



REVIEW ARTICLE

Cutting-edge genetic techniques for optimizing eggplant (*Solanum melongena*) cultivar performance

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Abstract

Brinjal (*Solanum melongena* L.), a crucial solanaceous vegetable crop, faces significant challenges from biotic stressors like pests and diseases, as well as abiotic stressors such as drought and salinity. Conventional breeding methods are limited in effectively addressing these complex traits. Nevertheless, advancements in molecular breeding, genetic engineering and tissue culture techniques have revolutionized brinjal improvement. Marker-assisted selection (MAS) has enabled the identification and incorporation of quantitative trait loci (QTLs) associated with resistance to bacterial wilt, shoot and fruit borer and enhanced yield attributes. Genetic engineering approaches, such as the development of Bt brinjal, have provided effective pest resistance while minimizing pesticide dependency. Tissue culture methods, including anther culture, have facilitated the rapid development of double haploid (DH) lines with improved fruit quality and tolerance to low temperatures. These biotechnological tools present promising solutions to mitigate stress factors while improving yield, quality and sustainability in brinjal cultivation. Future research should focus on integrating CRISPR/Cas9 gene editing with MAS to accelerate trait-specific improvements and utilize wild relatives for novel gene introgression.

Keywords: abiotic stress; biotic stress; CRISPR/CAS9; molecular breeding; tissue culture

Introduction

Eggplant (*Solanum melongena* L., $2n = 2x = 24$) is a globally cultivated vegetable crop of significant agronomic and economic importance, particularly in tropical and subtropical regions. Its adaptability to diverse agro-climatic conditions and high yield potential has led to widespread cultivation. In 2023, global eggplant production reached 12.61 million metric tonnes, highlighting its increasing demand and relevance in global food systems. Additionally, related wild species of *Solanum* are known to possess considerable medicinal properties, with over 77 distinct therapeutic uses reported across Asia alone (1). Despite its importance, eggplant cultivation is severely constrained by numerous biotic and abiotic stressors. Major biotic stresses include bacterial and fungal pathogens, root-knot nematodes and insect pests (2). Although some level of innate resistance exists within the germplasm, it is often incomplete and insufficient under field conditions (3, 4). The limited effectiveness of conventional pest control strategies, compounded by the concealed nature of certain pests, frequently leads to the indiscriminate use of synthetic pesticides. This not only contributes to the development of pesticide resistance but also raises concerns about food safety, ecological imbalance and economic sustainability (3).

Eggplant is recognized as a functional food due to its rich profile of health-beneficial compounds, including dietary fiber, vitamins, flavonoids, anthocyanins and phenolic acids, all of which contribute to its antioxidant and anti-inflammatory properties (4). The crop also contains alkaloids that exhibit medicinal potential; however, their excessive accumulation can result in bitterness and reduced palatability. Fortunately, under normal cultivation practices, cultivated varieties typically maintain alkaloid levels below the threshold of sensory and toxicological concern, unless subjected to extreme environmental stress (5). With the global population expected to exceed 9 billion by 2050 (6). There is an urgent need to enhance the productivity, resilience and nutritional quality of staple and horticultural crops, including eggplant. However, the rapid pace of climate change and biodiversity loss exacerbates the challenges of maintaining food security. Traditional breeding approaches, such as interspecific hybridization and selection, have been employed to improve eggplant traits. While effective, these methods are often labor-intensive, time-consuming and constrained by interspecific incompatibility barriers (7). To date, approximately 25 wild *Solanum* species have been successfully hybridized with cultivated brinjal, although the success rate remains relatively low (8).

To overcome these limitations, advanced molecular approaches such as genetic engineering and genome editing have emerged as powerful tools for targeted trait improvement. Among them, CRISPR/Cas9 (Clustered Regularly Interspaced Short Palindromic Repeats/CRISPR-associated protein 9) represents a breakthrough technology that enables precise genome modification. Originally derived from the adaptive immune system of bacteria and archaea, CRISPR/Cas9 facilitates site-specific DNA cleavage via Cas9 endonuclease guided by single-guide RNA (sgRNA), with cleavage dependent on the presence of a protospacer adjacent motif (PAM) sequence (9). The resultant double-strand breaks are repaired via either non-homologous end joining (NHEJ), which may introduce insertions or deletions, or homology-directed repair (HDR), which allows for precise sequence replacement or insertion (10).

Complementing genome editing, plant tissue culture techniques have also proven indispensable in eggplant improvement. These *in vitro* methods facilitate rapid propagation, regeneration and transformation of explants derived from stem, root, leaf, seed and embryo tissues. Optimization of culture media, hormone concentrations and stress elicitors has enabled enhanced regeneration efficiency and allowed for the development of stress-tolerant, disease-resistant and high-yielding cultivars within a relatively short time frame (11). This review aims to critically examine recent advances in genetic improvement strategies in *Solanum melongena* L., with a focus on molecular breeding, genome editing and tissue culture. Special emphasis is placed on addressing the challenges posed by both biotic and abiotic stressors and identifying innovative and sustainable solutions to enhance productivity, resilience and fruit quality in eggplant cultivation.

Molecular breeding approach

Brinjal (*Solanum melongena* L.) possesses extensive genetic diversity, which constitutes a critical reservoir for breeding programs aimed at enhancing key agronomic traits such as yield, biotic and abiotic stress tolerance and fruit quality. Numerous studies have demonstrated significant genotypic variation across cultivated and wild brinjal accessions, thereby facilitating the selection of superior lines for targeted

trait improvement (12). The advent of molecular markers, including RAPD and SSR, has revolutionized the assessment of genetic diversity and enabled the identification of robust marker-trait associations, particularly for resistance to devastating pests like the shoot and fruit borer (SFB) (12). Markers linked to specific traits-such as larval weight under infestation and extent of fruit damage-have proven invaluable in marker-assisted selection (MAS), substantially improving the efficiency and precision of breeding workflows (12). The availability of high-quality reference genome sequences has further empowered functional genomics, enabling genome-wide association studies (GWAS), fine mapping of quantitative trait loci (QTLs) and high-resolution marker development to accelerate trait introgression (13). Complementary to molecular strategies, combining ability analyses have identified genotypes with strong general and specific combining abilities for traits like fruit yield, earliness and marketable quality, offering reliable parental combinations for hybrid development (14). Heterosis breeding has also been effectively employed to exploit non-additive genetic variance, resulting in the release of high-performing hybrids with enhanced yield potential and resistance to major biotic stresses (Fig. 1). However, conventional breeding remains time-intensive and often constrained by linkage drag, sexual incompatibilities and the unintended introgression of undesirable traits such as bitterness or susceptibility to pathogens like *Colletotrichum gloeosporioides*, particularly when using wild relatives like *Solanum turvum* or *S. linnaeanum* (15, 16). These limitations underscore the utility of transgenic and genome editing approaches, which offer greater specificity and efficiency. For instance, the susceptible variety 'Pusa Purple Long' was crossed with the wilt-resistant line CARI-B-1 and advanced to the F₃ generation, where plants exhibited confirmed resistance in controlled sick plot evaluations (17). Similarly, Malaysian fusarium wilt-resistant lines LS1934 and LS2436 were hybridized with the susceptible line NSFB99 to generate F₁, F₂ and backcross populations, wherein resistance followed Mendelian segregation, indicating monogenic or oligogenic control (18). In the cross '305E40' × '67/3', F₂ progeny revealed QTLs conferring resistance to both *Fusarium* and *Verticillium* wilts (19). Moreover,

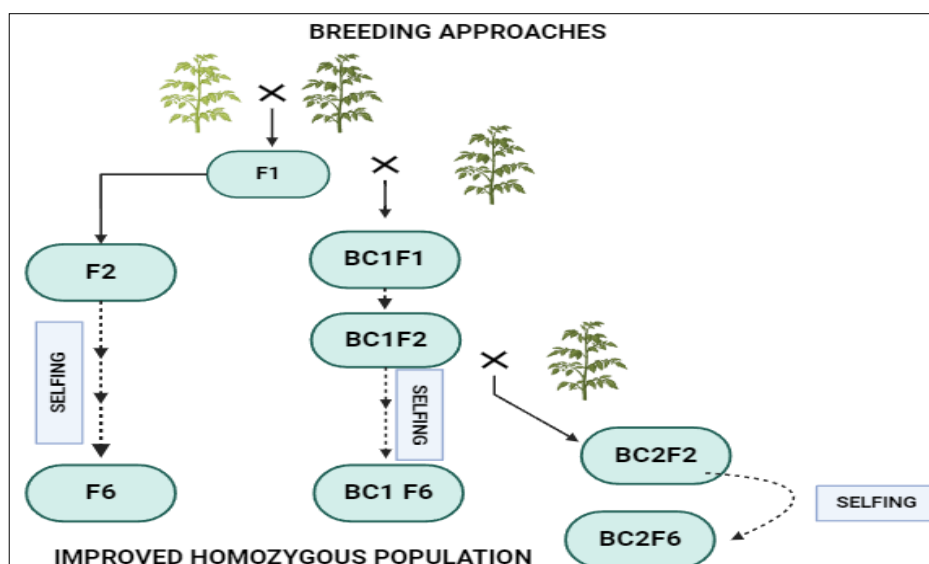


Fig. 1. Molecular breeding approaches.

interspecific hybrids between *Solanum incanum* and *S. melongena*, followed by backcrossing, have successfully yielded lines with elevated chlorogenic acid content, a natural compound with biopesticidal properties against SFB (20, 21). While these approaches have demonstrated substantial promise, the complex and polygenic nature of several economically important traits, such as abiotic stress tolerance and nutritional enhancement, necessitates deeper molecular dissection. Future breeding strategies must integrate advanced genomics tools, including high-throughput sequencing, gene editing technologies like CRISPR/Cas and developing trait-linked markers, alongside traditional methods to enable rapid, precise and sustainable genetic improvement in brinjal (13, 22). Such a holistic approach is imperative for accelerating cultivar development, ensuring resilience against climate-induced challenges and securing long-term productivity and nutritional security (Table 1).

Transformation for stress resistance

Genetic transformation in brinjal (*Solanum melongena* L.), a crop of significant economic and nutritional importance, has emerged as a pivotal approach for the targeted enhancement of complex traits that are difficult to improve through conventional breeding alone. These include resistance to major insect pests, notably the shoot and fruit borer (SFB), as well as improvements in yield stability and nutritional quality. Among the various transformation methods, *Agrobacterium tumefaciens*-mediated transformation remains the most efficient and widely utilized technique due to its ability to facilitate stable integration of transgenes with relatively low copy number and minimal somaclonal variation. In this method, genetically engineered *Agrobacterium* strains carrying the gene of interest are used to infect explants, typically derived from hypocotyls or cotyledons. Optimization of transformation parameters-such as explant type, pre-culture duration, acetosyringone concentration and co-cultivation time-has led to significant improvements in transformation efficiency (23, 24). Notably, the brinjal cultivar 'Arka Samhitha' exhibited a high transformation efficiency of 45.66 % using an in planta seed transformation approach, which bypasses the need for tissue culture and simplifies the transformation pipeline (23). These advances in genetic engineering complement findings from conventional

breeding, which have revealed substantial genotypic variability for key agronomic traits such as fruit weight, plant height and total yield. High heritability estimates coupled with significant genetic advance for these traits suggest a strong additive genetic component, thereby enabling effective selection-based improvement. The integration of precise genetic transformation strategies with traditional breeding frameworks offers a robust and accelerated route for the development of improved brinjal cultivars. Such integration holds the potential to produce varieties with enhanced pest resistance, better adaptability to biotic and abiotic stresses and enriched nutritional profiles-contributing not only to increased agricultural productivity but also to long-term food and nutritional security (12, 25) (Fig. 2).

Biotic stress

The incorporation of biotic stress resistance through genetic transformation in brinjal (*Solanum melongena* L.) has become an imperative strategy in modern crop improvement, driven by the extensive yield losses and economic setbacks caused by persistent pests and pathogens. Chief among these is bacterial wilt, caused by *Ralstonia solanacearum* and the fruit and shoot borer (*Leucinodes orbonalis*), both of which severely constrain brinjal productivity across major growing regions. Traditional management approaches, such as cultural practices, crop rotation and chemical control, have shown limited efficacy, particularly against *R. solanacearum*, a soil-borne bacterium characterized by a broad host range, high genetic variability and the ability to survive for prolonged periods in diverse environmental reservoirs. Similarly, the internal feeding habit and rapid life cycle of *L. orbonalis* make it poorly responsive to conventional insecticidal interventions. Considering these limitations, genetic transformation offers a highly targeted and durable solution by enabling the direct introduction of well-characterized resistance genes into elite brinjal cultivars without linkage drag or the need for extensive backcrossing. Genes such as *cry1Ac* and *cry1F*, derived from *Bacillus thuringiensis* (Bt), have been successfully deployed to confer high levels of resistance against SFB, markedly reducing pest incidence and reliance on chemical pesticides. Furthermore, the integration of resistance genes through transformation can be combined with molecular markers for efficient selection, expediting the breeding process. Overall, genetic engineering not only addresses the shortcomings of conventional methods

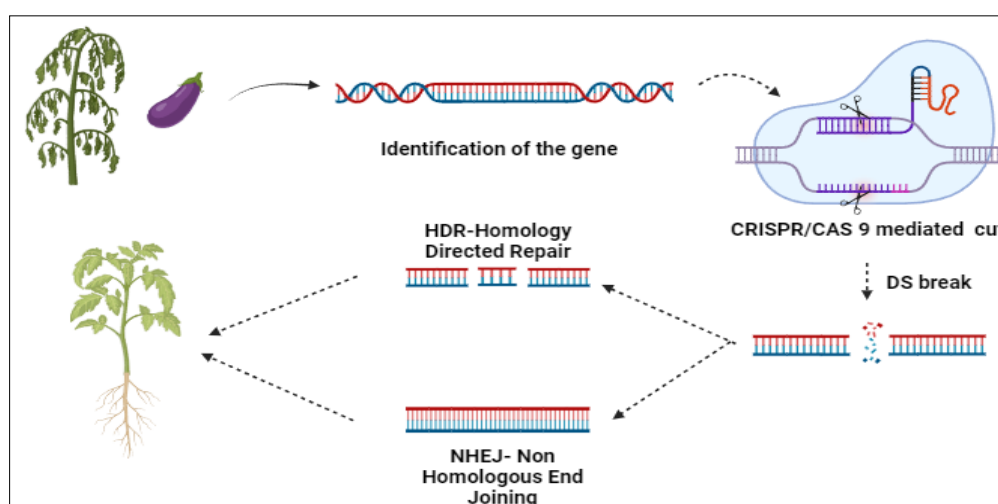


Fig. 2. CRISPR/Cas9 mediated transformation (DS - double strand).

Table 1. Different varieties released using marker-assisted selection

S.No.	Varieties	Key Features	Resistance Traits	Marker Name(s)	QTL Name	QTL Position	LOD Score	Variance Explained (%)	References
1	CHES WS-1	Elite genotype resistant to Shoot and Fruit Borer (SFB)	Resistance to SFB infestation	RAPD: OPN04_4; SSR: smSSR03_1, smSSR04	Not specified	Not specified	Not reported	Not reported	(95)
2	BBSR 117-1	Genotype with resistance against SFB	Resistance to SFB infestation	RAPD: OPN04_4; SSR: smSSR03_1, smSSR04	Not specified	Not specified	Not reported	Not reported	(95)
3	BB44	Genotype with moderate tolerance to SFB	Tolerance to SFB infestation	RAPD: OPC05_8	Not specified	Not specified	Not reported	Not reported	(95)
4	BBSR 200	Genotype with moderate tolerance to SFB	Tolerance to SFB infestation	RAPD: OPC05_8	Not specified	Not specified	Not reported	Not reported	(95)
5	Goa Brinjal-1	Bacterial wilt-resistant variety	Resistance to bacterial wilt	SSR markers	<i>qBWR-2.1, qBWR-11.1</i>	2 and 11	~9.0	18.5 %	(96)
6	Goa Brinjal-2	Bacterial wilt-resistant variety	Resistance to bacterial wilt	SSR markers	<i>qBWR-2.1, qBWR-11.1</i>	2 and 11	~7.5	15.2 %	(96)
7	Arka Nidhi (BWR 12)	Medium-long, blue-black, glossy fruits	Resistance to bacterial wilt	SSR markers	<i>qBWR-2.1</i>	2	~9.0	18.5 %	(96)
8	Arka Neelkanth	Short purple fruits borne in clusters of two	Resistance to bacterial wilt	SSR markers	<i>qBWR-2.1</i>	2	~9.0	18.5 %	(96)
9	Surya and Swetha	Early use of RAPD markers in wilt resistance	Resistance to bacterial wilt	RAPD markers OPA-11, OPD-8	Not specified	Not specified	Not reported	Not reported	(97)
10	EG203	Stable parthenocarp QTL; high breeding value; SSR-based MAS validated	Parthenocarp	SSR markers emf21H22 and emh11J10	<i>Cop8.1</i>	8	Not reported	~40 %	(98)
11	67/3 and SM6	Mapped organ-specific pigmentation traits; useful in improving market appeal	Anthocyanin pigmentation	SNP and SSR markers from RAD-seq	<i>UndcalE10 / PnccE10</i>	10	Not reported		(99)
12	Experimental F6 lines (<i>S. melongena</i> × <i>S. incanum</i>)	Major QTL clusters on E10; useful in developing high-anthocyanin lines	Fruit and shoot borer resistance	RAD tag-derived SNP markers	Multiple	Multiple	Up to 73.2	Up to 77.2 %	(100)
13		Major QTL; stable across environments; potential candidate gene near ANT1 (anthocyanin regulator)	Adaxial leaf anthocyanin (adlan)	15158_PstI_L379	adlanE10.ML / MT	10	36.9 / 44.9	60 % / 92 %	
14		Co-localizes with multiple anthocyanin traits; strong additive effect	Stem anthocyanin (stean)	1891_PstI_L363	steanE10.ML / MT	10	36.6 / 32.5	48.7 % / 44.7 %	
15		Novel QTL; specific to MT environment; high phenotypic contribution	Abaxial leaf anthocyanin (ablan)	11760_PstI_L333	ablanE10.MT	10	23.3	55.2 %	
16	'305E40' × '67/3' F ₂ population	Robust QTL; overlaps with calyx pigmentation hotspot; breeding value for pigment intensity	Calyx anthocyanin (calan)	1891_PstI_L363	calanE10.ML / MT	10	47.5 / 52.2	55.3 % / 73.6 %	
17		One of the strongest QTLs; very high heritability; target for MAS	Leaf venation anthocyanin (lvean)	1891_PstI_L363	lveanE10.ML / MT	10	58.9 / 61.8	83.3 % / 86.9 %	
18		Strongest QTL in study; nearly complete phenotypic explanation in MT; ideal for functional gene mining	Fruit peduncle anthocyanin (pedan)	35442_PstI_L404	pedanE10a.ML / MT	10	73.2 / 48.3	76.4 % / 99.8 %	
19		Distinct from other QTLs; mapped to E05; associated with ornamental value	Corolla color (corcol)	3311_PstI_L361	corcolE05.ML / MT	5	34.0 / 32.7	63.7 % / 57.3 %	

but also provides a robust platform for developing resilient brinjal cultivars, thereby enhancing yield stability and contributing to sustainable pest and disease management under intensifying biotic stress conditions (26, 27).

Disease resistance

The development of transgenic brinjal (*Solanum melongena* L.) lines through genetic engineering has emerged as a promising strategy for enhancing resistance against a broad spectrum of biotic stresses, including fungal, bacterial, viral and phytoplasmal diseases. This approach offers several advantages over traditional methods, including greater precision, durability of resistance, reduced reliance on chemical pesticides and cost-effectiveness in the long term. One of the major challenges in transgenic research, however, is the variability in resistance levels among independent transformants, which is often attributed to position effect-mediated differences in transgene expression depending on the genomic integration site (28). A notable target for antifungal resistance in transgenic plants is the class I chitinase family-vacuolar enzymes capable of degrading the chitin-rich cell walls of phytopathogenic fungi. Expression of *chi* genes in transgenic brinjal has been linked to enhanced resistance against wilt-causing pathogens such as *Verticillium dahliae* and *Fusarium oxysporum* (29).

Beyond pathogenesis-related proteins, metabolic engineering has also contributed to disease resistance. Overexpression of a yeast $\Delta 9$ -desaturase gene in eggplant resulted in elevated levels of palmitoleic acid, oleic acid and trienoic fatty acids, which correlated with increased resistance to *Verticillium* wilt. Palmitoleic acid, in particular, has been shown to directly inhibit the growth of *Verticillium in vitro*, suggesting a dual structural and antimicrobial role for these fatty acids (30). Similarly, transgenic brinjal expressing the alfalfa acidic glucanase gene demonstrated resistance to both *Fusarium* and *Verticillium* wilt, owing to the enzyme's ability to hydrolyze β -glucan components of fungal cell walls (31, 32). The *mtlD* gene, encoding mannitol-1-phosphate dehydrogenase, has been introduced into brinjal to induce mannitol accumulation—a sugar alcohol that acts as an osmoprotectant and antioxidant. Transgenic plants expressing *mtlD* exhibited enhanced tolerance to *Verticillium* wilt, *Fusarium* wilt and damping-off disease, with mannitol levels absent in wild-type lines but positively correlated with resistance in transgenics (28).

Incorporation of antifungal proteins such as hevein, introduced into the cultivar 'Arka Neelkanth', has also conferred broad-spectrum fungal resistance due to its chitin-binding activity (28). Similarly, the introduction of the ADC gene (arginine decarboxylase) has been shown to increase the synthesis of polyamines, which play a key role in plant stress responses, including resistance to *Fusarium oxysporum* (28). To target foliar pathogens, the Wasabi defensin gene from *Wasabia japonica* has been introduced into eggplant to confer resistance against *Alternaria solani*, the causative agent of Alternaria leaf spot (33). For viral resistance, transgenic brinjal lines expressing the coat protein gene have exhibited protection against Cucumber Mosaic Virus (CMV) and Tomato Chlorotic Spot Virus (TCSV), particularly in the susceptible cultivar 'Pusa Purple Long' (34). Furthermore,

transformation with the SW-5 gene, originally derived from tomato, has imparted resistance to Tospoviruses, including Tomato Chlorotic Virus (35). In addition to transgenic approaches, candidate genes such as RPN10, a conserved ubiquitin receptor protein implicated in proteasomal regulation, have been identified for genome editing. RPN10 has shown potential in enhancing resistance against little leaf disease caused by phytoplasma and represents a valuable target for CRISPR-based improvement (36).

Together, these genetic engineering strategies underscore the expanding toolkit for biotic stress management in brinjal. By leveraging both transgenic and genome-editing approaches, it is now feasible to develop brinjal cultivars with durable and broad-spectrum resistance, thereby improving crop productivity, reducing pesticide usage and contributing to sustainable agricultural practices.

Pest resistance

Agrobacterium-mediated transformation has played a pivotal role in the advancement of genetic engineering in brinjal. Guri and Sink first demonstrated this method in 1988, wherein co-cultivation of leaf explants with *Agrobacterium tumefaciens* led to the successful generation of kanamycin-resistant transgenic plants in the cultivar 'Picientia'. Since then, several studies have contributed to the optimization of transformation protocols in eggplant, focusing primarily on enhancing transformation efficiency and regeneration capacity (37, 38). Although the technical aspects of eggplant transformation are now well-established, the generation of transgenic lines with agronomically significant traits remains limited. One of the earliest attempts to impart insect resistance involved the introduction of the *chloramphenicol acetyltransferase* (*cat*) gene to confer resistance against the Colorado potato beetle (*Leptinotarsa decemlineata*), a major pest in solanaceous crops (39). Additionally, several reporter genes, including *gus* (encoding β -glucuronidase) and *luc* (encoding luciferase), have been employed in brinjal to develop efficient transformation systems and evaluate gene expression patterns (40).

The deployment of resistance genes from other plant species has also been successful. For instance, the *Mi-1.2* gene, originally identified in tomato, was introduced into brinjal cv. HP 83, resulting in resistance to the root-knot nematode *Meloidogyne incognita* (41, 42). One of the most impactful applications of genetic transformation in brinjal has been the introduction of genes from *Bacillus thuringiensis* (Bt), a bacterium that produces crystal (Cry) proteins— δ -endotoxins toxic to specific insect orders such as Lepidoptera, Coleoptera and Diptera (43, 44). Transgenic brinjal expressing various *cry* genes, including *cry1Ac*, *cry1Ab* and *cry1F*, has demonstrated high levels of resistance to the shoot and fruit borer (*Leucinodes orbonalis*), a major pest known for its resistance to conventional insecticides. For example, the cultivar 'Ruchira' showed a transformation efficiency of 19.8 % when engineered with the *cry1F* gene, leading to effective suppression of SFB infestation (45). Furthermore, synthetic *cry1Ab* genes have been engineered for broader lepidopteran resistance (46, 47) and have also shown potential against *M. incognita* (48). Transgenic lines expressing cystatin genes—protease inhibitors such as rice

cystatin-exhibited resistance to both *M. incognita* and piercing-sucking insects like the green peach aphid (*Myzus persicae*) and the potato aphid (*Macrosiphum euphorbiae*) (35, 49).

Advances in co-transformation strategies have further refined the development of insect-resistant brinjal. The co-delivery of *cry2Ab* along with *gus* in separate plasmids has been used to generate marker-free transgenic lines, enabling insect resistance without the retention of selectable marker genes (50). Additionally, the *Berl* gene has been introduced to modulate the toxicity of *Cry3B* protein and improve crop yield (51). A highly efficient transformation system involving the EHA105 *Agrobacterium* strain carrying the *cry1Ab* gene was utilized to transform cotyledonary explants, offering a reliable pipeline for developing Bt brinjal (46). The incorporation of *cry1Ac* along with selectable marker genes such as *nptII* and *aad* (aminoglycoside N⁶-acetyltransferase) resulted in transgenic plants with stable and high-level expression of insecticidal proteins effective against SFB (15, 32).

The development of Bt brinjal marked a significant milestone in brinjal biotechnology. By conferring built-in resistance to the brinjal fruit and shoot borer—a pest notoriously difficult to manage through conventional methods—Bt brinjal represents a major advancement in integrated pest management. This genetically engineered cultivar not only reduces dependency on synthetic insecticides but also enhances yield and improves farmer profitability (32, 52). The success of Bt brinjal highlights the broader potential of genetic transformation in brinjal improvement, particularly when integrated with sustainable agricultural practices and regulatory frameworks (Table 2).

Abiotic stress resistance

CRISPR/Cas9-mediated mutagenesis of the *Solanum melongena* phytoene desaturase (*SmPDS*) gene was conducted to validate genome editing efficiency. A three-primer PCR-based genotyping approach was employed to confirm the homozygosity of the mutant lines. The resultant edited plants exhibited a characteristic albino phenotype, indicative of successful disruption of the *PDS* gene, thus validating the effectiveness of the gene-editing protocol and offering a visual marker for transgene confirmation (53). To enhance abiotic stress tolerance, the *mtlD* gene, encoding mannitol-1-phosphate dehydrogenase, was introduced into brinjal via *Agrobacterium*-mediated transformation. Co-cultivation was performed using one-month-old axenic seedlings, employing 1 cm leaf explants devoid of the midvein and marginal tissue. The transgenic lines demonstrated enhanced tolerance to salinity, drought and low-temperature stress, attributed to osmotic adjustment conferred by mannitol accumulation (54). Similarly, the introduction of the *rd29A-DREB1A* transcription factor gene, under the control of the stress-inducible *rd29A* promoter, significantly improved tolerance to moisture deficit conditions by activating downstream stress-responsive genes (55).

In another strategy, overexpression of the *adc* (arginine decarboxylase) gene led to elevated levels of polyamines, such as putrescine, spermidine and spermine. Notably, transgenic plants also exhibited increased diamine

oxidase (DAO) activity, suggesting a coordinated upregulation of polyamine catabolism. These polyamine-rich lines exhibited broad-spectrum abiotic stress tolerance, including resistance to salinity, drought, temperature extremes and heavy metal toxicity (28). Transgenic brinjal plants expressing the *HAL1* gene, isolated from *Saccharomyces cerevisiae*, demonstrated improved growth under high salinity stress. The *HAL1* gene is known to regulate ion homeostasis, thereby enhancing salt stress tolerance in heterologous systems (56). Phenotypically, salt-tolerant genotypes were characterized by higher chlorophyll content, improved photosynthetic efficiency, increased biomass accumulation and reduced canopy temperature under stress conditions, indicating enhanced physiological performance (57).

Moreover, under salt stress, elevated levels of anthocyanins, lycopene, malondialdehyde (MDA), hydrogen peroxide (H₂O₂) and antioxidant enzymes were observed. Among evaluated genotypes, the cultivar ICS-BR-1351 exhibited superior resilience, suggesting its potential utility in breeding programs targeting salt-prone environments (58). In another approach to delay stress-induced senescence, the *PMI* (phosphomannose isomerase) gene, conferring mannose selection capability, was excised using *PstI* and *XbaI* restriction enzymes and fused with the *IPT* (isopentenyl transferase) gene under the senescence-associated *pSAG12* promoter in a binary vector. Following *Agrobacterium*-mediated transformation and molecular validation through PCR, Southern blotting and RT-PCR, the transgenic lines were exposed to cold stress (4 °C) and a 30-day drought period. Remarkably, no abnormal cytokinin overproduction was observed and senescence was significantly delayed, highlighting the role of localized cytokinin synthesis in stress adaptation without detrimental phenotypic effects (59).

Genome editing for enhancing quality attributes

Recent breakthroughs in genome editing have enabled precise and targeted modifications in plant genomes, marking a significant advancement over traditional transgenic approaches that typically rely on random gene insertions. With the advent of high-quality genome sequences and the development of programmable endonucleases such as CRISPR/Cas systems, it is now feasible to introduce or modify genes at specific loci, thereby enhancing the predictability, efficiency and safety of genetic engineering efforts (60). In *S. melongena*, the CRISPR/Cas9 system has been utilized to induce targeted mutations in the *SIDMR6-1* gene, a homolog implicated in disease resistance. This editing was achieved through protoplast electrofusion techniques, demonstrating the potential of cell-based genome engineering methods for generating precise allelic variants (61). In addition, somatic hybrid genome characterization using genomic in situ hybridization (GISH) has provided valuable insights into the chromosomal behavior and stability of hybrid genomes, further supporting the utility of cytogenetic tools in genome engineering studies (62) (Fig. 2).

Transgenic brinjal plants have also been developed through targeted expression of the *iaaM* gene from *Pseudomonas syringae*, which encodes tryptophan monooxygenase—an enzyme involved in auxin biosynthesis.

This gene was placed under the control of the ovule-specific *DefH9* promoter from *Antirrhinum majus*. The transgenic lines exhibited parthenocarpic (seedless) fruit development in the absence of fertilization due to elevated auxin levels, while retaining the ability to produce seeded fruits upon pollination. Under greenhouse conditions, these engineered plants demonstrated higher fruit yield compared to non-transgenic controls, indicating the agronomic benefits of hormonal manipulation for fruit set and productivity (63, 64). Enzymatic browning, a major post-harvest quality concern in brinjal, has been linked to the activity of polyphenol oxidase (PPO), peroxidase (POD) and the accumulation of chlorogenic acid. These components collectively contribute to oxidative discoloration and loss of visual and nutritional quality during storage and processing (65, 66). Targeted suppression of PPO and related enzymatic pathways is being explored as a strategy to improve shelf life and marketability of brinjal cultivars.

The efficiency of *Agrobacterium tumefaciens*-mediated transformation in brinjal is significantly influenced by virulence (*vir*) gene induction, which is triggered by phenolic compounds released from wounded plant tissues. Among these, acetosyringone—a low molecular weight phenolic compound—has been widely employed to enhance transformation efficiency by acting as a potent inducer of *vir* genes (40, 67). Additionally, polyamines such as spermidine and putrescine have been reported to further stimulate *vir* gene expression and improve T-DNA transfer efficiency during co-cultivation, underscoring their potential role as transformation adjuvants (37, 68). Together, these advances in precise genome editing, targeted hormonal regulation, enzymatic pathway modulation and improved transformation protocols represent a comprehensive toolkit for developing improved brinjal cultivars with enhanced agronomic and post-harvest traits (Table 2).

Tissue culture

Tissue culture has emerged as a fundamental tool in the genetic improvement, conservation and rapid multiplication of brinjal (*Solanum melongena* L.), a crop of high nutritional and economic significance. It facilitates the development of elite cultivars with enhanced traits such as disease resistance, abiotic stress tolerance and yield potential. Among its most notable applications is the generation of doubled haploids through anther and microspore culture, significantly reducing the time required for homozygosity in breeding programs (69). Plant regeneration through tissue culture has been achieved using a wide range of explants, including leaf discs, stem segments, shoot apices and hypocotyls, with regeneration efficiency being strongly influenced by the type and concentration of plant growth regulators (70, 71). Protocols for

efficient callus induction and plantlet regeneration have been optimized for unique brinjal landraces such as *Mattu Gulla*, supporting both genetic transformation and germplasm conservation (72).

A robust regeneration protocol is a prerequisite for successful genetic transformation. The earliest report of *in vitro* regeneration in wild brinjal (*Solanum sisymbriifolium* Lam.) provided foundational insights into species-specific responses (73). Subsequently, the use of indole-3-acetic acid (IAA) in Murashige and Skoog (MS) medium enabled somatic embryogenesis (SE) from immature seeds, marking a significant milestone in brinjal tissue culture (74, 75). Polyamines (PAs), particularly putrescine, have been shown to play a regulatory role in somatic embryogenesis by modulating cell differentiation. Temporal analysis of endogenous free, conjugated and bound forms of putrescine, spermidine and spermine across different hypocotyl regions revealed dynamic shifts in PA concentrations, highlighting their involvement in the critical phases of SE (76). Notably, leaf discs from apical regions, characterized by higher endogenous PAs, produced a greater number of somatic embryos (77). In the *Wase Shinkuro* cultivar, digoxigenin (DIG) treatment has also been demonstrated to effectively induce SE (78). Somatic embryos derived from callus tissues exhibit the highest regeneration potential and artificial seed production using sodium alginate (pH 6.0) has shown promising results. However, the addition of gibberellic acid and sucrose negatively impacts synthetic seed viability and regeneration (79). In addition to embryogenesis, organogenesis—a process involving the formation of shoots and roots from various explants—has also been widely employed in brinjal tissue culture. Explants such as leaf bases, shoot tips, root tips and floral buds respond differently depending on the hormonal balance in the culture medium, with regeneration success being contingent on both explant type and plant growth regulator composition (80, 81).

Recent studies have explored the use of natural biostimulants in *in vitro* propagation. Seeds treated with seaweed liquid extracts (SLEs) from species such as *Gracilaria salicornia*, *Padina gymnospora*, *Padina boergesenii* and *Gelidiella acerosa* exhibited enhanced germination, shoot proliferation and root induction. This suggests that SLEs can serve as eco-friendly alternatives to synthetic phytohormones in large-scale propagation systems (82). In anther culture, increased concentrations of ammonium nitrate (NH_4NO_3) have been reported to enhance embryogenic response, resulting in the generation of doubled haploid lines, such as SDH-36, which are valuable for developing homozygous breeding material (83). Additionally, herbicide-resistant lines have been developed by culturing *Pusa Purple Long* seeds on

Table 2. Transgenic eggplants with improved agronomic traits

Gene	Traits	Reference
Bt (codon-optimized Cry2Aa)	Resistance against brinjal shoot and fruit borer	(89)
Synthetic Cry1Aa3	Resistance against shoot and fruit borer (<i>Leucinodes orbonalis</i>)	(90)
Bt (Cry1F)	Resistance against shoot and fruit borer (<i>Leucinodes orbonalis</i>)	(45)
Bt (Cry1Aabc)	Resistance against shoot and fruit borer (<i>Leucinodes orbonalis</i>)	(91)
Antisense SmelPPO 1,4,5,6	Reduction of enzymatic browning	(92)
Rfo-sa1	Resistance to fusarium wilt	(93)
DefH9-iaaM(j)	Parthenocarpic transgenic plants	(94)

MS media supplemented with atrazine, demonstrating the feasibility of selection-based *in vitro* techniques for trait incorporation (84).

Salicylic acid (SA), a known plant defense elicitor, has been widely studied for its role in enhancing pathogen resistance in brinjal. SA treatment via bare-root dipping significantly reduced root-knot nematode (*Meloidogyne* spp.) infestation, increased the activity of defense enzymes such as phenylalanine ammonia-lyase (PAL) and peroxidase (PO) and improved overall plant vigor (85, 86). Furthermore, SA seed priming induced cellular changes, including cell wall thickening, enhancing seed resilience against *Verticillium* wilt (87). To enhance resistance against vascular wilt caused by *Fusarium oxysporum*, somatic hybridization between *S. melongena* and *S. aethiopicum* has been employed. Dihaploid lines derived from these hybrids through anther culture have shown promising resistance, underlining the utility of wide hybridization and haploid technology in brinjal improvement (88) (Fig. 3).

Conclusion

There are many methods for improving brinjal's tolerance to biotic and abiotic stressors that are thoroughly explored in this paper. Recent years have seen tremendous progress due to genome editing methods like CRISPR/Cas9, which enable accurate alterations to the brinjal's genomic DNA, focusing on certain genes that confer tolerance. The techniques for genetic transformation, including the insertion of foreign genes through processes like *Agrobacterium*-mediated transformation, have also proven crucial. By introducing desirable features from other species, these strategies help to increase stress tolerance and widen the genetic basis. Development of improved varieties using breeding approaches may be time-consuming but provides prominent results. Furthermore, developing plants from tissue cultures using plant regeneration techniques has proved crucial in creating

genetically stable and homogenous plants that are resistant to a range of challenges. The study also covers new techniques and technological advancements that are improving our knowledge of the molecular and genetic processes behind Brinjal's ability to withstand stress.

Future prospects

Numerous cutting-edge technologies are available for enhancing both the qualitative and quantitative characteristics. Everything was mostly dependent on traditional crop development techniques, which have several drawbacks, including high labor and time requirements and little yield in terms of noticeable improvement in eggplant. A later development was plant tissue culture, which attempted to create plants with better traits but also failed to produce any significant improvements. Then, to be more exact, genome editing and transformation emerged. While they have shown promising effects in other crops, eggplant is still a complicated crop and little research has been done on it, so this opens the door for more research in the future like Advanced phenotyping methods (like high throughput imaging, thermal infrared imaging, fluorescence imaging and so forth), bioinformatics tools (like BLAST, Clustal, Galaxy, so on) and high-throughput sequencing (Sequencing-by-synthesis, RNA-seq, Nanopore, Roche/454 pyrosequencing) are a few of the developments that help generate more robust brinjal varieties and offer deeper insights. Even if we work to develop the crop, there are some hardships. For instance, most of the population in the country is Orthodox because they find it difficult to accept genetically modified plants for consumption. Shortly, everyone will be supportive of embracing it.

Authors' contributions

All authors have contributed to the writing, editing, summarizing and revising the manuscript. All authors read and approved the final manuscript.

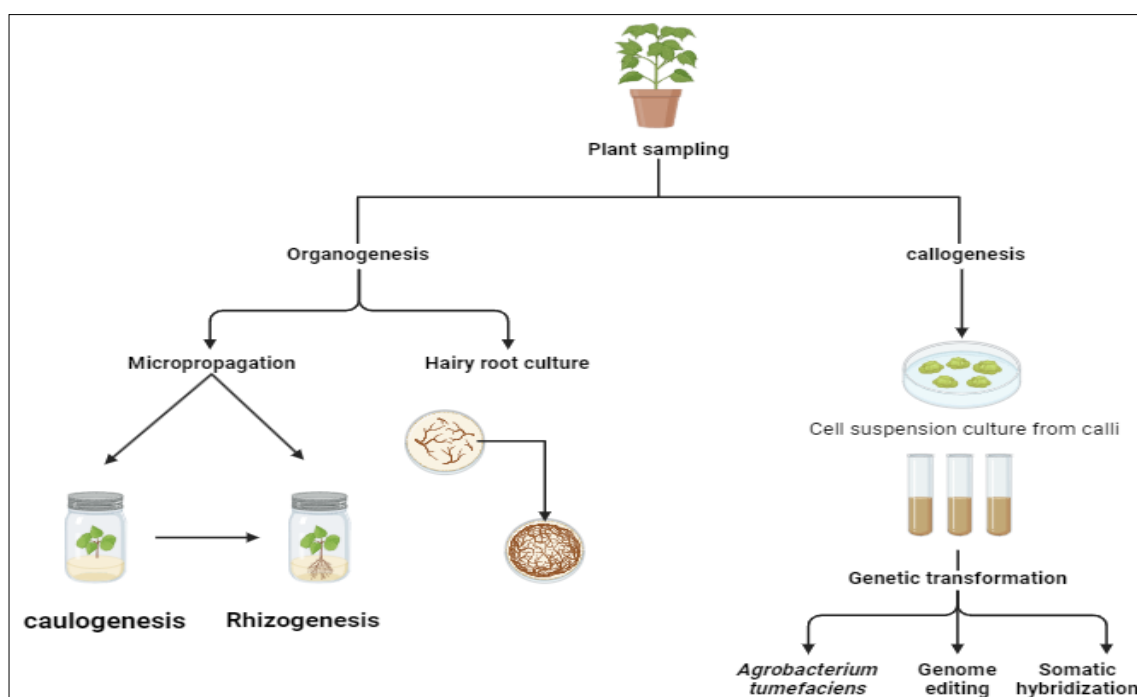


Fig. 3. Methods and application of tissue culture.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

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