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Review Paper on Genetically Modified Soybean Seed Development: Global Perspectives

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Abstract

Genetically modified soybean has gained significant attention and adoption worldwide due to its numerous agronomic, economic, and environmental benefits. This review paper explores the global perspectives on genetically modified soybean focusing on its development, adoption, benefits, concerns and future prospects. It provides an overview of traits incorporated into GN soybean, such as drought tolerance, enhanced quality, herbicide tolerance, disease tolerance and insect resistance, and delves into the socioeconomic impact of these biotechnological advancements on farmers, consumers, and the environment. Additionally, it discusses the scientific base, methods of gene transformation, and transgenic Soybean Seed development and production status of genetically modified soybean.

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Introduction

Globally, soybean [*Glycine max* (L.) Merr.] is the leading oilseed crop with a production of 363.27 million tonnes, accounting for 60.43% of the world oilseed production (601.14 million tonnes). Brazil leads the world in soybean production, accounting for 37.71% of total output, followed by the United States of America (30.97%), Argentina (12.66%), China (5.39%), India (2.87%), Paraguay (2.72%), and Canada (1.74%) (USDA, 2021). Soybean oil is the second most consumed vegetable oil in the world, after palm oil. In 2020-2021, global soybean oil production was 59.74 million tonnes, accounting for 28.85% of total vegetable oil production (207.01 million tonnes) (USDA, 2019). Soybean breeders have developed various breeding methodologies and have made tremendous progress in development of superior genotypes. Development of superior soybean varieties using traditional methods is very tedious as selection procedure of desirable genotypes using conventional approaches is complicated, inefficient and uncertain due to difficulties related to phenotyping procedures, which can be time-consuming, expensive, and unreliable for traits with a low heritability and subject to genotype × environment interactions (Francia *et al.,* 2005). Transgenesis, cisgenesis and intragenesis are the new breeding techniques that have been developed to meet these challenges. Advances in molecular genetics and genomics have revolutionized breeding procedures for development of superior genotypes.

A genetically modified (GM) crop is a plant into which one or more genes have been artificially inserted instead of the plant acquiring them under natural conditions of cross -breeding or natural recombination. The inserted

gene sequence, known as the transgene, may be from same species, a different species within the same kingdom or even from a different kingdom (e.g. genetically modified Bt corn, which produces the natural insecticide, contains a gene from a bacterium).

The world of biotechnology is moving very fast, more traits are emerging and more acres than ever before are being planted with genetically modified varieties of an ever-expanding number of crops. Genetic modification techniques allow novel traits to be introduced into animals, crops and microorganisms. Genetic modification is being used in the forest sector to create pest resistance, herbicide tolerance and wood quality traits (FAO, 2005).

Since the first stably transgenic plant produced in the early 1980s and the first commercialized transgenic plant in 1995, biotechnology has revolutionized plant agriculture. More than a billion acres of transgenic cropland has been planted worldwide, with over 50 trillion transgenic plants grown in the United States alone.

In the United States, over half of the corn and cotton and three-quarters of soybean produced are transgenic for insect resistance, herbicide resistance, or both. Biotechnology has been the most rapidly adopted technology in the history of agriculture and continues to expand in much of the developed and developing world (Pechlaner and Otero, 2008). The first staple crops with engineered traits first became commercially available in 1996; they were: maize (corn), rape (canola), soybean and cotton.

This review summarizes production status of soybean seeds, their scientific base, methods of gene transformation, transgenic Soybean Seed development and production status of genetically modified soybean.

Scientific base of Genetically modified Crops

Genetic transformation has become an important tool for crop improvement. The successful genetic transformation in plants requires the production of normal, fertile plants expressing the newly inserted gene(s). The process of genetic transformation involves several distinct steps, namely identification of useful gene, the cloning of the gene into a suitable plasmid vector, delivery of the vector into plant cell (insertion and integration) followed by expression and inheritance of the foreign DNA encoding a polypeptide. A gene construct consists typically of three elements: 1) The promoter functions as an on/off switch for when and where the inserted/modified gene is active in the recipient plant; 2) The transgene encodes a specifically selected trait, 3) The terminator functions as a stop signal for transcribing the inserted/altered gene (Tripathi, 2005).

Given that all genes in life on Earth are made from basically the same chemicals then there is no obvious reason why they cannot function when transferred from one species to another. Indeed genes can even be made in the laboratory and in theory it is possible to back-engineer a gene from the desired characteristics. This is what some refer to as 'synthetic biology' (Benner and Sismour, 2005).

Methods of Gene transformation

Several methods of production of genetically modified organisms (GMO) are known (Fig. 1.). The integration of transgene into the cell is carried out by different methods: (a) Transduction with the use of bacteriophages (b) Transgene injection using pronuclear microinjection; (c) Transfer using modified viruses and plasmids (d) Electroporation method by which higher permeability of cell membrane is achieved (Verma *et al.,* 2011).

Agrobacterium tumefaciens Method

Plant transformation mediated by the soil plant pathogen *Agrobacterium tumefaciens* has become the most commonly used method for plant transformation. *A. tumefaciens,* a gram-negative phytopathogen, naturally infects the wounded sites in dicotyledonous plant causing the formation of the crown gall tumours.

The basis of the crown gall formation is a transfer of a segment of bacterial tumour inducing plasmid (Ti) DNA, the T -DNA, into the nuclear genome of the infected plant cells. The T-DNA contains two types of genes: the oncogenic genes, encoding for enzymes involved in the synthesis of auxins and cytokinins and responsible for tumour formation; and the genes encoding for the synthesis of opines.

Outside the T -DNA are located the genes for the opine catabolism, the genes involved in the process of T-DNA transfer from the bacterium to the plant cell and for the bacterium-bacterium plasmid conjugative transfer genes (Hooykaas and Shilperoort, 1992; Zupan and Zambryski, 1995).

Agrobacterium tumefaciens is a natural genetic engineer used in the production of transgenic crops. It is a soil bacterium that infects plants at a site where the stem and the roots first meet. That site is called the crown. This bacterium causes rapid cell proliferation and induces crown gall disease in the plants. *A. tumefaciens* is able to work due to the presence of a tumor-inducing Ti plasmid.

The two most essential components present in the Ti plasmid are the T-DNA and the virulence region. The T-DNA contains 25 base pair repeats at the ends of the repeat called border sequences, known as right border (RB) sequences and left border (LB) sequences. The rest of the plasmid contains virulence genes such as virA, virB, virC, virD, virE, virF, and virG (Ghimire, 2017). The process starts when bacteria's receptors aid in recognizing and attaching to the plant cell. Once recognition and attachment have taken place, the bacterium infects the plant, and then the wounded plant releases chemical compounds.

A. tumefaciens recognizes the chemicals released. virA detects the signal and gets activated. It binds to the chemical compound. This interaction, in turn, activated virG via phosphorylation. This activated virG acts as a transcriptional activator for other vir genes such as virD1 and virD2. These virD genes act as endonucleases and cleave the border sequences present in the T-DNA. This result in a single-stranded T-DNA with virD2 attached to its end. T-DNA is then exported across the cell envelope of the host plant cell. This is done using a conjugation system called the type IV 390 Singh and Kaur secretion system (T4SS). Once the T-DNA is inside the nucleus, it gets integrated into the plant's genome. This integration of T-DNA into the nucleus is entirely. Any kind of specification does not mediate it. Then, it expresses specific encoded genes, some of which are responsible for the synthesis of plant hormones such as cytokinin and auxin. They are the genes responsible are the genes responsible for cell proliferation, tumor production, and opine production. The T-DNA also makes the plant produce "opines," a modified amino acid that serves as a nutritional source (carbon and nitrogen source) for the bacteria (Ghimire, 2017). Once the T-DNA is successfully incorporated into the plant's genome, the DNA modification part of the GMF production is complete. Lastly, it is bred just like other typical plants, and it grows normally, but once it is fully grown, the exhibited characteristics will differ from that of typical plants. This depends on the function of the chosen gene of interest inserted into the plant's nucleus.

Particle Gun Method

This method aims to introduce a new gene into the nucleus of a plant cell. In this method, the gene of interest does not need to be cloned into a unique transformation vector as we do with the *A. tumefaciens* method in order to be transformed into plant cells. This method uses microscopic gold or tungsten particles to deliver the gene of interest inside the nucleus (Oliver, 2014). Numerous gold particles are coated with many copies of our gene of interest. Another gene called the marker gene is also inserted along with the gene of interest.

This is inserted for easy identification of whether our target gene has been successfully transformed into the cell or not. This is done on a plastic disc present at the exit area of the firing piston. The coated gold particles are then accelerated at high air pressure and are shot at the plant cells such that the gene of interest penetrates the nucleus. There is a stopping plate just before the gene penetrates the plant cell. This stopping plate blocks the disc and allows only the DNA particles coated with gold or tungsten to penetrate. When a new gene is inserted into the chromosome, the chromosomal DNA separates the new gene's insertion without replacing existing genes. This can be compared to someone cutting a queue.

Once the target gene is inside, it is a part of the cell's DNA and will grow, multiply, and be passed onto the offspring (Ghimire, 2017). The *A. tumefaciens*-mediated gene transfer method is more widely used and is a comparatively more popular gene transfer method than the particle gun method. This bombardment process causes loss of integrity of the DNA because the target gene is shot into the nucleus at the high air pressure, and there are also size limitations on the target gene of interest. On the other hand, the *A. tumefaciens*-mediated gene transfer method has several advantages such as it is easy to use, it is not too expensive and results in a low copy number, and, most importantly, the integrity of the DNA is not lost when this method is used. Due to these reasons, the *A. tumefaciens* method is more popular (Ghimire, 2017).

Chemical mediated gene transfer

Cells or protoplasts can be stimulated to take up foreign DNA using some chemicals. Polyethylene glycol (PEG) is the most commonly used chemical for this purpose. It helps in precipitation of DNA, which can then be taken up by the calls through the process of endocytosis.

Liposome mediated gene transfer

Plasmid containing foreign desired gene can be enclosed in small lipid bags called liposomes, which can then be fused with protoplasts using chemicals like PEG.

Silicon carbide method

In this method, fibres of organic material like silicon carbide are used for gene transfer. These fibres, when mixed with plasmid DNA and plant tissue or cells, help in penetration of the foreign DNA into the plant tissue.

Transgenic Soybean Seed development

Transformation in soybean was first reported in 1988 by Christou *et al.,* (1988) and Hinchee *et al.,* (1988), and genetically modified soybean was first introduced commercially in 1996. Transgenic soybean plants have been obtained by two predominant methods for plant transformation, i.e. particle bombardment-based method and the Agrobacterium-mediated transformation method (Hinchee *et al.,* 1988; McCabe *et al.,* 1988). Agrobacterium-mediated gene transfer method is preferred over particle bombardment-based method due to requirement of minimal equipment costs, possibility of transferring relatively large segments of DNA, lower number of transgene copy integration into plant genomes, rare transgene rearrangement, lower frequency of genomic DNA interspersion and reduced abnormal transgene expression (Gelvin, 2003).

Particle bombardment method involves the use of complicated and expensive equipment (McCabe *et al.,* 1988) and results in complex integrations, fragmentation and reconstitution of transgenes that may lead to transgene silencing). Agrobacterium-mediated transformation method attributes about 85% of the transgenic plant production (Yu *et al.,* 2010). This method has been extensively used to introduce agronomical important traits like herbicide tolerance (Padgette *et al.,* 1995), amino acid modification (Falco *et al.,* 1995), virus resistance (Di *et al.,* 1996), insect resistance (Stewart *et al.,* 1996) and nematode resistance (Yamada *et al.,* 2012) in soybean cultivar. A detailed list of traits introduced in soybean through transgenic method is given in Table 1.

Despite production of fertile transgenic plants through Agrobacterium-mediated transformation, reported transformation efficiencies are generally low in soybean (Somers *et al.,* 2003; Rani *et al.,* 2012; Verma *et al.,* 2014). The transfer of T-DNA and its integration into the plant genome is influenced by several plant tissue-specific factors. These factors include plant genotype, explant vigour, Agrobacterium strain, vector-plasmid and selection system including selection agent and method (Cheng *et al.,* 2004; Shukla *et al.,* 2020). Additionally, inoculation and co-culture media composition, osmotic treatments, vir-gene-inducing synthetic phenolic compounds, tissue damage, suppression and elimination of *A. tumefaciens* infection after co-cultivation also affect the transformation efficiency (Klee, 2000; Cheng *et al.,* 2004). To develop an efficient genotype-independent Agrobacterium-mediated transformation system and high efficiency, modification should be done in factors affecting transformation. Although a number of factors that affect transformation efficiency have been studied and manipulated that includes sonication-assisted Agrobacterium-mediated transformation (Trick and Finer, 1997), the use of cystine, dithiothreitol and thiol compounds (Olhoft *et al.,* 2007), co-cultivation at 22C and use of Silwet-77 as surfactant (Liu *et al.,* 2007), use of antioxidant during co-cultivation (Wang and Xu, 2008), 4-day co-cultivation time period (Ko and Korban, 2004) and selection by direct placement of explant at low concentration of antibiotic (Yan *et al.,* 2000). Successful transformation using Agrobacterium depends not only on the efficiency of the plant regeneration systems but also on the subsequent elimination of this bacterium from transformed cells.

The elimination of Agrobacterium is usually achieved by adding one or more antibiotics to the culture medium and is quite important because the continued presence of Agrobacterium can present a problem for identifying transformants or interfere with the growth and development of the transformed plant cells or cause the death of the cultures (Horsch *et al.,* 1985; Matzk *et al.,* 1996). Carbenicillin and cefotaxime are the most commonly used antibiotics for this purpose. An effective and foolproof selection strategy is very important for successful transformation.

Five different selection markers have been utilized in soybean transformation. They include cat, npt II, hpt, bar and manA and neomycin phosphotransferase II (npt II). The most successful and popular selection marker is the bar gene, derived from *Streptomyces hygroscopicus* which encodes the enzyme phosphinothricin acetyltransferase (PAT) conferring resistance to the herbicide phosphinothricin (PPT) or its analogues Basta (with its active ingredient glufosinate ammonia) or bialaphos (Harshavardhan *et al.,* 2003).

Table.1 Agronomically important genes transferred into soybean

Target tissue	Gene	Selectable marker	Phenotype	References
Somatic embryo	Cry1Ac	HPT	Resistance against soybean looper (*Pseudoplusia includens*)	Stewart *et al.*, 1996
Cotyledonary nodes	BPMV-CP-P	NPTII	Resistance phenotype against BPMV	Di *et al*., 1996
Somatic embryos	β-casein	HPT	Expression of a milk protein in soybean	Maughan *et al.*, 1999
Hypocotyl	SMV-CP-3'-UTR	NPTII	Resistance against SMV virus	Wang *et al*., 2001
Somatic embryo	Maize 15 kDa zein protein gene	HPT	Increased methionine and cysteine content	Dinkins *et al*., 2001
Cotyledon	CRC	HPT	Enhanced accumulation of isoflavones in seed	Yu *et al*., 2003
Somatic embryo	Bean-chitinase gene (chi) and ribosome inactivating protein gene (rip)	NPTII	Bioassay not done	Li *et al*., 2004
Immature cotyledon	SMV-CP-3'-UTR	HPT	Bioassay not done	Lim *et al.*, 2005
Somatic embryo	CP-SMV	HPT	Resistance against SMV	Furutani *et al.*, 2006
Somatic embryo	SMV-HC-Pro	HPT	Exhibited resistance response against SbDV	Tougou *et al.*, 2006
Embryonic axes	Cry1Ac	NPAT	Resistance to cotton bollworm	Dang and Wei, 2007
Cotyledon	SbDV-CP	CP4 EPSPS & NPTII	Protection against soybean looper, soybean podworm and velvet bean caterpillar	Miklos *et al.*, 2007
Cot-node	FAD3	PAT	Significant reduction in linolenic acid (18:3) content, ranging from 1.0% to 3.1%	Flores *et al.*, 2008
Cotyledon	CPs	NPTII	Enhanced accumulation of isoflavones in seed	Marra *et al.*, 2009
Cotyledon	γ-TMT	PAT	41-fold increase in α tocopherol	Lee *et al.*, 2011
Half-seed cotyledonary explant/ nodes	Bar gene	PPT	Resistance against herbicide	Li *et al*., 2017a
Half seed	AtABF3	Phosphinothricin (PPT)	Drought tolerance	Kim *et al.*,2018

Fig.1 Methods of gene transfer in plants

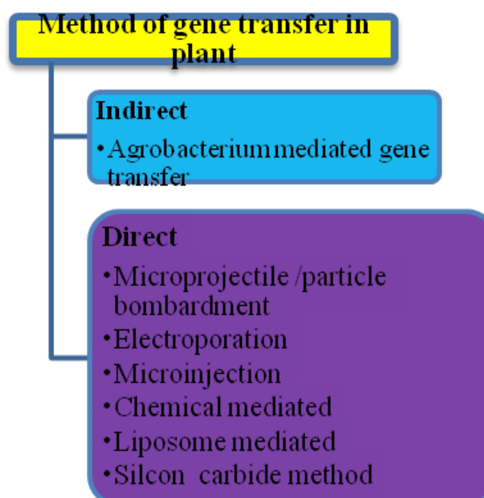
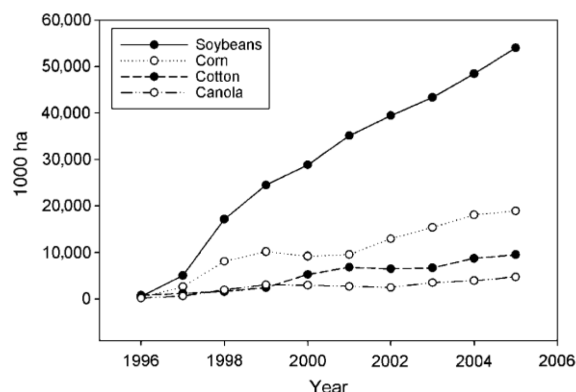


Fig.2 Area of global GM crops in 1996–2005. (Sources: ISAAA, Canola Council of Canada, Crop Life Canada, USDA, CSIRO, ArgenBio.)



A new technology for genome editing the CRISPR (clustered regularly interspaced short palindromic repeat)/Cas (CRISPR-associated) system has been successfully used for genome engineering in many important crops in recent years. Since 2015, CRISPR/Cas9-mediated genome editing in soybean has shown an initial success. This technology provides a powerful tool for accurate genetic modification and gene function identification, but it also relies on transformation efficiency (Chen *et al.,* 2018). Soybean genetic transformation is limited to few laboratories due to low transformation and regeneration efficiencies.

Production Status of Genetically modified Soybean

Biotechnology has been the most rapidly adopted technology in the history of agriculture and continues to expand in much of the developed and developing world. More than a billion acres of transgenic cropland has been planted worldwide, with over 50 trillion transgenic plants grown in the United States alone. In 2000, 68% of all GM crops were grown by U.S. farmers. In comparison, Argentina, Canada and China produced only 23%, 7% and 1%, respectively. Other countries that grew commercial GM crops in 2000 are Australia, Bulgaria, France, Germany, Mexico, Romania, South Africa, Spain, and Uruguay. Soybeans and corn are the top two most widely grown crops (82% of all GM crops harvested in 2000), with cotton, rapeseed (or canola) and potatoes trailing behind. 74% of these GM crops were modified for herbicide tolerance, 19% were modified for insect pest resistance, and 7% were modified for both herbicide tolerance and pest tolerance. Globally, acreage of GM crops has increased 25-fold in just 5 years, from approximately 4.3 million acres in 1996 to 109 million acres in 2000 - almost twice the area of the United Kingdom. Approximately 99 million acres were devoted to GM crops in the U.S. and Argentina alone (Whitman, 2000).

Almost all of the global GM crop area derives from soybean, maize (corn), cotton, and canola (Fig. 2.). In 2005, GM soybean accounted for the largest share (62%) of total GM crop cultivation, followed by maize (22%), cotton (11%), and canola (5%). In terms of the share of total global plantings to these four crops accounted for by GM crops, GM traits accounted for a majority of soybean grown (59%) in 2005 (i.e., non-GM soybean accounted for 41% of global soybean acreage in 2005). For the other three main crops, the GM shares in 2005 of total crop production were 13% for maize, 27% for cotton, and 18% for canola (i.e., the majority of global plantings of these three crops continued to be non-GM in 2005). The trend in plantings of GM crops (by crop) from 1996 to 2005 is shown in Figure 1 (John *et al.,* 2008).

In 2004, soybean accounted for 60% of all GM crops, maize for 23% and cotton for 11 percent. The global area under genetically modified (GM) crops grew from 1.7 million hectares in 1996 to 134 million hectares in 2009. Today, 14 million farmers worldwide grow GM crops in 25 countries, including 16 developing countries (James, 2009). The use of genetically modified (GM) crops in large-scale farm production in the past decade has created a demand for laboratory techniques that can track plant genes and transgenes in the environment and through the food chain. GM crops were grown on 58.7 million hectares in 2002, 99% of which was grown in the USA, Argentina, Canada and China as cited by Carol A. Auer (2003).

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Future Prospect and Challenges

Advance in biotechnology offer opportunities to develop soybean varieties with enhanced nutritional composition, abiotic stress tolerance and disease resistance. Research efforts are underway to improve the nitrogen fixation capacity of soybean, reducing dependence on synthetic fertilizers. However, challenges exist, including societal acceptance, public perception, and the need for transparent communication regarding the benefits and potential risks associated with genetically modified soybean. Adequate data on long term environmental impacts and socioeconomic aspects are crucial for informed decision making and evidence based policies.

The production and adoption of genetically modified soybeans have been revolutionized global soybean production, demonstrating numerous benefits in terms of productivity, weed and pest management, and environmental sustainability. However, concerns related to safety, environmental impact, and socioeconomic aspects require careful evaluation and management. Regulatory frame works play a crucial role in ensuring the safe and responsible use of genetically modified soybean. The future potential of genetically modified soybean lies in further advancements, such as increased nutrient composition, stress tolerance, and disease resistance.

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