Agrobacterium-mediated genetic transformation studies in soybean (*Glycine max* (L.) Merrill) for sustainable food and nutritional security: A Review

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Highlights

- The essential stress-responsive genes and transcription factors are *DREB*, *NAC*, *bZIP*, *WRKY*, *MYB*. These contribute to the improved tolerance in soybean against drought, salinity and biotic stress which are also critically analysed.
- Some of the *Agrobacterium*-mediated transformation parameters are systematically analysed, such as the type of explant, bacterial strain, parameters of infection and selection systems
- Genetic determinants that control ion homeostasis, osmoprotection, antioxidant defence and yield stability under stressful conditions are fully summarized.
- Transgenic approaches such as pathogen and pest resistance genes, and pathways that improve stress resilience in soybean are considered.
- Metabolic engineering of the protein composition, tocopherol, carotenoid and fatty acid biosynthesis pathways used to advance soybean biofortification are addressed.
- The existing constraints, such as genotype dependency, low transformation efficiency, are highlighted. New approaches like gene stacking, combination with genome editing technology, are discussed.

Abstract

Soybean (*Glycine max* (L.) Merrill), is a major legume crop in the family Fabaceae. It is significant source of plant-based protein and oil, which is important determinant in the food and nutritional security of the world. However, its productivity is progressively being limited by the abiotic stresses (drought and salinity), and biotic stresses (diseases and pests). Conventional breeding has limited success due to the complex genetics of stress-responsive traits and prolonged breeding cycles. Therefore, this review critically evaluates recent advances in *Agrobacterium tumefaciens*-mediated transformation for soybean improvement, focusing on stress tolerance, nutritional enhancement, and transformation efficiency. Accumulating evidence has established important roles for stress-responsive transcription factors, including *DREB*, *NAC*, *bZIP*, and *WRKY* families, together with Osmo protective, antioxidant, and protein- and oil-associated genes, in regulating soybean responses to environmental stresses and seed-quality traits. However, the reported effectiveness of individual genes and transformation protocols varies considerably among soybean genotypes and experimental systems, indicating that transformation efficiency and trait performance remain strongly genotype- and protocol-dependent**.** Furthermore, optimized transformation parameters, including explant selection, infection conditions, and selection strategies, are comparatively evaluated to identify factors affecting transformation efficiency and reproducibility. Despite progress, genotype dependency, low transformation efficiency, poor regeneration, and limited reproducibility remain major challenges. Gaps also persist in validating candidate genes under combined field-relevant stresses and translating laboratory protocols into scalable systems. Emerging approaches such as gene stacking, genome editing, improved vectors, and functional genomics offer promising solutions. Unlike previous reviews, this study integrates transformation efficiency, stress tolerance, nutritional improvement, and sustainable soybean development, highlighting priorities for climate-resilient and nutritionally enhanced cultivars.

Keywords: soybean; *Agrobacterium*-mediated transformation; abiotic stress tolerance; transcription factors; nutritional enhancement; genetic engineering.

1. Introduction

Ensuring global food and nutritional security in the changing climatic conditions around is one of the key scientific and agricultural challenges. Soybean (*Glycine max* (L.) Merrill) is protein and oil containing legume. Soybean is important component of global agri-food systems because it has numerous applications. Some of which include human nutrition, animal feed, and industrial applications [1, 2]. It is one of the most important oil seed crops worldwide. Also, it is a significant

source of protein across the globe [3]. But the abiotic stresses like drought, salinity, temperature extremes, and the biotic stresses like pathogens, insects, and nematodes are significant constraints to soybean production as they adversely affect the stability of yield and seed quality [4, 5]. Climate change has further made these limitations worse by making the events of stress conditions more frequent and severe, that adversely affect the productivity of soybean [4, 5]. Furthermore, biotic stresses have remained to be a major cause of huge yield losses worldwide. This has become a great challenge to the sustainable production systems [5]. These challenges highlight the need to develop effective and accurate strategies to improve stress tolerance and productivity in soybean. However, despite substantial progress in soybean genetic engineering, there remains a lack of comprehensive reviews integrating advances in *Agrobacterium*-mediated transformation, stress-responsive genes, nutritional trait enhancement, and the limitations affecting transformation efficiency [6]. Previous studies focus either on transformation methodologies or on individual trait improvements, resulting in fragmented knowledge and limited understanding of their collective implications for sustainable food and nutritional security. Therefore, there is a critical need to consolidate recent findings and identify future research priorities in this field. Moreover, the comparative evaluation of transformation parameters and the validation of candidate genes under combined or field-relevant stresses remain insufficiently synthesized [7]. Therefore, an updated and integrated assessment is required to clarify the current state of knowledge, identify inconsistencies and knowledge gaps, and highlight emerging strategies for improving the efficiency and applicability of soybean genetic transformation [8]. Accordingly, the objective of this review is to critically examine the latest developments in *Agrobacterium*-mediated genetic transformation in soybean focusing on (i) key genes and transcription factors associated with abiotic and biotic stress tolerance, (ii) genetic determinants of nutritional quality improvement, and (iii) major challenges and emerging strategies to enhance transformation efficiency and applicability.

Traditional approaches for soybean improvement, including classical breeding and marker-assisted selection, which have contributed significantly to the development of superior cultivars. Nevertheless, these methods are often constrained by lengthy breeding cycles, limited genetic diversity, and the complex inheritance patterns associated with stress-responsive traits [9]. Consequently, there is an increasing demand for technologies that enable precise manipulation of genes governing agronomic performance and seed quality. Genetic engineering has emerged as a powerful tool for crop improvement by facilitating the targeted introduction and regulation of desirable genes[10]. Among the available methods, *Agrobacterium tumefaciens*-mediated transformation remains the most widely adopted method owing to its relatively stable gene

integration, low transgene copy number, and high efficiency of gene transfer [11]. Significant progress has been made for the identification of major stress-responsive genes and transcription factors including DREB, NAC, bZIP and WRKY families that control plant responses to abiotic and biotic stresses [12]. Also, genetic engineering methods have been effective to enhance seed composition such as protein and oil content [13]. A comprehensive summary of genes associated with stress tolerance and nutritional improvement is presented in **Table 1** [14- 47]. Although these advancements have been made, soybean is still a recalcitrant species to genetic transformation with problems like genotype dependency, low transformation efficiency and low reproducibility limiting its more widespread use [48]. The overall optimized Agrobacterium-mediated transformation procedure in soybean is illustrated in **Figure 1.** This review address challenges essential for developing robust, scalable, and economically viable transformation platforms capable of accelerating soybean improvement programs. Integrating advances in transformation technologies with functional genomics and trait engineering will be instrumental in realizing the full potential of soybean as a climate-resilient crop that contributes to sustainable agriculture, global food security, and improved nutritional outcomes.

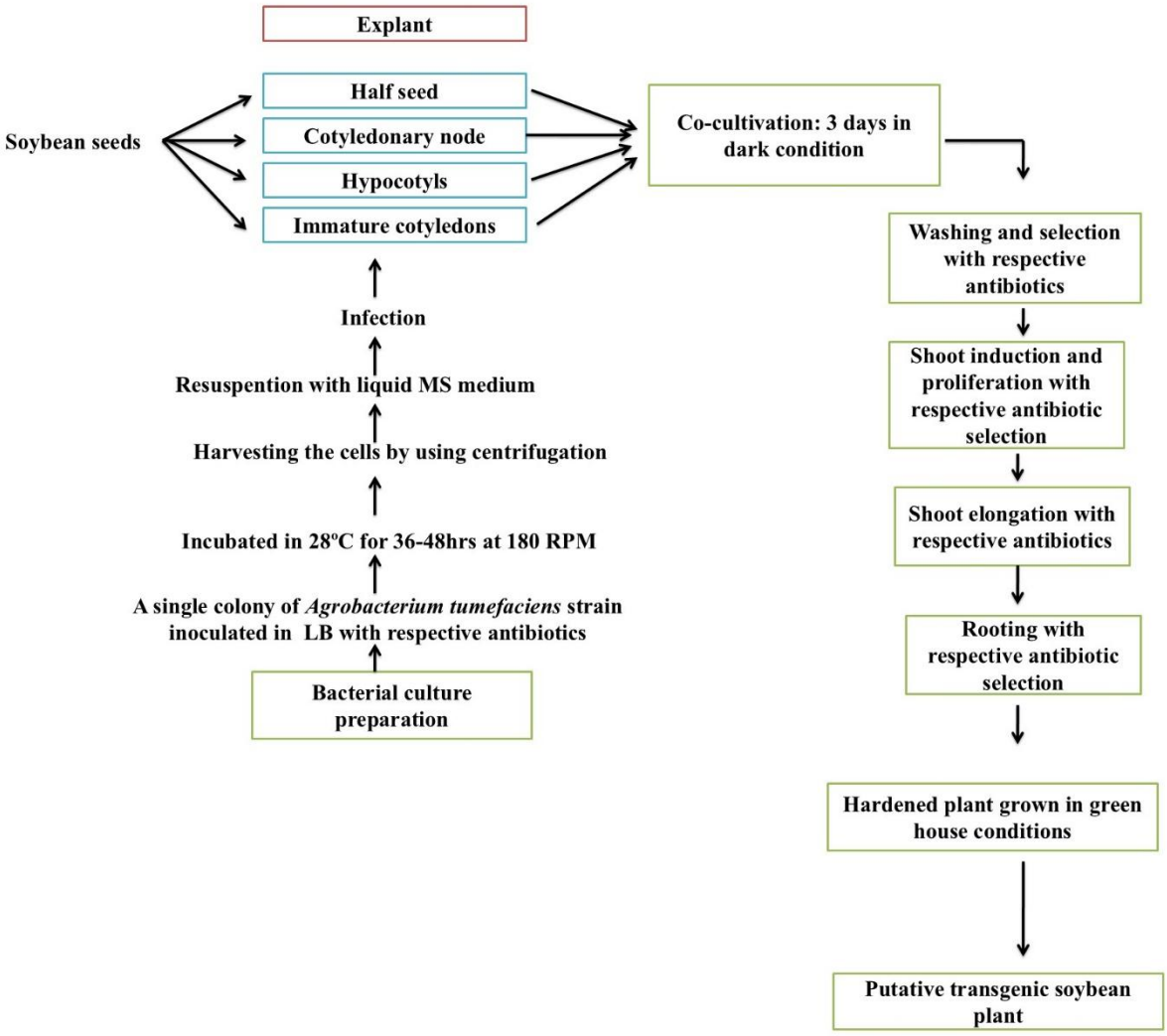

Figure 1. Schematic overview of the optimized *Agrobacterium tumefaciens*-mediated transformation protocol in soybean using different explants, leading to the development of putative transgenic plants. (Source: authors own image).

2 *Agrobacterium*-mediated technology to improve traits in soybean

2.1 Abiotic stress tolerance in soybean

Some of the key factors restricting the productivity of soybean worldwide are abiotic stresses like salinity and drought. These stresses cause disturbance of ionic balance, osmotic regulation and metabolism, and eventually lower the plant growth and yield [49]. These environmental constraints underscore the pressing need to come up with stress-resilient soybean varieties. In soybean, genetic

engineering has been used to target these stress-response pathways through *Agrobacterium*-mediated transformation, providing functional evidence for the roles of specific transporters, transcription factors, and protective proteins [50-51]. However, the strength of the evidence varies considerably among genes, genotypes, transformation systems, and stress-assessment conditions [52].

2.2 Salinity stress and ion toxicity

The salinity stress causes ionic and osmotic imbalance in plants mainly due to excessive accumulation of Na^+ and Cl^- ions that interfere with water uptake and cellular metabolism [53]. Salinity stress is met by plants via ion exclusion, compartmentalization and vacuole sequestration mechanisms [54]. A major adaptive mechanism involves vacuolar Na^+/H^+ antiporters (NHX proteins), which sequester Na^+ into vacuoles using the proton electrochemical gradient generated by vacuolar H^+ ATPase and H^+pyrophosphatase activities [55-58]. Vacuole *NHX* transporters like *NHX1* and *NHX2* preserve homeostasis of intracellular pH and K^+ [56]. Soybean functional studies have demonstrated that salinity tolerance in *NHX*-related genes is enhanced by manipulating the genes via *Agrobacterium*-mediated transformation systems [57]. Although several of these gene were initially characterized in model plant system including *Arabidopsis*, their conserved physiological functions suggest potential applicability in soybean; however, further soybean-specific validation is necessary to confirm their effectiveness under diverse environmental conditions [58-59]. Previous research result of stress tolerance is more dependent on the genotype and the environmental conditions [60].

2.2.1 Transcriptional regulation of stress responses

The transcription factors play the major role of controlling the abiotic stress in plants. Large families of soybean-related proteins are AP2/EREBP (DREB/ERF), MYB, NAC, bZIP and WRKY [61]. Functional classification and mechanistic trends of transgenes used for soybean improvement are shown in **Table 2** [62- 74]. DREB transcription factors control the Stress-inducible genes via binding to DRE/CRT promoter elements and increasing the tolerance to drought and salinity [30]. MYB transcription factors control growth and stress adaption pathways **[75].** *GmMYB68* increases photosynthetic performance and stress resistance in soybean [22,76], whereas, *GmNAC085* boosts antioxidant response and osmotic regulation under stress conditions [77]. Under salinity stress conditions, ABA-dependent signalling pathways are regulated, and antioxidant enzyme activity is enhanced by bZIP transcription factors [78]. Hormone signalling and expression of stress-responsive genes are regulated by *WRKY* transcription factors by binding the W-box promoters, which helps to enhance salinity tolerance in soybean [79]. Among the major stress-responsive regulators, DREB,

NAC, and bZIP transcription factors appear to exert broader downstream effects by coordinating multiple stress-response pathways simultaneously [80]. In contrast, MYB and WRKY proteins predominantly function as modulators of specific developmental and hormone-signaling processes. This hierarchy suggests that transcriptional regulators may represent more promising targets for engineering broad-spectrum stress tolerance in soybean [81-82].

2.3 The Calcium signalling and stress regulation

Hormone signalling, ion transport, and stress-responsive gene networks are regulated by *Calcium-dependent protein kinases* (*CDPKs*) [83]. Hence calcium signalling is an important aspect of plant perception and responses to stress [84-85]. The drought and salinity stress adaptation in soybean are mediated by *CDPK* pathway which is achieved by regulating the physiological and biochemical responses [86]. Nevertheless**,** Calcium signaling should be considered as an upstream regulatory component connecting stress perception with downstream transcriptional and metabolic responses rather than as an isolated transformation target [87]. Compared with DREB and ion-transporter genes, however, relatively fewer soybean *Agrobacterium*-mediated transformation studies have directly demonstrated that manipulation of a specific calcium-signaling component produces stable improvements in whole-plant stress tolerance [88]. Therefore, evidence for this pathway remains comparatively limited and warrants further soybean-specific functional validation [89].

2.4 Osmotic adjustment and protective mechanisms

Abiotic stress causes osmotic stress and oxidative damage of plant cells. Plants overcome these effects by accumulating osmolytes, activating antioxidant enzymes and by stress-protective proteins [90-91]. A PR5 family protein, Osmotic, is also a protein that improves the ability of plants to tolerate both abiotic and biotic stresses by stabilizing cell structures in stressful conditions [92-93]. However, the effectiveness of Osmo protective and antioxidant genes should be evaluated beyond changes in biochemical markers [94]. Increased proline, antioxidant enzyme activity, or reduced reactive oxygen species does not necessarily demonstrate improved agronomic performance [95]. Therefore, transformation studies should ideally assess multiple endpoints, including survival, biomass, photosynthetic performance, reproductive development, seed yield, and seed quality under stress. Consequently, these pathways are best considered complementary components of broader stress-response networks [96]. The signal of inositol phosphate is also involved in the regulation of ABA- and calcium-mediated stress responses [97].

2.5 Role of *Agrobacterium*-mediated transformation

The transformation of soybean by *Agrobacterium tumefaciens* is an important platform that facilitates the integration of genes, and functional validation of stress-responsive genes [98]. It allows the expression of transgenes in a manner that is heritable and also evaluate the stress tolerance traits in the long term. Compared with transient expression systems and RNA interference (RNAi)-based approaches, *Agrobacterium*-mediated transformation provides stable and heritable integration of transgenes, making it particularly valuable for long-term trait evaluation and crop improvement. However, transient expression systems remain advantageous for rapid functional screening, whereas RNAi approaches continue to offer an effective strategy for targeted gene silencing [99]. Precision breeding in soybean has been further improved with integration with genome editing technology, e.g., CRISPR/Cas [100-101]. But, factors like the dependency of genotype, regeneration efficiency, and inconsistent transgene expression are still a major problem [102]. Collectively, ion transporters, transcription factors, calcium-signaling pathways, and osmoprotective mechanisms constitute interconnected stress-response networks rather than independent pathways. Among these, transcriptional regulators such as DREB, NAC, and bZIP appear to exert the broadest effects on stress adaptation, whereas ion transporters primarily maintain cellular homeostasis [103].

3. Drought stress tolerance in soybean

3.1 Overview of Drought Stress

The drought stress is described briefly and includes a summary of its impact on the plant. One of the most serious environmental limitations to soybean productivity, in the changing climatic conditions is drought stress. Water deficit interferes with the photosynthetic efficiency, stomatal control and metabolic homeostasis, and eventually lowers the yield by 20-46 % based on the stress intensity [104-105]. At the physiological scale, drought affects electron transport, carbon fixation, and the CO_2 exchange at the stomata, resulting in oxidative stress, and a metabolic imbalance [106].

3.2 ABA-mediated hormonal regulation

The hormone abscisic acid (ABA) plays a key role in controlling the drought stress response in plants. When there is a lack of water, ABA is stored in roots and then it is moved to aerial tissues, where it controls stomatal closure to minimize transpiration loss [107]. ABA causes the activation of the ABA signalling pathway by binding to the PYR/PYL/RCAR receptors that suppresses PP2C phosphatases and activates *SnRK2* kinases. This cascade results in phosphorylation of ABRE- binding transcription factors (AREB/ABF) which control the expression of drought-responsive genes [108-109]. However, the relevance of this pathway to soybean improvement is better demonstrated by transformation studies than by the general description of ABA signaling. The Arabidopsis-derived transcription

factor *AtABF3* has been introduced into soybean through *Agrobacterium*-mediated transformation, where its expression was associated with enhanced drought tolerance. This study provides evidence that a heterologous ABA-responsive regulator can function in soybean; however, its broader applicability remains uncertain because the response may depend on soybean genotype, promoter activity, transformation event, and stress conditions [110]. Likewise, *LOS5*/*ABA3* increases the endogenous ABA production and increases drought tolerance by activating downstream stress-sensitive genes and physiological responses [111]. Nevertheless, increased ABA production may have pleiotropic effects, including excessive stomatal closure and growth penalties. Therefore, the effectiveness of ABA-related engineering should be evaluated not only by survival or biochemical responses but also by biomass production, reproductive performance, seed yield, and seed quality [112].

3.3 Transpiration factor networks (TFNs) in drought responses

The transcription factor families, such as DREB, MYB, NAC, bZIP and WRKY, highly regulates drought tolerance and they act downstream of ABA-dependent and ABA-independent pathways [113]. Binding of DREB transcription factors to dehydration-responsive elements (DRE/CRT) activates the stress-inducible genes that are associated with osmotic protection [114]. Among soybean-specific transformation studies, DREB-related genes provide comparatively direct evidence for genetic enhancement of drought tolerance. For example, *GmDREB2* overexpression in transgenic soybean has been associated with increased proline accumulation and enhanced expression of stress-responsive genes, accompanied by improved drought tolerance [115]. These findings support the functional relevance of DREB-mediated regulation; however, the magnitude of the phenotype should be interpreted in relation to the soybean genotype, promoter used, transformation event, and severity of the imposed drought stress[116]. MYB transcription factors are known to control metabolic adaptation and stability of photosynthesis leading to enhanced stress tolerance [117]. The stress-responsive pathways and antioxidant defence together with cellular detoxification systems are all regulated by NAC transcription factors [118]. bZIP transcription factors combine the ABA signal and control the ABRE-dependent gene expression of the soybean [119]. WRKY transcription factors also regulate the hormone signalling pathways and stress adaptation mechanisms [120]. Among these regulatory proteins, DREB and NAC transcription factors appear to exert the broadest influence on drought adaptation owing to their ability to coordinate multiple downstream stress-responsive pathways [121]. Conversely, MYB and WRKY proteins primarily function as modulators of specific metabolic and hormone-signaling processes, suggesting a hierarchical organization within drought-response networks [122].

3.4 Osmotic adjustment and metabolic regulation

Osmotic imbalance and build-up of reactive oxygen species (ROS) are induced by drought stress. Plants respond by activating synthesis of osmoprotectants, antioxidants defence system, and reorganizing metabolism [123]. Osmotin (PR-5 family protein) promotes cell stability and resistance to stress by safeguarding the membrane integrity and improving osmotic adjustment. *SnOLP* expression enhances physiological functioning in soybean during drought conditions [124]. The metabolism of fatty acid is also a regulatory factor in the adaptation to stress. The *FAD3* overexpression enhances the stability of the membrane, chlorophyll retention and stomatal control during the conditions of drought stress [125]. These studies suggest that metabolic and Osmo protective genes can complement transcriptional regulators in improving drought responses. However, biochemical improvements such as increased proline, antioxidant activity, or membrane stability should not be considered sufficient evidence of agronomic drought tolerance unless accompanied by measurements of biomass, reproductive development, seed yield, or recovery after stress [126]. Furthermore, the stability of these phenotypes across independent transformation events and generations remains insufficiently documented in several studies [127].

3.5 Secondary signalling and kinase pathways

Signalling pathways of protein kinases play a significant role in drought tolerance. *Glycogen synthase kinase -3* (*GSK-3*)- like proteins regulate the hormonal and stress responses in soybean. *GmBIN2*, as a soybean GSK3 homolog, controls the proline concentration, antioxidant and stability of membrane under drought stress via the *Agrobacterium*-mediated expression systems [128]. The *GmBIN2* study provides evidence that manipulation of signaling components can modify multiple physiological responses simultaneously [129]. Nevertheless, kinase-mediated engineering remains less extensively validated in soybean than transcription-factor-based approaches. In particular, the possibility of developmental or hormonal trade-offs and the reproducibility of the reported phenotype across soybean genotypes require further investigation [130].

3.6 Auxin and developmental regulation

Auxin signalling helps to adapt to drought by controlling root architecture and oxidative homeostasis. Plants have *YUCCA* enzymes controlling the biosynthesis of indole-3-acetic acid (IAA) [131]. Transformation of soybean with *AtYUCCA6* via *Agrobacterium* transformation improves drought tolerance as it improves root growth and minimizes the formation of reactive oxygen species [132]. Nevertheless, an important soybean-specific example is the introduction of the heterologous *AtYUCCA6* gene through *Agrobacterium*-mediated transformation. Transgenic soybean plants

showed enhanced root growth and reduced oxidative damage under drought conditions, suggesting that modification of auxin biosynthesis can improve drought adaptation by altering root development and stress homeostasis [133].

3.7 Cross-kingdom gene transfer and functional conservation

Arabidopsis sp., Brassica sp., and fungal species have several drought-responsive genes which have been successfully introduced into soybean using *Agrobacterium*-mediated transformation[134]. While these studies provide important mechanistic insights and demonstrate the conservation of stress-responsive pathways across species, their performance remains influenced by soybean genotype, environmental conditions, and transgene expression stability [135]. These studies demonstrate the functional conservation of several stress-response pathways and provide useful proof-of-concept evidence for heterologous gene transfer [136]. However, heterologous genes should be distinguished from soybean-native genes because differences in promoter compatibility, protein interaction networks, expression levels, and host genotype can influence the resulting phenotype [137]. For example, *FvC5SD* in *Flammulina velutipes* has been shown to promote sterol metabolism and membrane stability in soybean which increases drought tolerance [32]. Furthermore, these cross-species gene transfers are also effective because, in spite of evolutionary conservation of membrane stress and hormonal signalling pathways, the efficiency of expression can be variable, depending on the host genotype[138]. Consequently, broader field-level validation is required before their agricultural implementation can be established [139].

3.8 Integrated stress signalling model

The multi-layered regulatory network of stress response to drought in soybean are:

- The primary stress signal-ABA.
- *SnRK2* kinases are activated by the ABA receptors.
- AREB/ABF transcription factors control the expression of genes.
- Downstream TFs (DREB, NAC, MYB, and WRKY) enhance stress responses.
- The homeostasis of the cells is stabilized by osmotic and metabolic pathways.

Collectively, this ABA-dependent and ABA-independent regulatory framework illustrates that drought tolerance in soybean is governed by a highly interconnected network involving hormonal signaling, transcriptional regulation, metabolic adaptation, and developmental plasticity. Importantly, successful translation of these findings into commercial soybean improvement programs will require

improved transformation efficiency, reproducibility across genotypes, and integration with emerging technologies such as CRISPR/Cas-mediated genome editing and multiplex gene stacking [140]. *Agrobacterium*-mediated transformation, transient expression, and genome editing can serve as complementary approaches for soybean improvement. Transient systems enable rapid screening of candidate genes, whereas stable *A. tumefaciens*-mediated transformation allows evaluation of heritable drought-tolerance traits. Future studies should prioritize multi-generation and multi-genotype validation of promising genes, followed by genome editing or gene stacking where appropriate. Such integration can improve the stability, reproducibility, and agronomic relevance of drought tolerance and accelerate the development of climate-resilient soybean cultivars [141]. Therefore, future drought-improvement strategies are likely to benefit from integrating *Agrobacterium*-mediated transformation with complementary biotechnological approaches to achieve durable and predictable stress tolerance in soybean [142].

3.9. Role of *Agrobacterium*-mediated transformation.

Agrobacterium tumefaciens-mediated transformation continues to prove itself as an important platform to functionally validate drought-responsive genes in soybean. It allows the stable gene integration, heritable expression and trait evaluation in both controlled and field conditions [143]. Its principal value in drought research lies not simply in generating transgenic plants, but in enabling direct testing of whether manipulation of a candidate gene produces a stable and measurable phenotype[144]. Evidence from *GmDREB2*, *GmBIN2*, *AtABF3*, *AtYUCCA6*, and other candidate genes demonstrates the feasibility of this approach, but the reported outcomes remain influenced by genotype, transformation system, environmental conditions, and experimental design. Therefore, the current evidence supports *Agrobacterium*-mediated transformation as a powerful functional-genomics and crop-improvement platform, while also demonstrating that improved drought tolerance should not be inferred from single physiological measurements or individual transformation events [145]. Greater emphasis on independent events, multiple soybean genotypes, multi-generation stability, combined-stress conditions, reproductive traits, and field validation is required before these genetic strategies can be translated into broadly applicable drought-resilient soybean cultivars.

4. Biotic Stress Tolerance in soybean

4.1 Agronomic importance of soybean cyst Nematode (SCN)

The most financially devastating pathogen of soybean is the soybean cyst nematode (*Heterodera glycines*), which results in the loss of more than a billion USD in annual production of soybean in the largest soybean producing areas [146]. This is a serious pathogen which has led to resistance breeding

as a central goal in soybean improvement programs. Consequently, the development of SCN-resistant cultivars has become a central objective of soybean breeding programs aimed at improving yield stability and ensuring sustainable crop production. [147].

4.2. Genetic basis of SCN resistance

The control of SCN is mainly controlled by quantitative resistance loci with *Rhg1* and *Rhg4* being the most commonly mapped and characterized quantitative locus in soybean germplasm [148]. These loci regulate various defence related pathways showing that SCN resistance is a polygenic and system level trait as opposed to a resistance that is controlled by one gene. However, resistance conferred by *Rhg* loci is frequently partial and influenced by environmental conditions, soybean genotype, and nematode population dynamics, emphasizing the need for complementary molecular and breeding strategies to achieve durable resistance. [149].

4.3 Regulation of Nematode Defence by Hormones

Plant immunity to nematodes is controlled by a complex of hormonal interactions of salicylic acid (SA), jasmonic acid (JA), ethylene, and auxin signalling pathways [150]. SA-initiated signalling is a key component in systemic acquired resistance and controls pathogen colonization by triggering the expression of defence genes and inhibiting colonization. The local defence responses are contributed by JA and ethylene pathways, and the auxin signalling can be frequently manipulated by nematodes in order to enable infection [151]. This interaction of hormones suggests that the SCN resistance is regulated by a dynamic balance of hormones and not by one signalling pathway [152]. Among these pathways, salicylic acid-mediated signaling appears to play the predominant role in systemic defence activation, whereas jasmonic acid, ethylene, and auxin contribute to fine-tuning local and adaptive responses [153].

4.4 Molecular defence mechanism and gene regulation

On the molecular level, the salicylic acid (SA) biosynthesis and the signalling mechanisms, including *NPR1*, PR proteins, and Gibberellic acid (GA)-related defence regulators are important in the resistance of nematodes [154]. It has also been shown that the expression of *Arabidopsis* genes related to defence in the roots of soybean can be used to increase resistance responses through the common immune signalling pathways [155]. On the same note, *salicylic acid methyl transferase* (*GmSAMT1*) controls the SA homeostasis by transforming SA to methyl salicylate which in turn controls the intensity of defence signalling [156]. *GmSAMT1* overexpression in soybean hairy roots has been demonstrated to change the expression of genes involved in the synthesis of SA and improved the

response of soybean to nematodes [157,158]. Nevertheless, most studies involving *NPR1* and *GmSAMT1* have been conducted in controlled experimental systems, and their effectiveness across diverse soybean cultivars and field environments remains to be fully validated [159].

4.5 Biotechnological strategies using *Agrobacterium*-mediated transformation

The *Agrobacterium tumefaciens*-mediated transformation has been extensively employed to functionally test SCN resistance genes in soybean systems, especially in hairy root systems, and stable transformation systems [159-160].

This approach enables:

- Functional testing of Candidate resistance gene
- Moving forward, the assessment of SA/JA pathway modulation is carried out.
- Constant expression of the defence genes [161].

However, the majority of *Agrobacterium*-mediated studies remain limited to hairy root or laboratory-based systems, and the long-term stability and reproducibility of SCN resistance under field conditions have yet to be comprehensively evaluated.

4.6 Comparative effectiveness and integrated resistance strategy.

Though several genes including *Rhg1*, *Rhg4*, *NPR1* and *GmSAMT1* play a role in the resistance of SCN, their mechanisms vary considerably:

- *Rhg* loci: structural quantitative resistance.
- *NPR1*-related genes: systemic immune activation.
- *GmSAMT1*: hormonal regulation of the SA levels.

These components work as a whole in a genetic resistance and hormonal regulation integrated defence network rather than functioning alone. Among the identified resistance determinants, *Rhg1* and *Rhg4* represent the primary genetic basis for soybean cyst nematode resistance, whereas *NPR1* and *GmSAMT1* predominantly function as modulators of downstream defence signalling [162,163]. Therefore, durable resistance is likely to require the integration of quantitative resistance loci with hormone-mediated defence pathways, with *NPR1* and *GmSAMT1* contributing to the magnitude and adaptability of downstream defence responses [163]. Such coordinated integration of quantitative resistance loci with hormone-mediated signalling pathways is expected to support durable resistance.

4.7 Resistance to SCN- integrated conceptual model

SCN resistance in soybean can be summarized to be a multi-layered defence system:

- Pathogen recognition (activation of defence by *Rhg* loci)
- Hormonal interaction (SA -JA -ethylene -auxin network interaction)
- Activation of defence gene (PR proteins, *NPR1* pathway)
- Metabolic (SA methylation through *SAMT* genes)
- Defence responses of the cells (development and reproduction of nematodes restricted)

Collectively, SCN resistance in soybean is governed by coordinated genetic, hormonal, and metabolic interactions. However, further field validation and integration with modern breeding technologies are essential for its effective deployment [164].

5. *Phytophthora* root and Stem rot resistance in soybean

5.1 Agronomic Significance and Disease Effect

Phytophthora root and stem rot (PRR), which is a disease caused by *Phytophthora sojae*, a soil -borne pathogen, is one of the most destructing diseases that impact soybean production worldwide causing severe losses in the production of the affected crops [165]. Under favourable conditions, the pathogen infects roots and basal stems leading to tissue maceration, vascular disruption and plant collapse [166]. Due to its soil-borne persistence, PRR continues to be one of the greatest limitations of soybean production systems.

5.2 Integrated defence Strategy against PRR

The defence system of resistance of soybean to PRR is multi-layered defence system that entails metabolite, structural and immune signalling responses. These include:

• Isoflavonoid biosynthesis: Metabolic defence activation: *CHI, IFR*-mediated phytoalexins

• Structural reinforcement: The deposition of lignin and lignans via *DIR* proteins

• Pathogenesis-related enzymes

• Effector-triggered immunity: *hrpZm* activation

• Direct Antimicrobial peptide activation: AMP activity

Collectively, these mechanisms function in a hierarchical manner, where metabolic and structural defences constitute the first line of protection, while immune signaling pathways amplify and sustain resistance responses during pathogen invasion [167].

5.3 Isoflavonoid-Mediated Defence

The isoflavonoids are major phytoalexins in soybean which play a key role in pathogen defence and in plant microbe interactions. Their production is controlled by chalcone isomerase (CHI) which converts chalcones to flavanones which are the backbones of flavonoid pathways [168]. *GmCHI1A* is much expressed in roots and localized to the cortical endoplasmic reticulum in soybean. *GmCHI1A* overexpression can improve daidzein levels, reinforce early defence mechanisms against *P. sojae* infection [169]. These metabolites are the biochemical defence amplifiers which directly connects metabolism to disease resistance.

5.4 Lignin and structural defence reinforcement

One of the important physical barriers against invasion of pathogen is cell wall reinforcement. When the infection is caused by PRR, soybean enhances the deposition of lignin, lignocellulose and callose, which inhibits the spread of the pathogen [170, 171]. The lignan biosynthesis is controlled by dirigent proteins (*DIRs*). *GmDIR22* overexpression enhances lignan concentration and prevents the *P. sojae* hyphae growth, resulting in increased resistance [35]. This supports the idea that the lignification is a component of a structural immunity module and not a solitary reaction.

5.5 *Isoflavone reductase* and phytoalexin pathway

Glyceollins are among the key phytoalexins in soybean that need *Isoflavone reductase* (*IFR*) to be synthesized. *GmIFR* is a soybean gene which is important in resistance against PRR, overexpression of which boosts resistance to *P. sojae* as well as regulates SA, ethylene and ABA signalling, suggesting effective coordination of metabolic and hormonal defence mechanisms [171,172]. Among the identified defence determinants, phytoalexin-associated pathways appear to play a central role in early resistance, whereas hormonal signaling predominantly contributes to the amplification and maintenance of defence responses [173].

5.6 Effector-triggered immune activation

Virulence factors of the pathogen are identified by the immune system of the plants, which trigger defence mechanisms. In soybean, *Agrobacterium*-mediated transformation has been used to activate immune responses by the introduction of the engineered gene *hrpZm*, isolated from *Pseudomonas syringae.* Hypersensitive response-like signalling, stimulated by overexpression of *hrpZm* leads to resistance against PRR due to the activation of a range of defence pathways [174].

5.7 Antimicrobial peptides and defence amplification

Antimicrobial peptides (AMPs) are direct antimicrobial agents, which interfere with the membranes and metabolism of the pathogen. Overexpression of *CaAMP1* in soybean leads to an increase in PRR resistance, which activates salicylic acid (SA) and jasmonic acid (JA) signalling pathways, showing that can be a multi-pathway immune enhancer [175]. Nevertheless, the majority of AMP-based studies have been conducted under controlled conditions, and their long-term effectiveness under field environments remains to be established [176].

5.8 *Agrobacterium*-Mediated Transformation: PRR Research

Agrobacterium tumefaciens-mediated transformation is a common method of functional validation of PRR resistance genes in soybean. It enables:

- Stable gene integration
- Functional gene validation
- Pathway-level resistance analysis

However, genotype dependency, environmental variability, and limited field validation remain significant challenges for the large-scale deployment of PRR-resistant soybean cultivars. Collectively, resistance to *Phytophthora sojae* is mediated through coordinated metabolic, structural, and immune mechanisms. However, further studies are required to establish their relative contributions and reproducibility under field conditions [177].

6. Viral resistance in soybean

6.1 Soybean Mosaic Virus (SMV): Pathogenesis and Constraints to Resistance

One of the most economically significant viral pathogens earlier known to impact on soybean productivity on the global stage is Soybean mosaic virus (SMV) which is a positive-sense single-stranded RNA virus belonging to the Potyviridae family [178]. The infection causes mosaic foliar patterns, systemic chlorosis, stem browning, tip necrosis, and discoloration of seed coat all of which result into a high yield loss [179]. Conventional breeding to develop SMV resistance is limited by large viral genetic variation, several host susceptibility sites, and quick evolution of viral virulence factors [180]. These shortcomings require the creation of molecular and transgenic methods of long-term resistance in soybean.

6.2 Homeostasis of Ions and Indirect action of Potassium in Viral Defence

Potassium (K^+) is one of the most important macronutrients that contributes to the maintenance of the osmotic balance, enzyme activity, and regulation of the phloem transport in plants [181]. Transport of K^+ occurs through special ion channels, such as Shaker-type voltage-gated potassium channels [182]. One of these, *AKT serine/threonine kinase 2* (*AKT2*), found in phloem tissues, guard cells and vascular areas controls the redistribution of K^+ between source and sink tissues. Even though *AKT2* has no direct impact on viral replication, it has been shown that its part in sustaining phloem conductivity and homeostasis of cellular energy indirectly affect the viral movement and effectiveness of systemic infection. Functional research indicates that the expression of *GmAKT2* increases in SMV-tolerant soybean cultivars, but decreases in the susceptible cultivars. Notably, the *GmAKT2* overexpression of the susceptible soya bean cultivar Williams 82 improved SMV tolerance, which means that improved ion homeostasis can indirectly help limit viral infection at the entire plant scale [183]. However, *AKT2*-mediated resistance appears to function indirectly through the maintenance of cellular homeostasis and is therefore considered a supportive, rather than primary, determinant of antiviral defence in soybean [184].

6.3 Peptide signalling and Snakin /GAST-Mediated Defence Modulation

Snakin-like proteins are plant antimicrobial peptides (AMPs). They are a part of innate immune systems. Members of GAST (gibberellin acid-stimulated transcript) have cysteine-rich motifs which are conserved. These motifs ensure structural stability and responsive stress signalling [185]. *GmSN1*, a snakin-like peptide, in soybean improves viral tolerance. It achieves viral tolerance by regulating the expression of immune-related genes. Instead of having independent action, *GmSN1* affects downstream signalling networks, such as ion transporter gene, like *GmAKT2*, defence regulatory networks [186]. This suggests that there is functional cross-talking of peptide-mediated immunity and ion homeostasis rather than independent antiviral pathways. *GmSN1* is therefore best regarded as a defence amplifier that enhances existing immune responses rather than acting as an independent antiviral factor [187].

6.4 Molybdenum Cofactor-Dependent Metabolic Regulation in Viral Defence

Many enzymes that are involved in the metabolism of nitrogen, redox homeostasis, and in the detoxification processes. The activity of these enzymes depends on molybdenum cofactor (Moco) [188]. Moco-dependent enzymes, like nitrate reductase (NR) and aldehyde oxidase (AO) play an indirect role in viral resistance, by ensuring metabolic stability regulating oxidative stress levels [189]. Similarly, *GmCnx1* contributes indirectly to antiviral defence by maintaining metabolic stability and redox homeostasis, highlighting the importance of cellular fitness during viral infection

[190]. This gene has demonstrated a positive response on enhancement of SMV tolerance upon overexpression. Transgenic plants show higher NR and AO enzyme activities, better metabolic regulation, and increased tolerance to the virus [191]. The results suggest that the antiviral defence is tightly connected with the metabolic balance of the cells and is not directly related to the virus-targeting mechanisms.

6.5 Cross-species viral model (TuMV): Relevance and limits

Turnip mosaic virus (TuMV), belongs to the family Potyviridae, infects a large variety of dicotyledonous species and is commonly employed as model system to study the interactions between plants and viruses. The *Arabidopsis*–TuMV system is particularly valuable for dissecting conserved molecular mechanisms of potyvirus infection. It is also an important system to understand the replication of TuMV genome, movement and host defence signalling. Although TuMV-based studies provide important mechanistic insights, their findings should not be directly extrapolated to soybean owing to species-specific differences in host–virus compatibility [192]. Therefore, while the TuMV model is highly informative for understanding conserved antiviral pathways, validation in soybean–Soybean mosaic virus (SMV) systems remain essential to establish their functional relevance. Consequently, conclusions derived from TuMV-based studies should be interpreted cautiously and considered complementary to soybean-specific investigations. Moreover, the majority of TuMV-based findings remain to be validated across diverse soybean genotypes and field environments [193].

6.6 The hormonal control of antiviral defence networks

The plant hormones, salicylic acid (SA), jasmonic acid (JA) and ethylene, correlates systemic and local antiviral defence responses [194]. These signalling pathways control the activation of defence genes, resistance priming and systemic acquired resistance during viral infection. It is important to note that hormonal signalling does not act alone. They form an integrated defence network upon interaction with ion transport systems, peptide signalling molecules, and metabolic regulators. Additionally, hormone-mediated signaling networks act as central coordinators of antiviral defence by integrating ion homeostasis, peptide-mediated immunity, and metabolic regulation [195].

6.7 Integrated conceptual framework for viral resistance

Soybean plant employs a coordinated multi-layered system against viral resistance rather than a single dominant pathway. The interconnected key components include:

- Ion homeostasis (regulation of K^+ - via *AKT2*)
- Peptide mediated immunity (*GAST*/snakin family)

• Regulation of metabolism (Moco-dependent enzymes)
• Hormonal (SA–JA–ethylene) communications.

Together, these pathways regulate the movement of viruses, their replication ability and the activation of host defence, providing an integrated antiviral response system in soybean. Nevertheless, most studies have been conducted under controlled experimental conditions, and their reproducibility across soybean genotypes and field environments remains insufficiently characterized [196]. Future efforts integrating *Agrobacterium*-mediated transformation, genome editing, and molecular breeding approaches are expected to facilitate the development of durable antiviral resistance in soybean.

7 Improvement in Nutritional Quality of Soybean

7.1 Integrated approach to nutritional biofortification

Genetic engineering of metabolic pathways is the primary way of improving nutritional quality. This regulates the composition of soybean seeds including proteins, fatty acids, vitamins and carotenoids. Although there is a high number of reported transgenic approaches, most of the literature is centred on single-gene perturbations [197]. The single-gene perturbations are shown to yield trait-specific benefits, but fail to reflect all agronomic trade-offs and interdependencies in metabolic responses. Therefore, nutritional enhancement should be interpreted within a systems-level metabolic framework.

7.2 Yield traits, seed size and developmental regulation

The size of soybean seeds and the weight of grains are major determinants of the yield of the soybean. These are regulated by cytochrome P450 monooxygenases. The *CYP78A* genes regulate organ growth through hormonal and developmental signalling pathways [198]. In soybean KLU has an ortholog-*GmCYP78A72*, which enhances seed number and influences seed development. But even though overexpression helps in boosting yield traits, its impact on nutritional characteristics is indirect. This suggests that the increase in yield is does not always equate to nutritional enhancement. Knockdown studies indicate no significant effects on seed size, suggesting functional redundancy in growth regulation networks [199].

7.3 Tocopherols (Vitamin E): Nutritional trade-offs and bioavailability

Tocopherols are antioxidants that are lipid-soluble and are essential for human nutrition. α-tocopherol has the highest bioavailability with γ- and δ-tocopherol are abundant in seeds [200]. Engineering of the γ-tocopherol methyl transferase (*γ-TMT*) enhances the amount of γ- and δ -tocopherols in the

soybean seeds[201]. However, this tends to decrease the content of α-tocopherol, causing a composition trade-off isoforms instead of absolute nutritional gain . As a result, nutritional impact depends on isoform balance and the ability of the human body to absorb it, rather than the total tocopherol content.

7.4 Carotenoids and vitamin A biofortification

Carotenoids such as β-carotene are precursors of vitamin A. The accumulation of β-carotene increases significantly by transgenic expression of phytoene synthase and carotene desaturase genes soybean seeds [202]. However, dietary fat, digestion efficiency, and matrix effects influences carotenoid bioavailability. Therefore, increased accumulation, is not directly proportional to vitamin A bioavailability in humans.

7.5 Ketocarotenoids: Functional feed vs human nutrition

Engineering ketocarotenoids like astaxanthin and canthaxanthin, in soybean is mainly focused towards aquaculture and poultry feed industries. Multi-gene stacking (*crtB, crtW, bkt1)* enhances carotenoid diversity. But it can impose metabolic load on endogenous isoprenoid pathways, which could affect the stability of plant growth [203].

7.6 Protein quality and amino acids trade-offs

Soybean protein lacks sulphur amino acids like methionine and cysteine. Expression of maize zein protein (15kDa) increases methionine content in soybean seeds. This increase in metabolic efficiency is however associated with metabolic trade-offs in the nitrogen allocation and storage protein balance and does not always improve overall protein digestibility. Protein digestibility is determined by amino acid balance and not by single amino acid enrichment [204].

7.7 Fatty acid engineering and oil quality constraints

Fatty acid modification using *FAD3* and *DGAT1* genes modifies lipid composition. This improves nutritional profiles such as omega-3 fatty acid (ALA) content [205]. It is important to note that increased ALA decreases oxidative stability of soybean oil, which has a negative impact on the shelf life and industrial usability. Similarly, changes in oleic acid content influences frying stability. Fatty acid engineering, therefore, is a trade-off between nutrition and industry rather than a simple improvement [206]. Moreover, nutritional engineering strategies should be evaluated not only on the basis of metabolite accumulation but also in terms of their effects on bioavailability, storage stability, and consumer relevance [207].

7.8 Central metabolism genes and indirect effects of nutrition

Broader metabolic pathways like stress response, lipid metabolism and seed development are controlled by genes such as *ThIPK2* and *DGAT1*. Though these genes do affect seed composition; their primary role is in core metabolic and stress regulatory pathways. Nutritional changes are secondary outcome and not a direct nutritional engineering objective [208].

7.9 Limitations of single-gene nutritional engineering

Majority of nutritional improvement strategies are based on the single-gene overexpression. Most of these strategies does not reflect the complexity of seed metabolism. Some of the interacting pathways involves carbon flux, transcriptional regulation, and environmental effects. Such pathways control nutritional traits. Hence, single-gene techniques frequently lead to imbalance in metabolic outputs, and undesirable trade-offs, which highlights the need for multi-gene and systems-level engineering approaches [209].

7.10 Integrated Perspective

The nutritional enhancement of soybean is a multi-dimensional trait that includes the vitamins, proteins and lipids. However, nutritional enhancement is not only based on the metabolite accumulation, but also on the bioavailability, metabolic balance and agronomic performance. Future strategies must integrate multi-pathway metabolic engineering and systems biology approaches to achieve balanced improvement in yield, nutrition, and industrial quality [210]. Accordingly, soybean nutritional improvement should be considered a systems-level process requiring the coordinated optimization of metabolic pathways, agronomic traits, and end-use quality. Future strategies should therefore prioritize multi-trait engineering approaches to achieve balanced and sustainable nutritional enhancement [211].

8.0 Regulatory Biosafety Commercialization Challenges

Despite considerable advances in *Agrobacterium*-mediated transformation, the commercialization of transgenic soybean remains associated with several challenges [212]. Regulatory approval processes differ substantially among countries and require extensive biosafety assessments, environmental risk evaluations, and food safety studies [213]. In addition, intellectual property considerations, public acceptance of genetically modified crops, and the economic feasibility of large-scale deployment continue to influence commercialization. Addressing these challenges through harmonized regulatory frameworks, transparent risk assessment procedures, and effective stakeholder engagement will be essential for translating laboratory-scale innovations into sustainable agriculture [214].

9. Conclusion

Transgenic and genome-assisted crop improvement strategies offer considerable potential to enhance stress tolerance, nutritional quality, and yield stability in soybean. However, their successful implementation will depend on continued technological advancements, regulatory acceptance, and integration with conventional breeding and sustainable agricultural practices. These approaches are expected to contribute significantly toward addressing future challenges related to food and nutritional security.

Authors' Contributions:

K.S.: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Visualization, Supervision, Project administration; P.U.: Validation, Formal analysis, Writing – original draft, Writing – review & editing; S.D.: Writing – original draft, Writing – review & editing; C.D.: Writing – original draft, Writing – review & editing. All authors have read and agreed to the published version of the manuscript.

List of Abbreviations:

- **ABA** – Abscisic acid
- **AKT2** – Arabidopsis K^+ Transporter 2
- **ALA** – α-Linolenic acid
- **AMPs** – Antimicrobial peptides
- **AO** – Aldehyde oxidase
- **AREB/ABF** – ABA-responsive element-binding/ABRE-binding factors
- **bZIP** – Basic leucine zipper
- **CDPKs** – Calcium-dependent protein kinases
- **CHI** – Chalcone isomerase
- **Cl^-** – Chloride ion
- **CRISPR** – Clustered regularly interspaced short palindromic repeats
- **DRE/CRT** – Dehydration-responsive element/C-repeat
- **DREB** – Dehydration-responsive element-binding
- **DIRs** – Dirigent proteins
- **GAST** – Gibberellic acid-stimulated transcript
- **GmSAMT1** – Salicylic acid carboxyl methyltransferase 1
- **GSK3** – Glycogen synthase kinase 3

- **IAA** – Indole-3-acetic acid
- **IFR** – Isoflavone reductase
- **JA** – Jasmonic acid
- **K^+** – Potassium ion
- **MoCo** – Molybdenum cofactor
- **MYB** – Myeloblastosis
- **NAC** – NAM, ATAF1/2, and CUC
- **NHX proteins** – Na^+/H^+ antiporters
- **NPR1** – Nonexpressor of pathogenesis-related genes 1
- **NR** – Nitrate reductase
- **PR proteins** – Pathogenesis-related proteins
- **PRR** – *Phytophthora* root and stem rot
- **PYR/PYL/RCAR** – Pyrabactin resistance/Pyrabactin resistance-like/Regulatory components of ABA receptors
- **RNAi** – RNA interference
- **ROS** – Reactive oxygen species
- **SA** – Salicylic acid
- **SCN** – Soybean cyst nematodes
- **SMV** – Soybean mosaic virus
- **SnRK2** – SNF1-related protein kinase 2
- **TuMV** – Turnip mosaic virus
- **WRKY** – WRKY transcription factor family
- **γ-TMT** – γ-Tocopherol methyltransferase

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Supplementary Materials

Supplementary Tables S1 and S2 provide detailed information on the genetic determinants and

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AI Declaration

The authors confirm that Grammarly and Quillbot were used exclusively for language polishing, paraphrasing, and improving the readability of content originally written by them. These tools were not used to source, generate, or contribute to any substantive data, information, or literature included in the manuscript. All concepts, results, and literature reviews presented herein reflect the authors' original work. The authors take full responsibility for the accuracy, originality, integrity, and scientific content of the manuscript.

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Tables

Table 1. Genetic determinants of abiotic stress tolerance, biotic stress resistance, and nutritional quality improvement in soybean via *Agrobacterium*-mediated transformation

Target Gene/ Transcription Factor	Functional Category	Molecular Mechanism / Role	Transformation System (Strain / Vector)	Improved Trait	References
Abiotic Stress Tolerance – Salinity					
GmDREB6	Transcription factor (DREB)	Regulates stress-responsive genes via ABA-independent pathway	CV58 / pBI121	Enhanced proline accumulation and salt tolerance	[14]
TaNHX2	Ion transporter (Na^+/H^+ antiporter)	Vacuolar Na^+ sequestration maintaining ionic homeostasis	EHA101 / pTF101.1	Improved salt tolerance	[15]
GmCLC1	Anion transporter	Regulates Cl^- transport and ion balance under salt stress	GV3101, K599 / pCAMBIA1300	Enhanced salt tolerance	[16]
StNHX1	Ion transporter	Vacuolar Na^+ compartmentalization	EHA105 / pCAMBIA3301	Improved salt tolerance	[17]
AtNHX5	Ion transporter	Intracellular ion homeostasis and vesicular trafficking	— / pCAMBIA3300	Enhanced salt tolerance	[18]
OsDREB2A	Transcription factor (DREB)	Activation of stress-inducible gene expression	EHA101 / pZY101	Improved salt tolerance	[19]
Tbosm	Osmoprotectant protein	Osmotic adjustment and cellular protection	— / —	Salt tolerance and fungal resistance	[20]
GmCDPK3	Protein kinase	Calcium-mediated stress signal transduction	— / pCAMBIA3301	Enhanced salt tolerance	[21]
GmMYB68	Transcription factor (MYB)	Regulation of stress-responsive gene networks	EHA101 / pTF101	Salt and alkaline stress tolerance	[22]
GmNAC085	Transcription factor (NAC)	Regulation of stress signalling pathways	— / —	Improved salt tolerance	[23]

GmFDL19	Transcription factor (bZIP-like)	Modulates ABA-mediated stress responses	— / —	Improved salt tolerance	[24]
MsWRKY11	Transcription factor (WRKY)	Regulation of stress and defence-related genes	EHA101 / pTF101.1	Enhanced salt tolerance	[25]
Abiotic Stress Tolerance – Drought					
GmNFYA5	Transcription factor (NF-YA)	Regulates ABA-dependent and independent drought pathways	K599 / pCAMBIA3301	Enhanced drought tolerance	[26]
AtABF3	Transcription factor (bZIP)	ABA-mediated regulation of drought-responsive genes	EHA105 / pB2GW7.0	Improved drought tolerance	[27]
LOS5/ABA3	Enzyme (ABA biosynthesis)	Enhances ABA accumulation under stress	EHA105 / pCAMBIA1300	Improved drought tolerance	[28]
GsWRKY20	Transcription factor (WRKY)	Regulates stress-responsive gene expression	EHA101 / pBA	Improved drought and salinity tolerance	[29]
GmBIN2	Protein kinase (BR signalling)	Modulates stress signalling via brassinosteroid pathway	K599 / pCAMBIA3301	Enhanced drought tolerance	[30]
AtYUCCA6	Enzyme (auxin biosynthesis)	Regulates auxin-mediated stress adaptation	— / —	Improved drought tolerance	[31]
FvC5SD	Enzyme (sterol biosynthesis)	Maintains membrane stability under stress	EHA101 / pTF101.1	Enhanced drought tolerance	[32]
Biotic Stress Resistance					
GmSAMT1	Enzyme (SA methyltransferase)	Converts salicylic acid to methyl salicylate for systemic resistance	K599 / pCAMBIA1305.2	Soybean cyst nematode resistance	[33]
GmCHI1A	Pathogenesis-related protein (chitinase)	Degrades fungal cell walls and induces phytoalexins	K599 / pBin	Phytophthora resistance and increased daidzein	[34]
GmDIR22	Dirigent protein	Lignan biosynthesis and cell wall reinforcement	LBA4404 / pCAMBIA3301	Phytophthora resistance	[35]
GmIFR	Enzyme (isoflavone reductase)	Phytoalexin (daidzein) biosynthesis	LBA4404 / pCAMBIA3301	*Phytophthora sojae* resistance	[36]

CaAMP1	Antimicrobial peptide	Direct pathogen inhibition and membrane disruption	EHA101 / pCAMBIA3300	*Phytophthora sojae* resistance	[37]
GmAKT2	Potassium channel	Regulates ion transport affecting viral movement	EHA101 / pB7RWG2.0	Soybean mosaic virus resistance	[38]
GmCnx1	Enzyme (Moco biosynthesis)	Enhances redox metabolism and defence enzymes	— / pB7FWG2.0	Soybean mosaic virus resistance	[39]
Nutritional Quality Improvement					
GmCYP78A72	Cytochrome P450 enzyme	Regulates seed development and size	GV3101 / pCAMBIA1301	Improved seed development	[40]
γ-TMT (Perilla frutescens)	Tocopherol methyltransferase	Converts γ- to α-tocopherol	EHA105 / pCAMBIA1304	Increased tocopherol content	[41]
BnTMT	Tocopherol methyltransferase	Enhances α-tocopherol biosynthesis	LBA4404 / pBin438	Improved tocopherol content	[42]
PSY-2A* + *CRTI	Carotenoid biosynthesis enzymes	Enhances carotenoid biosynthetic pathway	EHA105 / pB2GW7.0	Increased carotenoid content	[43]
crtB* + *ketolase	Metabolic enzymes	Ketocarotenoid biosynthesis	— / —	Enhanced ketocarotenoids	[44]
ThIPK2	Signalling enzyme	Regulates lipid metabolism and stress responses	LBA4404 / pCAMBIA3300	Improved fatty acid composition	[45]
SiDGAT1	Lipid biosynthesis enzyme	Triacylglycerol accumulation	EHA105 / pCAMBIA3301	Increased oil content	[46]
FAD3-1	Fatty acid desaturase	Converts fatty acids to α-linolenic acid	EHA105 / pB2GW7.0	Increased linolenic acid content	[47]

Table 2. Functional classification and mechanistic trends of transgenes used for soybean improvement

Functional Category	Representative Genes	Primary Mechanism	Target Trait	Key Outcome	References
Transcription Factors (TFs)	*GmDREB6, OsDREB2A, GmMYB68, GmNAC085, GsWRKY20, MsWRKY11, GmNFYA5, AtABF3*	Regulation of stress-responsive gene expression via ABA-dependent and independent pathways	Abiotic stress (salinity, drought)	Broad-spectrum stress tolerance through gene network modulation	[62-63]
Ion Transporters / Channels	*TaNHX2, StNHX1, AtNHX5, GmCLC1, GmAKT2*	Maintenance of ionic homeostasis via Na^+ sequestration, K^+ transport, and Cl^- regulation	Salinity stress, viral resistance	Improved cellular ion balance and stress adaptation	[64]
Protein Kinases / Signalling Molecules	*GmCDPK3, GmBIN2, ThIPK2*	Signal transduction via calcium signalling, brassinosteroid pathways, and stress signalling cascades	Abiotic stress tolerance	Enhanced stress perception and downstream response activation	[65-66]
Osmoprotectants & Stress Proteins	*Tbosm*	Cellular osmotic adjustment and protection of macromolecules	Salinity and combined stress	Stabilization of cellular structures under stress	[67]
Pathogenesis-Related Proteins / Defence Enzymes	*GmCHI1A, GmIFR, GmSAMT1, GmDIR22*	Antifungal activity, phytoalexin production, and systemic acquired resistance	Biotic stress (fungi, nematodes)	Enhanced pathogen resistance and defence signalling	[38,68-69]
Antimicrobial Peptides	*CaAMP1*	Direct pathogen inhibition via membrane disruption	Biotic stress (Phytophthora)	Increased disease resistance	[70]
Metabolic Enzymes (Nutritional Enhancement)	*γ-TMT, BnTMT, SiDGAT1, FAD3-1*	Modification of lipid, tocopherol, and fatty acid	Nutritional quality	Improved oil content and fatty acid composition	[47,71]

		biosynthesis pathways			
Carotenoid Biosynthesis Enzymes	*PSY-2A, CRTI, crtB + ketolase*	Enhancement of carotenoid and ketocarotenoid biosynthetic pathways	Nutritional quality	Increased carotenoid accumulation	[72]
Cytochrome P450 Enzymes	*GmCYP78A72*	Regulation of seed development and growth processes	Yield and seed traits	Improved seed size and development	[73]
Redox and Cofactor Biosynthesis Enzymes	*GmCnx1*	Molybdenum cofactor biosynthesis influencing redox enzymes	Viral resistance	Enhanced defence enzyme activity	[74]

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