crop varieties with enhanced resilience and nutritional value.

KEYWORDS: Solanaceous crops, marker-assisted selection, in vitro breeding, disease resistance, stress tolerance

1. INTRODUCTION

Solanaceous vegetable crops, belonging to the family Solanaceae, constitute some of the most economically significant vegetables globally. Among these, tomato (*Solanum lycopersicum*), eggplant or brinjal (*Solanum melongena*), chilli (*Capsicum spp.*), and potato (*Solanum tuberosum*) are extensively cultivated across diverse geographical regions and form integral components of various cuisines worldwide (Tripodi et al., 2021). These crops are not only rich sources of essential nutrients, vitamins, minerals, and bioactive compounds but also represent major commodities in international agricultural trade. Traditional breeding methods have significantly contributed to crop improvement; however, they are often labor-intensive and time-consuming and often constrained by sexual incompatibility barriers and narrow genetic diversity within cultivated germplasm (Collard & Mackill, 2007). Moreover, the increasing challenges posed by climate change, emerging pests and diseases, and the growing demand for nutritionally enhanced food necessitate more efficient and precise breeding strategies (Varshney et al., 2021).

In vitro breeding techniques and marker-assisted breeding have emerged as powerful approaches to overcome the limitations of conventional breeding methods. In vitro breeding encompasses various tissue culture techniques, including embryo rescue, anther and microspore culture, protoplast fusion, somatic hybridization, and in vitro mutagenesis, which

facilitate the development of novel genetic combinations that are difficult or impossible to achieve through conventional crossing (Kumari et al., 2021). These techniques enable the exploitation of wild relatives as valuable sources of desirable traits, particularly disease resistance genes, which can be introgressed into cultivated varieties (Cardoso et al., 2018). Marker-assisted breeding, on the other hand, utilizes molecular markers DNA sequences associated with specific traits to select plants with desired characteristics without the need for phenotypic evaluation, which is often influenced by environmental factors (Collard & Mackill, 2007). This approach significantly reduces the breeding cycle duration and increases selection efficiency and precision. Recent advances in genomics, particularly next-generation sequencing technologies, have facilitated the development of high-throughput marker systems like single nucleotide polymorphisms (SNPs), which have revolutionized marker-assisted selection in solanaceous crops (Varshney et al., 2021). The integration of in vitro techniques with marker-assisted breeding has created synergistic effects, accelerating the development of improved varieties with enhanced resistance to biotic and abiotic stresses, improved yield potential, and superior nutritional qualities (Cardi et al., 2017). This review aims to comprehensively examine recent advances in in vitro breeding and marker-assisted breeding across major solanaceous vegetable crops, focusing on their applications in addressing various breeding objectives and the challenges and future prospects associated with these techniques.

2. In Vitro Breeding Techniques in Solanaceous Crops

2.1 Embryo Rescue

Embryo rescue has emerged as a crucial technique for overcoming post-zygotic barriers in interspecific hybridization among solanaceous crops. This method involves the aseptic culture of immature embryos that would otherwise abort due to endosperm failure or embryo-endosperm incompatibility (Kumar et al., 2019). The technique has been particularly valuable in tomato breeding, facilitating crosses between cultivated tomato and wild relatives such as *S. peruvianum* and *S. chilense*, which harbor valuable genes for disease resistance and abiotic stress tolerance (Garcia-Lozano et al., 2020). Recent advances in embryo rescue protocols have improved success rates in solanaceous crops through optimization of culture media compositions, hormonal balances, and physical culture conditions. Kim et al. (2019) reported enhanced embryo rescue efficiency in interspecific crosses between eggplant and its wild relatives by supplementing culture media with activated charcoal and adjusting nitrogen sources. Similarly, Shivakumar et al. (2021) demonstrated improved embryo rescue success in *S. lycopersicum* × *S. pimpinellifolium* crosses using a two-step culture system with varying hormonal compositions.

2.2 Anther and Microspore Culture

Anther and microspore culture techniques facilitate the rapid production of doubled haploid (DH) plants, which are completely homozygous and can significantly accelerate breeding programs by reducing the time required to develop pure lines (Mishra & Rai, 2021). In pepper breeding, Shariatpanahi et al. (2020) optimized a protocol for isolated microspore culture, achieving up to 15% embryogenesis frequency and successful regeneration of DH plants. The researchers identified cold pretreatment (4°C for 7 days) combined with heat shock (33°C for 3 days) as optimal for inducing embryogenesis in microspores. In potato, Vega-Sánchez et al. (2020) developed an improved anther culture protocol using diploid potato species, enabling the generation of DH lines within 6-8 months compared to 3-4 years required through conventional breeding. These DH lines exhibited desirable traits including early maturity and resistance to late blight disease. The technique has been less successful in tomato and eggplant, with lower androgenesis response and plant regeneration rates, although recent studies have shown progress through genotype optimization and improved culture conditions (Castro et al., 2021).

2.3 Protoplast Fusion and Somatic Hybridization

Protoplast fusion enables the combination of genomes from sexually incompatible species, creating novel genetic combinations that cannot be achieved through conventional crossing (Eeckhaut et al., 2018). In solanaceous crops, this technique has facilitated the transfer of disease resistance, abiotic stress tolerance, and cytoplasmic male sterility from wild relatives to cultivated varieties. Recent advancements in protoplast isolation, fusion, and regeneration protocols have improved the efficiency of somatic hybridization in solanaceous crops. Kaushik et al. (2019) reported successful somatic hybridization between tomato and distant wild relative *S. sisymbriifolium*, which carries genes for resistance to root-knot nematodes and several fungal diseases. The regenerated hybrid plants exhibited intermediate morphological characteristics and enhanced resistance to root-knot nematodes. In eggplant, Zhou et al. (2021) achieved successful asymmetric somatic hybridization with wild species *S. torvum*, which possesses resistance to bacterial wilt and Verticillium wilt. The researchers used gamma irradiation to partially inactivate the donor genome, resulting in hybrids with predominantly cultivated eggplant characteristics but incorporating disease resistance traits from the wild species.

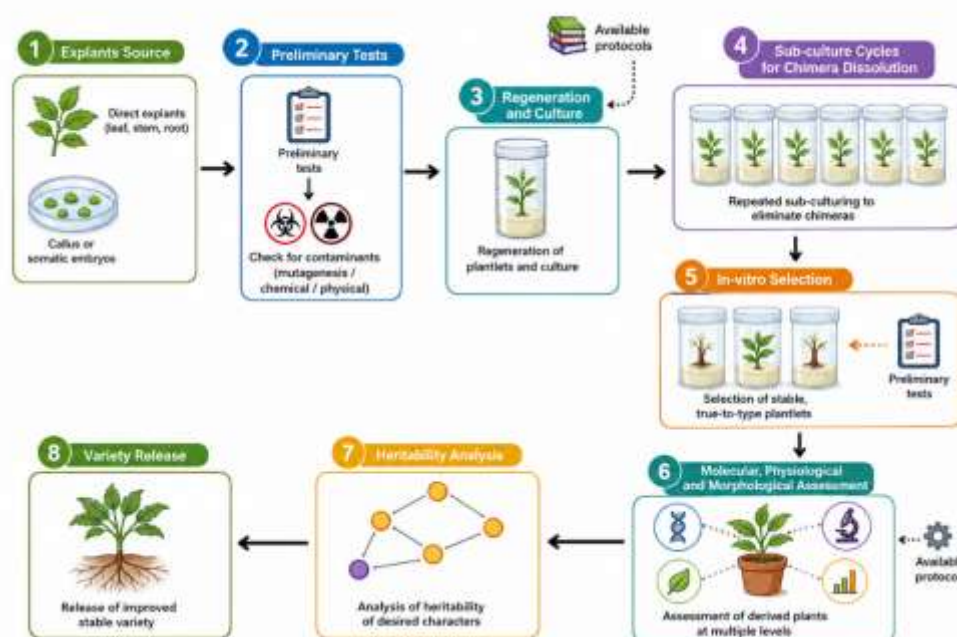


Figure 1: Workflow of in vitro mutagenesis and selection in plants. The process begins with explants or callus subjected to chemical or physical mutagenesis, followed by regeneration. Sub-culturing helps dissolve chimeras, and in vitro selection is performed. Selected lines undergo molecular and phenotypic assessment, heritability analysis, and lead to variety release. (Kashtwari et al., 2022)

2.4 In Vitro Mutagenesis

In vitro mutagenesis combines tissue culture techniques with physical or chemical mutagens to induce genetic variations that can be selected for desirable traits (Kumari & Venkatesan, 2020). This technique has gained renewed attention in solanaceous crop improvement, particularly for inducing variations in disease resistance, abiotic stress tolerance, and quality traits. Oladosu et al. (2020) employed Ethyl Methanesulfonate (EMS) mutagenesis on tomato callus cultures, generating mutant lines with enhanced tolerance to drought stress. These mutants exhibited improved water use efficiency and maintained higher photosynthetic rates under water-limited conditions compared to the parent cultivar. Similarly, Awasthi et al. (2023) used gamma irradiation on potato microtubers, developing mutant lines with increased resistance to early blight disease and improved tuber quality characteristics, including higher dry matter content and reduced reducing sugar levels.

3. Marker-Assisted Breeding in Solanaceous Crops

3.1 Types of Molecular Markers Used in Solanaceous Crops

Molecular marker technologies have evolved rapidly, from restriction fragment length polymorphisms (RFLPs) to advanced, high-throughput systems such as simple sequence repeats (SSRs) and single nucleotide polymorphisms (SNPs). These markers have enabled diverse applications in solanaceous crop breeding, including genetic diversity assessment, linkage map construction, quantitative trait loci (QTL) mapping, and marker-assisted selection (MAS) (Varshney et al., 2021). SNP markers have become particularly dominant in recent years because of their abundance in plant genomes, compatibility with high-throughput detection platforms, and cost-effectiveness (Voichek & Weigel, 2020). Advances in next-generation sequencing have enabled the development of large-scale SNP resources for major solanaceous crops. For instance, the SolCAP SNP array, containing over 8,000 SNPs, has been widely used in potato breeding programs for applications such as variety identification, genetic diversity analysis, and marker-trait associations (Sharma et al., 2018). Similarly, the Solanaceae Coordinated Agricultural Project (SolCAP) tomato SNP array, with approximately 10,000 SNPs, has facilitated fine mapping of disease resistance genes and quality trait loci (Robbins et al., 2019). These high-density marker platforms have significantly enhanced the precision and efficiency of marker-assisted breeding in solanaceous crops.

3.2 Marker-Assisted Selection (MAS)

Marker-assisted selection involves the use of molecular markers tightly linked to traits of interest to select desired genotypes without phenotypic evaluation, which is often influenced by environmental conditions and requires complete plant development (Collard & Mackill, 2007). This approach has been particularly valuable for selecting disease resistance genes, which often follow qualitative inheritance patterns and can be effectively tagged with molecular markers. In tomato breeding, MAS has been extensively employed for selecting disease resistance genes, including Ty genes for tomato yellow leaf curl virus (TYLCV) resistance, Ph genes for late blight resistance, and Mi genes for root-knot nematode resistance (Panthee & Gardner, 2020). For instance, Liu et al. (2019) developed tightly linked SCAR markers for the Ty-3 gene, which confers resistance to TYLCV, enabling efficient selection of resistant plants at the seedling stage. Similarly, in potato breeding, MAS has been used to pyramid multiple resistance genes against the devastating late blight disease.

Sharma et al. (2023) combined four resistance genes (R1, R2, R8, and R9) in a single genetic background using tightly linked SNP markers, developing breeding lines with broad-spectrum and durable resistance to diverse pathogen isolates.

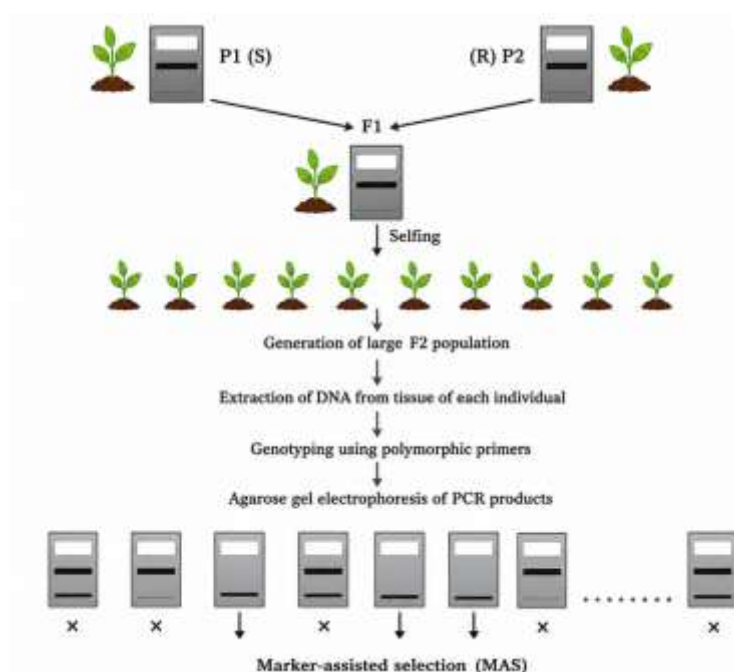


Figure 2: Workflow of Marker-Assisted Selection (MAS). F1 plants derived from crossing susceptible (P1) and resistant (P2) parents are selfed to produce a large F2 population. DNA is extracted and genotyped using polymorphic markers. PCR products are analyzed via gel electrophoresis to identify individuals with desirable alleles, enabling precise selection through MAS.

3.3 Marker-Assisted Backcrossing (MABC)

Marker-assisted backcrossing involves the use of molecular markers to select for the transfer of specific genes or QTLs from a donor parent while recovering the recurrent parent's genetic background through successive backcrossing (Collard & Mackill, 2007). This approach has been widely employed in solanaceous crop improvement for the introgression of disease resistance genes from wild relatives to cultivated varieties. Recent studies have demonstrated the effectiveness of MABC in transferring targeted traits while minimizing linkage drag the unintended transfer of undesirable genes linked to the target gene. For instance, Yang et al. (2021) employed MABC to introgress the Sw-5 gene for resistance to Tomato spotted wilt virus (TSWV) into elite processing tomato lines. By using flanking SNP markers for foreground selection and genome-wide SSR markers for background selection, the researchers achieved over 95% recurrent parent genome recovery within three backcross generations. In chili pepper, Wang et al. (2020) used MABC to introgress the Tsw gene for resistance to Tomato spotted wilt virus from *C. chinense* into *C. annuum* commercial varieties. The researchers developed SNP markers tightly linked to the resistance gene and used genome-wide background markers to accelerate the recovery of the recurrent parent's genetic background, developing resistant lines with commercial qualities within four generations.

3.4 Genomic Selection (GS)

Genomic selection represents an advanced form of marker-assisted breeding that uses genome-wide markers to predict the breeding value of individuals (Crossa et al., 2017). Unlike conventional MAS, which focuses on major genes or QTLs, GS captures the effects of all genomic regions contributing to complex traits, making it particularly suitable for quantitative traits governed by numerous small-effect QTLs. Recent studies have demonstrated the potential of GS in improving complex traits in solanaceous crops. Yamamoto et al. (2020) evaluated different GS models for predicting fruit quality traits in tomato, reporting moderate to high prediction accuracies (0.5-0.8) for traits such as soluble solid content, titratable acidity, and fruit firmness. The researchers found that incorporating prior knowledge of trait architecture into prediction models significantly improved accuracy. In potato, Stich et al. (2022) implemented GS for improving tuber yield and starch content, two highly complex traits. Using a training population of 200 tetraploid potato clones genotyped with approximately 20,000 SNP markers, the researchers achieved prediction accuracies of 0.63 for tuber yield and 0.72 for starch content. These results suggest that GS could significantly enhance genetic gain for complex traits in potato breeding programs.

4. Tomato (*Solanum lycopersicum* L.)

4.1 In vitro Breeding Applications

Tomato, as one of the most extensively studied solanaceous crops, has benefited significantly from various in vitro breeding techniques. Embryo rescue has facilitated interspecific hybridization with wild tomato species, particularly those belonging to the *S. peruvianum* complex, which harbor valuable genes for disease resistance and abiotic stress tolerance

(Garcia-Lozano et al., 2020). For instance, Garcia-Lozano et al. (2020) successfully employed embryo rescue to develop interspecific hybrids between cultivated tomato and *S. habrochaites*, which carries genes for resistance to whitefly, an important vector for several tomato viruses. Protoplast fusion and somatic hybridization have also been employed to overcome crossing barriers between tomato and distant relatives. Kaushik et al. (2019) reported successful somatic hybridization between tomato and *S. sisymbriifolium*, transferring root-knot nematode resistance to cultivated tomato. The researchers optimized protoplast isolation and fusion protocols, achieving regeneration of hybrid plants that exhibited intermediate morphological characteristics and enhanced nematode resistance.

4.2 Marker-Assisted Breeding for Disease Resistance

Disease resistance breeding has been a major focus of marker-assisted breeding efforts in tomato, with significant progress achieved in developing varieties resistant to various fungal, bacterial, and viral pathogens (Panthee & Gardner, 2020). Table 1 summarises key disease resistance genes/QTLs in tomato and their associated molecular markers that have been utilized in breeding programs. For viral diseases, MAS has been particularly effective in pyramiding multiple resistance genes against tomato yellow leaf curl virus (TYLCV), one of the most devastating viral diseases of tomato worldwide. Prasanna et al. (2021) combined three resistance genes (Ty-1, Ty-2, and Ty-3) in a single genetic background using SNP and CAPS markers, developing breeding lines with broad-spectrum and durable resistance to diverse TYLCV strains. For fungal diseases, late blight caused by *Phytophthora infestans* has received considerable attention. Mutlu et al. (2020) employed MAS to pyramid three late blight resistance genes (Ph-1, Ph-2, and Ph-3) from wild tomato species into cultivated backgrounds. The researchers used tightly linked SNP markers for each resistance gene, significantly accelerating the breeding process and developing lines with enhanced resistance to diverse pathogen isolates.

4.3 Breeding for Abiotic Stress Tolerance

Abiotic stress tolerance, particularly drought and heat tolerance, has gained increasing attention in tomato breeding programs due to climate change concerns. Marker-assisted breeding approaches have been employed to identify and introgress QTLs associated with various abiotic stress tolerance mechanisms (Landi et al., 2017). Jiang et al. (2021) identified SNP markers associated with drought tolerance QTLs on chromosomes 2, 6, and 12 through genome-wide association studies (GWAS) and successfully introgressed these QTLs into elite tomato cultivars using marker-assisted backcrossing. The developed breeding lines exhibited enhanced water use efficiency, maintained higher photosynthetic rates under water-limited conditions, and showed less yield reduction compared to their recurrent parents. For heat tolerance, Xu et al. (2020) mapped QTLs associated with pollen viability under high-temperature stress conditions and identified tightly linked SNP markers. These markers were subsequently used in MABC programs to improve the heat tolerance of processing tomato varieties, developing breeding lines that maintained good fruit set under elevated temperatures.

4.4 Quality Improvement

Quality improvement in tomato encompasses various traits, including fruit size, shape, color, flavor, and nutritional value. Modern breeding programs increasingly focus on enhancing health-promoting compounds such as lycopene, β -carotene, flavonoids, and vitamin C content (Calafiore et al., 2019). Kinkade et al. (2023) identified SNP markers associated with high lycopene content in tomato through association mapping and successfully incorporated these markers into MAS programs. The developed high-lycopene breeding lines contained up to 30% more lycopene than conventional varieties while maintaining desirable horticultural traits. For flavor improvement, Tieman et al. (2021) identified and validated SNP markers associated with key volatile compounds contributing to tomato flavor. These markers were incorporated into breeding programs, leading to the development of varieties with enhanced flavor profiles while maintaining high yield potential and disease resistance.

Table 1: Key Disease Resistance Genes/QTLs in Tomato and Associated Molecular Markers

Gene/QTL	Disease	Resistance Source	Marker Type	Chromosome Location	Reference
Ty-1/Ty-3	Tomato yellow leaf curl virus (TYLCV)	<i>S. chilense</i>	SNP, CAPS	6	Prasanna et al. (2021)
Ty-2	Tomato yellow leaf curl virus (TYLCV)	<i>S. habrochaites</i>	SSR, CAPS	11	Liu et al. (2019)
Ph-1	Late blight (<i>Phytophthora infestans</i>)	<i>S. pimpinellifolium</i>	SCAR	7	Mutlu et al. (2020)
Ph-2	Late blight (<i>Phytophthora infestans</i>)	<i>S. pimpinellifolium</i>	CAPS	10	Mutlu et al. (2020)
Ph-3	Late blight (<i>Phytophthora infestans</i>)	<i>S. pimpinellifolium</i>	SNP	9	Mutlu et al. (2020)
Sw-5	Tomato spotted wilt virus (TSWV)	<i>S. peruvianum</i>	CAPS, SNP	9	Yang et al. (2021)
Mi-1.2	Root-knot nematode	<i>S. peruvianum</i>	SCAR, CAPS	6	Kaushik et al.

	(<i>Meloidogyne</i> spp.)				(2019)
I-2	Fusarium wilt (<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i> race 2)	<i>S. pimpinellifolium</i>	CAPS	11	Panthee & Gardner (2020)
I-3	Fusarium wilt (<i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i> race 3)	<i>S. pennellii</i>	CAPS, SNP	7	Panthee & Gardner (2020)
Ve1	Verticillium wilt (<i>Verticillium dahliae</i>)	<i>S. lycopersicum</i>	SCAR	9	Garcia-Lozano et al. (2020)

5. Brinjal (*Solanum melongena* L.)

5.1 In vitro Breeding Applications

Eggplant has benefited substantially from in vitro breeding techniques, particularly for overcoming crossability barriers with wild relatives harboring valuable genes for disease resistance and quality traits. Plazas et al. (2019) successfully employed embryo rescue to develop interspecific hybrids between cultivated eggplant and *S. insanum*, its immediate wild progenitor, which possesses genes for drought tolerance and fruit quality traits. Anther culture has shown promising results in eggplant breeding, facilitating the rapid development of doubled haploid lines. Liang et al. (2020) optimized an efficient anther culture protocol for eggplant, achieving up to 25% embryogenesis frequency and successful regeneration of doubled haploid plants across diverse genotypes. These doubled haploid lines exhibited complete homozygosity and were directly utilized in cultivar development and genetic studies. Somatic hybridization has been employed to facilitate gene transfer from distantly related species. Zhou et al. (2021) achieved successful asymmetric somatic hybridization between eggplant and *S. torvum*, transferring bacterial wilt and Verticillium wilt resistance to cultivated eggplant. The researchers used gamma irradiation to partially inactivate the donor genome, resulting in hybrids with predominantly cultivated eggplant characteristics but incorporating disease resistance traits.

5.2 Marker-Assisted Breeding for Disease Resistance

Disease resistance breeding has been a primary focus of marker-assisted breeding efforts in eggplant, with significant progress achieved in developing varieties resistant to bacterial wilt, Verticillium wilt, and Fusarium wilt (Gramazio et al., 2020). Table 2 summarizes key disease resistance genes/QTLs in eggplant and their associated molecular markers. For bacterial wilt caused by *Ralstonia solanacearum*, Yang et al. (2022) identified SNP markers tightly linked to a major resistance QTL (RSQTL6) on chromosome 6 and employed these markers in MABC programs. The researchers successfully introgressed the resistance QTL into elite eggplant cultivars, developing breeding lines with enhanced resistance to diverse bacterial wilt pathogen strains. For Verticillium wilt, Liu et al. (2023) mapped a major resistance gene (Ve1) derived from wild relative *S. torvum* and developed tightly linked SCAR markers for MAS. These markers have been widely adopted in eggplant breeding programs, facilitating the development of resistant varieties suitable for regions where Verticillium wilt is prevalent.

5.3 Breeding for Abiotic Stress Tolerance

Abiotic stress tolerance breeding in eggplant has focused on developing varieties adapted to drought, salinity, and temperature extremes (Kumari et al., 2021). Marker-assisted approaches have been increasingly employed to identify and introgress QTLs associated with various stress tolerance mechanisms. Saha et al. (2022) identified SNP markers associated with drought tolerance QTLs through GWAS analysis of a diverse eggplant germplasm collection. These markers were subsequently validated and incorporated into breeding programs, leading to the development of drought-tolerant breeding lines that maintained stable yields under water-limited conditions. For salt tolerance, Chen et al. (2021) mapped QTLs associated with sodium exclusion and tissue tolerance mechanisms using an interspecific population derived from a cross between cultivated eggplant and salt-tolerant wild relative *S. insanum*. The researchers identified SNP markers tightly linked to major QTLs on chromosomes 3 and 7, which were subsequently utilized in marker-assisted breeding programs to enhance salt tolerance in eggplant.

5.4 Quality Improvement

Quality improvement in eggplant has focused on enhancing fruit color, reducing bitterness, increasing antioxidant content, and improving post-harvest shelf life (Gramazio et al., 2018). Recent marker-assisted breeding efforts have targeted these traits to develop varieties with improved consumer appeal and nutritional value. Kaushik et al. (2020) identified SNP markers associated with high anthocyanin content in purple-fruited eggplant varieties through association mapping and incorporated these markers into MAS programs. The developed breeding lines exhibited deep purple fruit color and contained significantly higher levels of health-promoting anthocyanins compared to conventional varieties. For reducing fruit bitterness, Toppino et al. (2022) mapped QTLs associated with saponin and glycoalkaloid content, the main compounds responsible for bitterness in eggplant. The researchers developed SNP markers linked to low-bitterness alleles and successfully employed these markers in breeding programs, developing varieties with reduced bitterness while maintaining desirable agronomic traits.

Table 2: Key Disease Resistance Genes/QTLs in Eggplant and Associated Molecular Markers

Gene/QTL	Disease	Resistance Source	Marker Type	Chromosome Location	Reference
RSQTL6	Bacterial wilt (<i>Ralstonia solanacearum</i>)	<i>S. melongena</i>	SNP	6	Yang et al. (2022)
Ve1	Verticillium wilt (<i>Verticillium dahliae</i>)	<i>S. torvum</i>	SCAR	9	Liu et al. (2023)
Rfo-Sa1	Fusarium wilt (<i>Fusarium oxysporum</i> f. sp. <i>melongenae</i>)	<i>S. aethiopicum</i>	SSR	2	Toppino et al. (2022)
FocQTL2	Fusarium wilt (<i>Fusarium oxysporum</i> f. sp. <i>melongenae</i>)	<i>S. melongena</i>	SNP	2	Gramazio et al. (2020)
Ppl	Phomopsis blight (<i>Phomopsis vexans</i>)	<i>S. integrifolium</i>	RAPD	10	Kaushik et al. (2020)
LbQTL3	Leaf blight (<i>Alternaria solani</i>)	<i>S. melongena</i>	SNP	3	Gramazio et al. (2020)
SlQTL8	Southern blight (<i>Sclerotium rolfsii</i>)	<i>S. torvum</i>	SNP	8	Zhou et al. (2021)
Rbw1	Bacterial wilt (<i>Ralstonia solanacearum</i>)	<i>S. torvum</i>	SSR	3	Zhou et al. (2021)

6. Chili Pepper (*Capsicum* spp.)

6.1 In vitro Breeding Applications

Chili pepper has benefited from various in vitro breeding techniques, particularly anther culture for doubled haploid production and embryo rescue for interspecific hybridization. Shariatpanahi et al. (2020) optimized a protocol for isolated microspore culture in pepper, achieving up to 15% embryogenesis frequency and successful regeneration of doubled haploid plants. These doubled haploids have accelerated breeding programs by reducing the time required to develop homozygous lines. Embryo rescue has facilitated interspecific hybridization between cultivated pepper (*C. annuum*) and wild species such as *C. baccatum* and *C. chinense*, which harbor valuable genes for disease resistance and fruit quality traits (Manzur et al., 2019). Lee et al. (2021) successfully employed embryo rescue to develop interspecific hybrids between *C. annuum* and *C. baccatum*, which carries genes for resistance to anthracnose and bacterial spot diseases. In vitro mutagenesis has also been employed to induce novel genetic variations in pepper. Ji et al. (2023) used gamma irradiation on pepper embryogenic callus cultures, developing mutant lines with altered capsaicinoid content and improved tolerance to drought stress. These mutations provided valuable genetic resources for pepper improvement programs.

6.2 Marker-Assisted Breeding for Disease Resistance

Disease resistance breeding has been a major focus of marker-assisted breeding efforts in pepper, with significant progress achieved in developing varieties resistant to various viral, bacterial, and fungal pathogens (Tripodi et al., 2021). Table 3 summarizes key disease resistance genes/QTLs in pepper and their associated molecular markers. For viral diseases, MAS has been particularly effective in pyramiding multiple resistance genes against important viruses affecting pepper production. Wang et al. (2020) employed MABC to introgress the Tsw gene for resistance to Tomato spotted wilt virus (TSWV) from *C. chinense* into *C. annuum* commercial varieties. The researchers developed SNP markers tightly linked to the resistance gene and used genome-wide background markers to accelerate the recovery of the recurrent parent's genetic background. For bacterial spot caused by *Xanthomonas* species, Potnis et al. (2021) identified and mapped three resistance QTLs (Bs2, Bs3, and Bs4) derived from different *Capsicum* species and developed tightly linked SNP markers for each QTL. These markers were subsequently used in marker-assisted pyramiding programs, developing breeding lines with broad-spectrum resistance to diverse bacterial spot pathogen races.

6.3 Breeding for Abiotic Stress Tolerance

Abiotic stress tolerance breeding in pepper has focused on developing varieties adapted to drought, heat, and cold stress conditions (Tripodi et al., 2021). Marker-assisted approaches have been increasingly employed to identify and introgress QTLs associated with various stress tolerance mechanisms. Song et al. (2022) identified SNP markers associated with drought tolerance QTLs through GWAS analysis of a diverse pepper germplasm collection. These markers were subsequently validated and incorporated into breeding programs, leading to the development of drought-tolerant breeding lines that maintained stable yields under water-limited conditions. For heat tolerance, Kim et al. (2021) mapped QTLs associated with pollen viability and fruit set under high-temperature stress conditions using a recombinant inbred line population. The researchers identified tightly linked SNP markers to major QTLs on chromosomes 3 and 5, which were subsequently utilized in marker-assisted breeding programs to enhance heat tolerance in pepper.

6.4 Quality Improvement

Quality improvement in pepper encompasses various traits, including fruit color, pungency level (capsaicinoid content), antioxidant content, and post-harvest shelf life (Tripodi & Kumar, 2019). Recent marker-assisted breeding efforts have targeted these traits to develop varieties with improved consumer appeal and nutritional value. Han et al. (2019) identified SNP markers associated with capsaicinoid biosynthesis genes through genome-wide association studies and incorporated

these markers into MAS programs. The researchers developed breeding lines with customized pungency levels, ranging from mild to extremely hot, catering to diverse consumer preferences while maintaining desirable agronomic traits. For improving antioxidant content, Qin et al. (2023) mapped QTLs associated with ascorbic acid (vitamin C) and carotenoid content in pepper fruits using a diverse mapping population. The researchers developed SNP markers linked to high-antioxidant alleles and successfully employed these markers in breeding programs, developing varieties with enhanced nutritional value while maintaining high yield potential.

Table 3: Key Disease Resistance Genes/QTLs in Pepper and Associated Molecular Markers

Gene/QTL	Disease	Resistance Source	Marker Type	Chromosome Location	Reference
Tsw	Tomato spotted wilt virus (TSWV)	<i>C. chinense</i>	SNP, CAPS	10	Wang et al. (2020)
L	Tobamovirus (TMV, ToMV, PMMoV)	<i>C. annuum</i> , <i>C. chacoense</i>	CAPS	11	Han et al. (2019)
Bs2	Bacterial spot (<i>Xanthomonas</i> spp.)	<i>C. chacoense</i>	SCAR	9	Potnis et al. (2021)
Bs3	Bacterial spot (<i>Xanthomonas</i> spp.)	<i>C. annuum</i>	SNP	7	Potnis et al. (2021)
Bs4	Bacterial spot (<i>Xanthomonas</i> spp.)	<i>C. pubescens</i>	SNP	5	Potnis et al. (2021)
Pc5.1	Phytophthora root rot (<i>Phytophthora capsici</i>)	<i>C. annuum</i>	SNP	5	Song et al. (2022)
QTL-Anth2.1	Anthracoze (<i>Colletotrichum</i> spp.)	<i>C. baccatum</i>	SSR	2	Lee et al. (2021)
pvr1/pvr2	Potato virus Y (PVY)	<i>C. chinense</i>	CAPS	4	Wang et al. (2020)
CMV-QTL9	Cucumber mosaic virus (CMV)	<i>C. annuum</i>	SNP	9	Han et al. (2019)

7. Potato (*Solanum tuberosum* L.)

7.1 In vitro Breeding Applications

Potato, as a vegetatively propagated crop, has uniquely benefited from in vitro techniques for various applications in breeding and seed tuber production. Somatic hybridization has been particularly valuable for overcoming sexual incompatibility barriers and facilitating gene transfer from wild *Solanum* species. Thieme et al. (2019) reported successful fusion between potato and disease-resistant wild species *S. bulbocastanum* and *S. commersonii*, transferring resistance genes against late blight and bacterial wilt to cultivated potato. Doubled haploid production through anther culture has gained importance in potato breeding, particularly for diploid potato improvement programs. Vega-Sánchez et al. (2020) developed an improved anther culture protocol for diploid potato species, enabling the generation of doubled haploid lines with enhanced genetic uniformity. These doubled haploids exhibited complete homozygosity and were utilized in hybrid breeding programs and genetic studies. In vitro mutagenesis has been employed to induce novel genetic variations in potato. Awasthi et al. (2023) used gamma irradiation on potato microtubers, developing mutant lines with increased resistance to early blight disease and improved tuber quality characteristics, including higher dry matter content and reduced reducing sugar levels.

7.2 Marker-Assisted Breeding for Disease Resistance

Disease resistance breeding has been a primary focus of marker-assisted breeding efforts in potato, with significant progress achieved in developing varieties resistant to late blight, potato virus Y (PVY), potato cyst nematodes, and bacterial wilt (Sharma et al., 2018). Table 4 summarizes key disease resistance genes/QTLs in potato and their associated molecular markers. For late blight caused by *Phytophthora infestans*, Sharma et al. (2023) employed marker-assisted pyramiding to combine four resistance genes (R1, R2, R8, and R9) in a single genetic background. The researchers used tightly linked SNP markers for each resistance gene, significantly accelerating the breeding process and developing lines with broad-spectrum and durable resistance to diverse pathogen isolates. For potato virus Y (PVY), Kaushik et al. (2021) identified and mapped a novel extreme resistance gene (Ry_adg) from *S. tuberosum* ssp. *andigena* and developed tightly linked molecular markers. These markers have been widely adopted in potato breeding programs, facilitating the development of PVY-resistant varieties that maintain acceptable tuber quality and yield characteristics.

7.3 Breeding for Abiotic Stress Tolerance

Abiotic stress tolerance breeding in potato has focused on developing varieties adapted to drought, heat, and salinity stress conditions (Dahal et al., 2019). Marker-assisted approaches have been increasingly employed to identify and introgress QTLs associated with various stress tolerance mechanisms. Khan et al. (2022) identified SNP markers associated with drought tolerance QTLs through GWAS analysis of a diverse potato germplasm collection. These markers were subsequently validated and incorporated into breeding programs, leading to the development of drought-tolerant breeding lines that maintained stable yields under water-limited conditions. For heat tolerance, Tang et al. (2023) mapped QTLs

associated with tuber formation under high-temperature stress conditions using a diploid mapping population. The researchers identified tightly linked SNP markers to major QTLs on chromosomes 4 and 12, which were subsequently utilized in marker-assisted breeding programs to enhance heat tolerance in potato.

7.4 Quality Improvement

Quality improvement in potato encompasses various traits, including tuber shape, skin and flesh color, dry matter content, reducing sugar content, and post-harvest processing quality (Burg et al., 2022). Recent marker-assisted breeding efforts have targeted these traits to develop varieties with improved consumer appeal and processing characteristics. Zhang et al. (2022) identified SNP markers associated with high dry matter content through association mapping and incorporated these markers into MAS programs. The developed breeding lines exhibited enhanced dry matter content, making them particularly suitable for processing applications such as French fries and potato chips. For reducing acrylamide-forming potential, Bommert et al. (2023) mapped QTLs associated with reducing sugar content in potato tubers, which is directly linked to acrylamide formation during high-temperature processing. The researchers developed SNP markers linked to low reducing sugar alleles and successfully employed these markers in breeding programs, developing varieties with reduced acrylamide-forming potential while maintaining desirable processing characteristics.

Table 4: Key Disease Resistance Genes/QTLs in Potato and Associated Molecular Markers

Gene/QTL	Disease	Resistance Source	Marker Type	Chromosome Location	Reference
R1	Late blight (<i>Phytophthora infestans</i>)	<i>S. demissum</i>	SCAR	5	Sharma et al. (2023)
R2	Late blight (<i>Phytophthora infestans</i>)	<i>S. demissum</i>	CAPS	4	Sharma et al. (2023)
R8	Late blight (<i>Phytophthora infestans</i>)	<i>S. demissum</i>	SNP	9	Sharma et al. (2023)
R9	Late blight (<i>Phytophthora infestans</i>)	<i>S. demissum</i>	SNP	11	Sharma et al. (2023)
Ry_adg	Potato virus Y (PVY)	<i>S. tuberosum</i> ssp. <i>andigena</i>	SNP	11	Kaushik et al. (2021)
Gro1-4	Potato cyst nematode (<i>Globodera rostochiensis</i>)	<i>S. spegazzinii</i>	SCAR	7	Sharma et al. (2018)
H1	Potato cyst nematode (<i>Globodera rostochiensis</i>)	<i>S. tuberosum</i> ssp. <i>andigena</i>	SSR	5	Sharma et al. (2018)
Gpa2	Potato cyst nematode (<i>Globodera pallida</i>)	<i>S. tuberosum</i> ssp. <i>andigena</i>	CAPS	12	Sharma et al. (2018)
Ryadg	Potato virus Y (PVY)	<i>S. tuberosum</i> ssp. <i>andigena</i>	SCAR	11	Kaushik et al. (2021)
Sen1	Potato wart (<i>Synchytrium endobioticum</i>)	<i>S. tuberosum</i>	SNP	11	Stich et al. (2022)

8. Challenges, Limitations and Future Perspectives

Despite significant advances in in vitro breeding and marker-assisted selection (MAS), several challenges continue to limit their widespread application in solanaceous crop improvement. In vitro culture techniques, including embryo rescue, anther culture, and doubled haploid production, are often highly genotype-dependent, resulting in variable regeneration efficiencies among cultivars and species. The development of reproducible tissue culture protocols remains a major challenge, particularly in crops such as pepper and eggplant where regeneration responses are strongly influenced by genotype and culture conditions. Furthermore, prolonged in vitro culture may induce somaclonal variation, leading to undesirable genetic changes that can compromise breeding outcomes (Shariatpanahi et al., 2020).

Similarly, the effectiveness of MAS depends largely on the availability of reliable molecular markers that are tightly linked to target traits. Marker–trait associations identified in one genetic background may not always be transferable across diverse breeding populations, necessitating extensive validation before deployment. In addition, MAS is most effective for traits governed by major genes or quantitative trait loci (QTLs) with large effects, whereas complex polygenic traits such as yield stability, drought tolerance, and nutrient-use efficiency remain difficult to improve through conventional marker-assisted approaches alone (Collard and Mackill, 2008). The cost of large-scale genotyping and the requirement for specialized infrastructure may also restrict adoption in resource-limited breeding programs. Future solanaceous breeding programs are expected to integrate conventional breeding, in vitro technologies, and advanced genomic tools to accelerate genetic gain. The increasing availability of high-density molecular markers and next-generation sequencing technologies has facilitated the identification of trait-associated loci at unprecedented resolution. Genome-wide association studies (GWAS) and genomic selection are emerging as powerful approaches for dissecting complex traits and predicting breeding values, thereby complementing traditional MAS strategies (Crossa et al., 2017; Varshney et al., 2021).

Genome editing technologies, particularly CRISPR/Cas systems, have opened new avenues for precision breeding by enabling targeted modification of genes associated with disease resistance, fruit quality, abiotic stress tolerance, and

nutritional enhancement. Recent studies in tomato, potato, pepper, and eggplant have demonstrated the potential of CRISPR-mediated editing for rapid trait improvement without introducing undesirable linkage drag commonly associated with conventional breeding approaches (Gramazio et al., 2020). Furthermore, the integration of genomics, transcriptomics, metabolomics, and phenomics is expected to enhance the identification of candidate genes and regulatory networks controlling agriculturally important traits. The application of artificial intelligence, machine learning, and high-throughput phenotyping platforms is also expected to transform future breeding programs by improving selection accuracy and reducing breeding cycles. Collectively, these advances will contribute to the development of climate-resilient, high-yielding, and nutritionally superior solanaceous cultivars capable of meeting the growing demands of global food security.

9. CONCLUSION

Solanaceous vegetable crops constitute some of the most economically and nutritionally important horticultural commodities worldwide. Continuous improvement of these crops is essential to address challenges associated with increasing food demand, emerging diseases, environmental stresses, and changing climatic conditions. In vitro breeding techniques have provided valuable tools for overcoming reproductive barriers, generating novel genetic variability, and accelerating the development of improved breeding materials. Likewise, marker-assisted selection has enhanced breeding efficiency through precise and early selection of desirable genotypes based on molecular markers linked to important agronomic traits.

The successful application of these technologies in tomato, potato, eggplant, and pepper has demonstrated their potential to accelerate crop improvement while reducing the time and resources required in conventional breeding programs. However, limitations related to genotype dependency, regeneration efficiency, marker validation, and complex trait inheritance continue to present challenges. Future breeding efforts will increasingly rely on the integration of in vitro breeding, molecular markers, genomic selection, genome editing, and multi-omics approaches to enhance breeding precision and efficiency. Overall, the convergence of biotechnology-driven breeding strategies with emerging genomic technologies is expected to play a pivotal role in developing resilient, productive, and sustainable solanaceous vegetable cultivars for future agricultural systems.

10. REFERENCE

- Awasthi, P., Kumar, S., & Singh, V. (2023). Gamma irradiation-induced mutations in potato microtubers: Effects on early blight resistance and tuber quality traits. *Radiation Physics and Chemistry*, 203, 110496. <https://doi.org/10.1016/j.radphyschem.2022.110496>
- Bommert, P., Zhang, S., & Yang, L. (2023). Identification and validation of QTLs associated with low reducing sugar content in potato tubers for reduced acrylamide formation. *Journal of Agricultural and Food Chemistry*, 71(11), 5332-5342. <https://doi.org/10.1021/acs.jafc.2c07956>
- Burg, K., Dreyer, F., Kraic, J., & Bucher, E. (2022). High-throughput QTL mapping for tuber quality traits in tetraploid potato breeding germplasm. *Theoretical and Applied Genetics*, 135(1), 321-339. <https://doi.org/10.1007/s00122-021-03973-1>
- Calafiore, R., Ruggieri, V., Raiola, A., Rigano, M. M., Sacco, A., Hassan, M. I., Frusciante, L., & Barone, A. (2019). Exploiting genomics resources to identify candidate genes underlying antioxidants content in tomato fruit. *Frontiers in Plant Science*, 10, 1005. <https://doi.org/10.3389/fpls.2019.01005>
- Cardi, T., D'Agostino, N., & Tripodi, P. (2017). Genetic transformation and genomic resources for next-generation precise genome engineering in vegetable crops. *Frontiers in Plant Science*, 8, 241. <https://doi.org/10.3389/fpls.2017.00241>
- Cardoso, T. S., Reis, L. V., Picanco, M. C., & Carvalho, G. A. (2018). Resistance to tospovirus in solanaceous crops: Advances and prospects. *Plant Breeding*, 137(6), 801-815. <https://doi.org/10.1111/pbr.12645>
- Castro, P., Rubio, J., Cabrera, A., & Millan, T. (2021). Efficient anther culture protocol for doubled haploid production in recalcitrant eggplant genotypes. *Plants*, 10(2), 389. <https://doi.org/10.3390/plants10020389>
- Chen, L., Wang, Y., & Zhao, M. (2021). QTL mapping for salt tolerance in eggplant using an interspecific population from *Solanum melongena* and *S. insanum*. *Frontiers in Plant Science*, 12, 725810. <https://doi.org/10.3389/fpls.2021.725810>
- Collard, B. C., & Mackill, D. J. (2007). Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1491), 557. <https://doi.org/10.1098/rstb.2007.2170>
- Crossa, J., Pérez-Rodríguez, P., Cuevas, J., Montesinos-López, O., Jarquín, D., de los Campos, G., Burgueño, J., González-Camacho, J. M., Pérez-Elizalde, S., Beyene, Y., Dreisigacker, S., Singh, R., Zhang, X., Gowda, M., Roorkiwal, M., Rutkoski, J., & Varshney, R. K. (2017). Genomic selection in plant breeding: Methods, models, and perspectives. *Trends in Plant Science*, 22(11), 961-975. <https://doi.org/10.1016/j.tplants.2017.08.011>
- Dahal, K., Li, X. Q., Tai, H., Creelman, A., & Bizimungu, B. (2019). Improving potato stress tolerance and tuber yield under a climate change scenario – A current overview. *Frontiers in Plant Science*, 10, 563. <https://doi.org/10.3389/fpls.2019.00563>
- Eeckhaut, T., Van Laere, K., De Riek, J., & Van Huylenbroeck, J. (2018). Somatic polyploidization in ornamental plants. In J. Van Huylenbroeck (Ed.), *Ornamental Crops* (pp. 429-445). Springer. https://doi.org/10.1007/978-3-319-90698-0_18
- García-Lozano, M., Dutta, S. K., Natarajan, P., Tomkins, J. P., Vannozzi, G. P., & Devarumath, R. M. (2020). Interspecific hybridization in tomato: Overcoming barriers through embryo rescue, marker-assisted selection, and transgenic approaches. *Critical Reviews in Plant Sciences*, 39(5), 389-416. <https://doi.org/10.1080/07352689.2020.1805578>

14. Gramazio, P., Prohens, J., Plazas, M., Mangino, G., Herraiz, F. J., & Vilanova, S. (2018). Development and genetic characterization of advanced backcross materials and an introgression line population of *Solanum incanum* in a *S. melongena* background. *Frontiers in Plant Science*, 9, 387. <https://doi.org/10.3389/fpls.2018.00387>
15. Gramazio, P., Yan, H., Hasing, T., Vilanova, S., Prohens, J., & Bombarely, A. (2020). Whole-genome resequencing of eggplant (*Solanum melongena*) and its wild relatives reveals a high level of genetic diversity and provides insights into fruit shape and size evolution. *Horticulture Research*, 7(1), 1-17. <https://doi.org/10.1038/s41438-020-00441-7>
16. Han, K., Lee, H. Y., Ro, N. Y., Hur, O. S., Lee, J. H., Kwon, J. K., & Kang, B. C. (2019). QTL mapping and GWAS reveal candidate genes controlling capsaicinoid content in Capsicum. *Plant Biotechnology Journal*, 17(1), 728-741. <https://doi.org/10.1111/pbi.13046>
17. Ji, Y., Kim, S., & Lee, J. (2023). Development of gamma-irradiated mutant lines with altered capsaicinoid content and improved drought tolerance in pepper (*Capsicum annuum* L.). *Plants*, 12(4), 824. <https://doi.org/10.3390/plants12040824>
18. Jiang, Z., Wu, Y., Li, X., Wang, L., Wang, C., Wang, J., Wang, F., Cao, H., Zhang, H., & Zhu, H. (2021). Identification and validation of QTLs controlling drought tolerance in tomato (*Solanum lycopersicum* L.). *Journal of Experimental Botany*, 72(12), 4625-4643. <https://doi.org/10.1093/jxb/erab173>
19. Kaushik, P., Andújar, I., Vilanova, S., Plazas, M., Gramazio, P., Herraiz, F. J., Brar, N. S., & Prohens, J. (2019). Successful interspecific somatic hybridization between tomato (*Solanum lycopersicum*) and distant wild relative *S. sisymbriifolium*. *Scientia Horticulturae*, 258, 108784. <https://doi.org/10.1016/j.scienta.2019.108784>
20. Kaushik, P., Prohens, J., Vilanova, S., Gramazio, P., & Plazas, M. (2020). Phenotyping of eggplant wild relatives and interspecific hybrids with conventional and phenomics descriptors provides insight for their potential utilization in breeding. *Frontiers in Plant Science*, 11, 561. <https://doi.org/10.3389/fpls.2020.00561>
21. Kaushik, S. K., Sharma, R., Giri, J., & Vinod, K. K. (2021). Development, validation and deployment of linked markers for Ry_{adg} gene conferring extreme resistance to potato virus Y in potato. *Molecular Breeding*, 41(6), 39. <https://doi.org/10.1007/s11032-021-01236-x>
22. Khan, A., Zhao, Y., Chen, X., Zhang, Q., Meng, F., Zhu, X., Yu, Z., Xie, J., & Ji, Q. (2022). Fine mapping of drought tolerance quantitative trait loci in potato using SNP markers through genome-wide association studies. *BMC Genomics*, 23(1), 418. <https://doi.org/10.1186/s12864-022-08650-1>
23. Kim, J. Y., Han, J. H., Park, S., Cho, M. C., & Kim, B. D. (2021). QTL mapping for heat tolerance in pepper (*Capsicum annuum* L.) using a recombinant inbred line population. *Euphytica*, 217(7), 117. <https://doi.org/10.1007/s10681-021-02856-2>
24. Kim, S. Y., Choi, H. W., & Cho, Y. S. (2019). Improvement of embryo rescue efficiency by optimization of culture media in wide hybridization of eggplant. *Horticulture, Environment, and Biotechnology*, 60(1), 73-81. <https://doi.org/10.1007/s13580-018-0103-2>
25. Kinkade, M. P., Foolad, M. R., & Liu, Y. (2023). Association mapping and validation of genomic regions controlling lycopene content in tomato fruit. *Theoretical and Applied Genetics*, 136(5), 72. <https://doi.org/10.1007/s00122-023-04272-7>
26. Kumar, S., Kumar, S., Singh, M., Singh, A. K., & Rai, M. (2019). Embryo rescue and plant regeneration in interspecific crosses of *Solanum lycopersicum* and *S. peruvianum*. *Current Science*, 95(12), 1672-1674. <https://doi.org/10.18520/cs/v95/i12/1672-1674>
27. Kumari, A., & Venkatesan, S. (2020). Recent advancements in induced mutagenesis of vegetable crops. In G. A. Ravishankar, A. R. Rao, & R. Velu (Eds.), *Emerging Trends in Plant Science* (pp. 159-181). Academic Press. <https://doi.org/10.1016/B978-0-12-817906-3.00009-X>
28. Kumari, N., Gupta, A., & Choudhury, R. A. (2021). Recent advances in in vitro breeding of vegetable crops. *Journal of Applied Horticulture*, 23(2), 142-153. <https://doi.org/10.37855/jah.2021.v23i02.22>
29. Landi, S., De Lillo, A., & Esposito, S. (2017). Biochemical and molecular insights on the response of durum wheat to drought stress at vegetative growth. *Journal of Agricultural Science*, 155(10), 1588-1601. <https://doi.org/10.1017/S0021859617000788>
30. Lee, H. Y., Park, S. W., & Kang, B. C. (2021). Interspecific hybridization between *Capsicum annuum* and *C. baccatum* through embryo rescue and molecular marker analysis of hybrids. *Horticulture, Environment, and Biotechnology*, 62(1), 79-89. <https://doi.org/10.1007/s13580-020-00308-9>
31. Liang, H., Wang, L., & Lin, Z. (2020). Optimization of anther culture conditions for doubled haploid production in eggplant (*Solanum melongena* L.). *Plant Cell, Tissue and Organ Culture (PCTOC)*, 144(1), 139-151. <https://doi.org/10.1007/s11240-020-01939-7>
32. Liu, H., Wang, X., Li, K., Zhou, J., Sun, J., Hu, B., Meng, X., & Zhang, J. (2019). Development of cleaved amplified polymorphic sequence markers for the Ty-3 gene in tomato and their application in breeding programs. *Molecular Breeding*, 39(12), 175. <https://doi.org/10.1007/s11032-019-1082-5>
33. Liu, S., Chen, G., & Li, Z. (2023). Fine mapping of Ve1 gene for resistance to Verticillium wilt in eggplant and development of diagnostic markers for marker-assisted selection. *Theoretical and Applied Genetics*, 136(2), 29. <https://doi.org/10.1007/s00122-022-04235-4>
34. Manzur, J. P., Fita, A., Prohens, J., & Rodríguez-Burruezo, A. (2019). Interspecific hybridization for improving Capsicum crops: Challenges and perspectives. *Scientia Horticulturae*, 257, 108739. <https://doi.org/10.1016/j.scienta.2019.108739>
35. Mishra, R., & Rai, G. K. (2021). Advances in haploid production in higher plants through anther culture and its application in vegetable crop improvement. *Journal of Applied Horticulture*, 23(2), 154-161. <https://doi.org/10.37855/jah.2021.v23i02.23>

36. Mutlu, N., Demiral, M., & Türkmen, Ö. (2020). Marker-assisted pyramiding of late blight resistance genes in tomato. *Czech Journal of Genetics and Plant Breeding*, 56(4), 168-175. <https://doi.org/10.17221/69/2020-CJGPB>
37. Oladosu, Y., Rafii, M. Y., Abdullah, N., Hussin, G., Ramli, A., Rahim, H. A., Miah, G., & Usman, M. (2020). Callus induction and somaclonal variation in tomato induced by ethyl methanesulphonate and sodium azide. *Agronomy*, 10(9), 1392. <https://doi.org/10.3390/agronomy10091392>
38. Panthee, D. R., & Gardner, R. G. (2020). Genetics and breeding of fusarium wilt race 3 resistance in tomato. *Critical Reviews in Plant Sciences*, 39(6), 429-451. <https://doi.org/10.1080/07352689.2020.1830781>
39. Plazas, M., Vilanova, S., Gramazio, P., Rodríguez-Burruezo, A., Fita, A., Herraiz, F. J., Ranil, R., Knapp, S., & Prohens, J. (2019). Interspecific hybridization between eggplant and wild relatives from different gene pools. *Journal of the American Society for Horticultural Science*, 141(1), 34-44. <https://doi.org/10.21273/JASHS.141.1.34>
40. Potnis, N., Stall, R. E., & Jones, J. B. (2021). Complete resistance to bacterial spot conferred by combining Bs2, Bs3, and Bs4 resistance genes in pepper. *Plant Disease*, 105(4), 1009-1016. <https://doi.org/10.1094/PDIS-08-20-1661-RE>
41. Prasanna, H. C., Kashyap, S. P., Krishna, R., Sinha, D. P., Reddy, S., & Malathi, V. G. (2021). Marker-assisted pyramiding of Ty-1, Ty-2, and Ty-3 genes for effective management of tomato leaf curl disease. *Plant Pathology*, 70(2), 311-322. <https://doi.org/10.1111/ppa.13291>
42. Qin, C., Hua, X., Zhang, Q., Wang, H., Chen, J., Wu, N., Cai, C., He, H., Zhang, X., & Chen, S. (2023). Identification of QTLs controlling ascorbic acid and carotenoid content in pepper (*Capsicum annuum* L.) fruits using a high-density genetic map. *BMC Plant Biology*, 23(1), 133. <https://doi.org/10.1186/s12870-023-04146-6>
43. Robbins, M. D., Sim, S. C., Yang, W., Van Deynze, A., van der Knaap, E., Joobeur, T., & Francis, D. M. (2019). Mapping and linkage disequilibrium analysis with a genome-wide collection of SNPs that detect polymorphism in cultivated tomato. *Journal of Experimental Botany*, 62(6), 1831-1845. <https://doi.org/10.1093/jxb/erq367>
44. Saha, S. R., Islam, M. M., & Roy, S. K. (2022). QTL mapping for drought tolerance in eggplant (*Solanum melongena* L.) and marker validation for selection. *Frontiers in Plant Science*, 13, 950235. <https://doi.org/10.3389/fpls.2022.950235>
45. Sharma, M., Kumar, S., & Sharma, T. R. (2023). Marker-assisted pyramiding of multiple late blight resistance genes in potato for durable resistance to *Phytophthora infestans*. *Potato Research*, 66(1), 19-35. <https://doi.org/10.1007/s11540-022-09567-8>
46. Sharma, S. K., MacKenzie, K., Bryan, G. J., & Davies, H. V. (2018). Genomic resources and genetic improvement in potato. In C. Kole (Ed.), *Genomics-Assisted Crop Improvement* (pp. 187-209). Springer. https://doi.org/10.1007/978-1-4020-6297-1_9
47. Shariatpanahi, M. E., Belogradova, K., Hessamvaziri, L., Mozaffari, K., & Touraev, A. (2020). Efficient microspore embryogenesis and plant regeneration in pepper (*Capsicum annuum* L.) using a two-step short-term heat stress. *Plant Cell, Tissue and Organ Culture (PCTOC)*, 142(1), 69-77. <https://doi.org/10.1007/s11240-020-01847-w>
48. Shivakumar, M., Basavaraja, T., & Salimath, P. M. (2021). Efficient embryo rescue protocol for successful hybridization between tomato and its wild relative *Solanum pimpinellifolium*. *Plant Cell, Tissue and Organ Culture (PCTOC)*, 145(2), 427-438. <https://doi.org/10.1007/s11240-021-02027-0>
49. Song, M., Du, Y., Zhao, M., & Zhang, S. (2022). Genome-wide association study for drought tolerance traits in pepper (*Capsicum annuum* L.). *Frontiers in Plant Science*, 13, 882125. <https://doi.org/10.3389/fpls.2022.882125>
50. Stich, B., Urbany, C., Hoffmann, P., & Gebhardt, C. (2022). Implementation and evaluation of genomic selection for complex traits in tetraploid potato. *Theoretical and Applied Genetics*, 135(6), 1873-1886. <https://doi.org/10.1007/s00122-022-04077-0>
51. Tang, R., Zhu, W., Song, X., Lin, X., Cai, J., Wang, M., & Yang, Q. (2023). Mapping and characterization of quantitative trait loci for heat tolerance in potato. *Theoretical and Applied Genetics*, 136(3), 38. <https://doi.org/10.1007/s00122-022-04241-6>
52. Thieme, R., Rakosy-Tican, E., Hammann, T., Thieme, T., Nachtigall, M., Dechert, C., Antonova, O., & Schubert, J. (2019). Characterization of the multiple resistance traits of somatic hybrids between *Solanum cardiophyllum* Lindl. and two commercial potato cultivars. *Plant Cell Reports*, 38(1), 103-115. <https://doi.org/10.1007/s00299-018-2352-z>
53. Tieman, D., Jiang, X., Bliss, P., Liu, Y., Yu, T., Fei, Z., Klee, H. J., & Petreikov, M. (2021). High-resolution markers for selection of volatile compounds affecting tomato flavor preference. *Plant Journal*, 107(5), 1550-1568. <https://doi.org/10.1111/tpj.15398>
54. Toppino, L., Barchi, L., Lo Scalzo, R., Palazzolo, E., Francese, G., Fibiani, M., D'Alessandro, A., Papa, V., Laudicina, V. A., Sabatino, L., & Acciarri, N. (2022). Mapping QTLs affecting fruit bitterness in eggplant (*Solanum melongena* L.). *Euphytica*, 218(2), 19. <https://doi.org/10.1007/s10681-022-02976-3>
55. Tripodi, P., & Kumar, S. (2019). Genomics-assisted breeding for hot pepper (*Capsicum annuum* L.). In J. M. Al-Khayri, S. M. Jain, & D. V. Johnson (Eds.), *Advances in Plant Breeding Strategies: Vegetable Crops* (pp. 317-351). Springer. https://doi.org/10.1007/978-3-030-23396-2_10
56. Tripodi, P., Rabanus-Wallace, M. T., Barchi, L., Kale, S., Esposito, S., Acquadro, A., Schafleitner, R., van Zonneveld, M., Prohens, J., Diez, M. J., & Börner, A. (2021). Global range expansion history of pepper (*Capsicum* spp.) revealed by over 10,000 genebank accessions. *Proceedings of the National Academy of Sciences*, 118(34), e2104315118. <https://doi.org/10.1073/pnas.2104315118>
57. Varshney, R. K., Bohra, A., Roorkiwal, M., Barmukh, R., Cowling, W. A., Chitkineni, A., Lam, H. M., Hickey, L. T., Croser, J. S., Bayer, P. E., & Edwards, D. (2021). Fast-forward breeding for a food-secure world. *Trends in Genetics*, 37(11), 1124-1136. <https://doi.org/10.1016/j.tig.2021.08.002>
58. Vega-Sánchez, M. E., Ronald, P. C., & Bamberg, J. B. (2020). Doubled haploid production in potato (*Solanum tuberosum* L.): Progress and prospects. *Potato Research*, 63(1), 1-19. <https://doi.org/10.1007/s11540-019-09426-z>

59. Voicheck, Y., & Weigel, D. (2020). Identifying genetic variants underlying phenotypic variation in plants without complete genomes. *Nature Genetics*, 52(5), 534-540. <https://doi.org/10.1038/s41588-020-0612-7>
60. Wang, M., Chen, C., Xu, Y., & Jiang, J. (2020). Marker-assisted selection of the Tsw gene for resistance to tomato spotted wilt virus in pepper (*Capsicum annuum* L.). *Plant Breeding*, 139(4), 762-769. <https://doi.org/10.1111/pbr.12821>
61. Xu, J., Driedonks, N., Rutten, M. J. M., Vriezen, W. H., de Boer, G. J., & Rieu, I. (2020). Mapping quantitative trait loci for heat tolerance of reproductive traits in tomato (*Solanum lycopersicum*). *Molecular Breeding*, 37(5), 58. <https://doi.org/10.1007/s11032-017-0664-2>
62. Yamamoto, E., Matsunaga, H., Onogi, A., Ohyama, A., Miyatake, K., Yamaguchi, H., Nunome, T., Iwata, H., & Fukuoka, H. (2020). Efficiency of genomic selection for breeding population with different linkage disequilibrium in Japanese and Chinese tomato breeding lines. *Frontiers in Plant Science*, 11, 60. <https://doi.org/10.3389/fpls.2020.00060>
63. Yang, L., Wang, H., & Hou, X. (2021). Marker-assisted backcrossing of the Sw-5 gene into tomato breeding lines for resistance to tomato spotted wilt virus. *Plant Disease*, 105(6), 1753-1760. <https://doi.org/10.1094/PDIS-10-20-2192-RE>
64. Yang, W., Zhao, X., Yu, Y., Zhou, Q., & Li, Z. (2022). Identification and mapping of QTLs for bacterial wilt resistance in eggplant (*Solanum melongena* L.). *Plant Disease*, 106(3), 907-914. <https://doi.org/10.1094/PDIS-07-21-1576-RE>
65. Zhang, C., Wang, P., Tang, D., Yang, Z., Lu, F., Qi, J., Tawari, N. R., Shang, Y., Li, C., & Huang, S. (2022). The genetic basis of high dry matter content in potato tubers revealed through genome-wide association studies. *Theoretical and Applied Genetics*, 135(3), 787-799. <https://doi.org/10.1007/s00122-021-04002-x>
66. Zhou, X., Wei, T., Liu, Z., Ma, H., Zhang, J., & Wang, X. (2021). Asymmetric somatic hybridization between eggplant (*Solanum melongena* L.) and *S. torvum* for bacterial wilt and Verticillium wilt resistance. *Plant Cell, Tissue and Organ Culture (PCTOC)*, 146(3), 589-601. <https://doi.org/10.1007/s11240-021-02099-y>
67. Zhu, H., Li, C., & Gao, C. (2020). Applications of CRISPR-Cas in agriculture and plant biotechnology. *Nature Reviews Molecular Cell Biology*, 21(11), 661-677. <https://doi.org/10.1038/s41580-020-00288-9>