



Plant Archives

Journal homepage: <http://www.plantarchives.org>

DOI Url : <https://doi.org/10.51470/PLANTARCHIVES.2026.v26.supplement-2.212>

GM CROPS IN AGROECOSYSTEM: A REVIEW OF EMERGING BENEFITS AND UNCERTAINTIES

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(Date of Receiving : 27-03-2026; Date of Revision : 15-05-2026; Date of Acceptance : 03-06-2026)

ABSTRACT

Genetically modified (GM) crops have become an essential component of contemporary agricultural practices, designed to meet the growing global need for food and to address challenges posed by pests and diseases, yield decline, and climate change. Recent advances in molecular breeding, such as stacked traits and precision genome editing, have extended the frontiers of crop modification beyond earlier-generation transgenics. These technologies have improved crop yield stability, minimized crop losses, and enhanced resistance to biotic and abiotic stresses, making GM crops essential components of sustainable intensification. Notwithstanding these advances, important scientific and policy controversies continue to surround long-term ecological and socio-economic implications. These include transgene escape into wild relatives and landraces, genetic erosion, and unintended effects on non-target species. There are also uncertainties regarding effects on soil microbial populations, nutrient cycling, and agroecosystem resilience. Beyond ecological considerations, agro-economic aspects, such as seed industry consolidation, farmer dependence on biotechnology, and inequitable distribution of benefits, especially for small farmers, remain contentious. While short-term analyses often indicate agronomic benefits and acceptable risks, holistic long-term and landscape-level analyses that consider biodiversity, soil quality, and rural economic sustainability are still underrepresented. This review combines current technological advancements with a critical analysis of negative impacts on agricultural systems, as it seeks to offer a balanced perspective for sustainable assessment and future use of GM crops.

Keywords : GM Crops, Agroecosystem, Genetic Modification, Agriculture.

Introduction

Genetically modified (GM) crops have evolved from an innovative biotech approach to the backbone of modern agriculture, having covered an area of around 206 million hectares worldwide in 2024 (Bekele-Alemu *et al.*, 2025). Although the initial acceptance was based on the gene transfer approach by random insertion, the technology has been completely transformed by the CRISPR/Cas method, which enables targeted and precise modifications of the genome (Jaganathan *et al.*, 2018). These developments have shifted beyond the basic herbicide resistance trait to tackle more intricate issues such as nutrient deficit and climate change.

Genetic modification is the direct manipulation of the genetic system of an organism. The WHO has defined Genetically Modified Organisms (GMOs) as Organisms (i.e. plants, animals or microorganisms) in which the genetic material (DNA) has been altered in a way that does not occur naturally by mating and/or natural recombination, while the FAO (Food and Agriculture Organization of the United Nations) and the European Commission define GMOs as products “not occur naturally by mating and/or natural recombination (Zhang *et al.*, 2016). Although there are differences between “GM crops” and traditional breeding, allowing for a more precise control over the desired characteristics, these definitions are still a subject of scientific controversy, as scientists question

the strict separation between natural and engineered (Raina *et al.*, 2018; Tagliabue, 2016).

The practical advantages of these technologies are substantial. GM crops have significantly improved global food security and farmers' livelihoods through increased crop yields. Additionally, GM technology is said to reduce environmental impacts by reducing toxicity from chemical pesticides and by facilitating carbon sequestration through reduced fuel emissions in their cultivation systems (Brookes & Barfoot, 2020; Klümper & Qaim, 2014).

On the flip side, GM monocultures pose ecological risks, such as herbicide-resistant weeds (Benbrook, 2012). In addition to weed resistance, there are also concerns about "gene flow" to wild relatives, which could endanger biodiversity integrity, and such crop plants, by their advantageous traits against natural selection pressure, may cause loss of wild varieties and so respective wild genes (Haygood *et al.*, 2003; Snow *et al.*, 2003). Further, some researchers suggest transgene flow to weeds may also result in the development of herbicide resistance in them (Adam, 2025). The effect of soil health, particularly the impact of microbial biomass and mycorrhizal fungi colonization in continuous glyphosate use, remains a topic of debate among scientists with conflicting evidence on soil fertility (AlSheboul & Aldeeb, 2025).

The socio-economic environment is increasingly characterized by high market concentration. Hostile takeovers have resulted in only a few companies dominating the majority of the global proprietary seed and agricultural input market (Howard, 2009, 2015). This has resulted in reduced competition and increased seed prices (Clapp, 2018). In developing countries, the high price and enforcement of patents can create a debt cycle for small farmers (Lianos *et al.*, 2016). In a nutshell, these phenomena can result in companies focusing on maximizing shareholder value rather than sustainability objectives such as crop diversity and farmer autonomy (Clapp, 2018).

Emerging GM crops and methods of Genetic Modification

As the global population in 2030 is expected to be 8.5 billion, and the corresponding increase in food demand, proportional to the population growth, is expected to be an estimated 11.6 billion tons of food, the productivity of agriculture needs to be enhanced significantly to avoid mass hunger and food insecurity (Ahmad *et al.*, 2021). Traditional agronomic advances may not be adequate because of the limitations of land and resources, climate change, pest attacks, etc. Genetically modified (GM) crops have been identified

as a major means of promoting food production through yield enhancement, loss reduction, and improved resistance to biotic and abiotic stress factors.

A historic meta-analysis shows that GM technology has led to a 22% increase in crop yield and a 68% increase in farmers' earnings (Klümper & Qaim, 2014). Moreover, from 1996 to 2018, GM technology contributed an additional 231 million metric tons of maize and 441 million metric tons of soybeans to global production, greatly enhancing food security. In terms of the environment, GM technology has enabled a 37% decrease in the use of chemical pesticides, resulting in crop-wise different reductions in the Environmental Impact Quotient (EIQ), which is a measure of the seasonal toxicity of pesticide use. In addition to chemical use, GM crop technologies have contributed to the mitigation of climate change; in 2018, the carbon sequestration effect of reduced tillage and lower fuel consumption was equivalent to the removal of 15.3 million cars from the road (Brookes & Barfoot, 2020; Klümper & Qaim, 2014).

Some emerging GM crops

Edible Cottonseed

RNAi-engineered cotton suppresses seed-specific gossypol, making seed meal protein-rich and edible while maintaining toxicity in leaves for pest control (Palle *et al.*, 2013; Rathore *et al.*, 2020).

Golden Rice

Golden Rice contains phytoene synthase and carotenoid biosynthesis genes, which accumulate β -carotene to fight vitamin A deficiency. Field trials demonstrate increased provitamin A content without affecting crop yields (Beyer *et al.*, 2002).

Flood-Tolerant Rice (SUB1)

At least 15 million hectares of rainfed lowland rice regions in South and Southeast Asia are frequently affected by submergence distress. The potential to use marker assisted backcrossing (MAB) to develop submergence-tolerant versions of varieties that are commonly produced in such areas (especially Swarna Variety) has been made possible by a major QTL (Quantitative Trait Locus) on chromosome 9, Sub1 (Neeraja *et al.*, 2007).

Virus-Resistant Papaya

PRSV coat protein transgenic papaya (SunUp/Rainbow) was resistant from ring-spot virus damage, allowing for sustainable production (Fermin *et al.*, 2004).

Bt Maize

Bt maize expresses *Bacillus thuringiensis* Cry proteins that protect the crop from Lepidoptera, thereby reducing the use of insecticides and improving crop stability (Klümper & Qaim, 2014; Koziel *et al.*, 1993).

Herbicide-Tolerant Soybean

Glyphosate-resistant soybeans represent the most prominent transgenic crop currently cultivated within the United States, which was originally revolutionized by the significant ease of weed control (Dill, 2005).

High-Oleic Soybean

Gene-edited soybean with high oleic acid content results in healthier oil profiles and oxidative stability for food and industrial applications (Haun *et al.*, 2014).

Low-Phytate Maize

When compared to regular maize, low-phytic acid maize seeds have been demonstrated to have substantially more bioavailable phosphorus for monogastric animals (Veum *et al.*, 2001).

Virus-Resistant Cassava

Transgenic cassava with RNAi-mediated resistance to Cassava brown streak virus exhibits long-term resistance in field tests, mitigating yield losses (Odipio *et al.*, 2014).

Jatropha (Biofuel Crop)

Jatropha curcas is an oilseed plant that is not edible and is considered suitable for biodiesel production because of the oil content (high lipid concentration) in its seeds, which is similar to palm oil (Achten *et al.*, 2008). Its growth in India has led to socio-political conflicts, especially when it was grown on the lands of tribal and marginal farmers (Ariza-Montobbio & Lele, 2010). Efforts to improve oil productivity and abiotic stresses in *Jatropha curcas* through breeding and genetic improvement programs focus on increasing yield efficiency without requiring large areas of land (Basha & Sujatha, 2007; Divakara *et al.*, 2010). Furthermore, oil from *Jatropha* has been examined for its possible use as a renewable resource for developing biodegradable polymeric products and bioplastics (Chiang *et al.*, 2017).

Methods of Genetic Modifications:

Long before the advent of molecular technologies, early agriculturalists practiced artificial selection in breeding crops with desirable phenotypic traits. This continuous process of selection breeding has dramatically changed plant genomes, resulting in the

evolutionary divergence of modern crops from their wild counterparts (Meyer & Purugganan, 2013).

Improvement in crops from phenotype-based selection to genetic manipulation began in the 20th century with advances in genetics and cell biology. Genes responsible for desirable traits in crops could now be introduced or altered with precision due to tissue culture, recombinant DNA technology, and, more recently, genome editing, as a more precise and successful method (Ahmad *et al.*, 2021; Gao, 2021). Moreover, the last few years have been another new age with new and more effective methods than the conventional molecular methods used previously.

One of the fundamental techniques in plant biotechnology, such as *Agrobacterium*-mediated transformation, leverages the inherent ability of *Agrobacterium tumefaciens* to transfer a specific segment of its Tumor-inducing (Ti) plasmid, termed Transfer DNA (T-DNA), into the plant nuclear genome. This biological technique uses virulence genes (vir genes), which facilitate the excision and transport of the T-DNA. In laboratory applications, the native T-DNA oncogenes are replaced with genes of interest within "disarmed" Ti plasmids. Once the T-DNA integrates into the host's chromosomal DNA, the transformed cells are regenerated into complete, transgenic plants through specialized tissue culture protocols. This method has been widely used for stable nuclear transformation across diverse dicotyledonous and several important monocotyledonous species (Gelvin, 2003).

Microparticle (Biolistic) Bombardment is a direct transfer or physical delivery approach, employed in much broader range of plant species that are less amenable to *Agrobacterium* transformation (such as cereals) (Altpeter *et al.*, 2005), where foreign DNA is precipitated onto heavy microcarriers, typically gold or tungsten particles. A helium-driven apparatus builds pressure using a rupture disk, propelling a macro carrier loaded with those DNA-coated microparticles. The macro carrier is arrested by a stopping screen, while the high-velocity microparticles continue forward, physically penetrating the plant cell wall and entering the nucleus (Klein *et al.*, 1987; SANFORD *et al.*, 1987). The foreign DNA then randomly integrates into the plant genome, a process that is typically unpredictable in terms of location and copy number. Successfully transformed cells are subsequently isolated using selection media, such as antibiotic or herbicide plates, to regenerate GM plants, which ultimately produce transgenic seeds. (Altpeter *et al.*, 2005; Klein *et al.*, 1987) (Figure 1).

Originally discovered as a bacterial adaptive immune system against viruses and plasmids, CRISPR loci consist of short palindromic DNA repeats alternating with variable phage-derived spacer sequences (Jinek *et al.*, 2012). CRISPR/Cas9 provides highly precise, programmable gene editing and so re-engineered as a precise molecular tool for targeted crop improvement (Bortesi & Fischer, 2015). This molecular tool is based on two primary molecular components: the Cas9 endonuclease and a customizable single guide RNA (sgRNA), typically introduced via a plasmid or as ribonucleoprotein complexes (Jinek *et al.*, 2012; Le *et al.*, 2013). The sgRNA directs Cas9 to a specific target DNA sequence adjacent to a Protospacer Adjacent Motif (PAM),

where the complex induces a targeted double-strand break (DSB) (Jinek *et al.*, 2012; Le *et al.*, 2013). The plant's natural repair mechanisms then resolve the DSB via two primary pathways: Non-Homologous End Joining (NHEJ), which typically introduces random insertions or deletions (indels) resulting in gene knockouts, or Homology-Directed Repair (HDR), which uses a supplied repair template to create precise, targeted modifications (Bortesi & Fischer, 2015; Le *et al.*, 2013). This method allows for precise endogenous edits while facilitating the development of lines that do not necessarily retain foreign DNA, achieved through the segregation of transgenes or the use of transgene-free delivery methods (Bortesi & Fischer, 2015) (Figure 1).

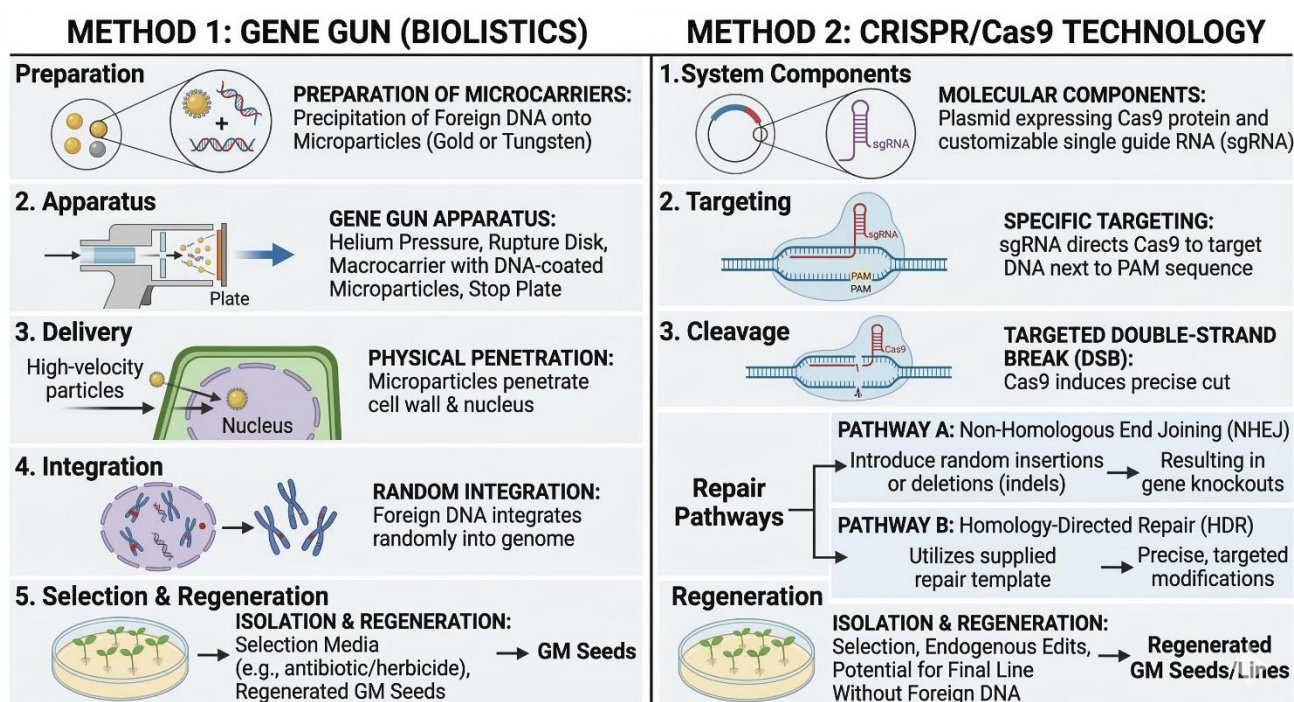


Fig. 1: The method of Gene Gun involves the introduction of foreign DNA into plant cells by high-velocity microparticles. However, CRISPR/Cas9 technology employs the Cas9-sgRNA complex for precise gene modification by introducing double-stranded breaks in the genome, resulting in no foreign DNA being left behind (Altpeter *et al.*, 2005; Bortesi & Fischer, 2015; Jinek *et al.*, 2012; Klein *et al.*, 1987; Le *et al.*, 2013; SANFORD *et al.*, 1987).

Arguably, the Tissue-Culture-Free Synthetic Regeneration System is the most significant recent discovery in this field. Unlike earlier long sterile laboratory efforts and frequent failure to grow a gene-edited cell into a complete plant, this novel method bypasses the petri dish method completely by using a "synthetic transcription cascade" to initiate the plant's own wound-healing response, which causes it to produce new, modified shoots straight from the cultivated plant (Kshetry *et al.*, 2025).

In virus-induced gene silencing (VIGS), plant viral vectors are genetically modified to express

inverted repeats of a target gene (Ratcliff *et al.*, 2001). Once the viral vector infects the cell, these sequences are transcribed and folded into double-stranded RNA (dsRNA) in the host plant cells, which acts as the molecular trigger to initiate the RNA interference (RNAi) pathway (Fire *et al.*, 1998; Unver & Budak, 2009). An endogenous host RNase III-like enzyme known as Dicer then recognizes and cleaves dsRNA into small interfering RNAs (siRNAs). These siRNAs are incorporated into the RNA-induced silencing complex (RISC). This complex with siRNA guides Agronaute protein bound to RISC complex towards

complementary viral mRNA for degradation (Ender & Meister, 2010; Unver & Budak, 2009). This sequence-specific degradation prevents the production of viral protein (Zulfiqar *et al.*, 2023). Consequently, the plant develops systemic resistance against viral infection and ensures agronomic stability (Ratcliff *et al.*, 2001; Unver & Budak, 2009) (Figure 2).

Virus-Mediated RNAi for GM Crops

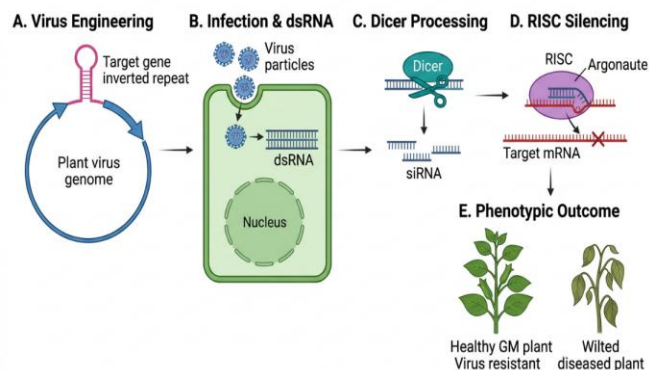
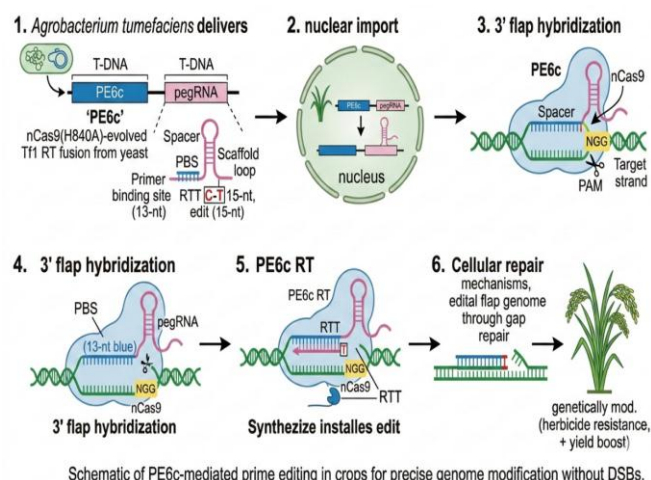


Fig. 2: In VIGS, modified viral vectors produce dsRNA, triggering plant RNAi. Dicer cleaves dsRNA into siRNAs, which direct the Argonaute-RISC complex to degrade complementary viral mRNA. This stops replication, resulting in healthy, virus-resistant GM crops, which are quite different from wilted, diseased crops. (Ender & Meister, 2010; Fire *et al.*, 1998; Ratcliff *et al.*, 2001; Unver & Budak, 2009; Zulfiqar *et al.*, 2023)

To prevent transgene escape via pollen, researchers are targeting the chloroplast genome to ensure maternal inheritance of engineered traits. A Transcription Activator-Like Effector (TALE) linked deaminase precisely converts adenine to guanine in the cpDNA (chloroplast DNA), conferring herbicide resistance without inducing DNA double-strand breaks (Mok *et al.*, 2024). Beyond standard CRISPR-Cas9 systems, base editing utilizes catalytically impaired Cas9 variants such as those possessing nicking activity fused to deaminases to achieve direct single-nucleotide transitions without fragmented DNA (Komor *et al.*, 2016). Furthermore, Genome editing by Reciprocal Addition of Nucleotides (GRAND editing) employs paired prime editing guide RNAs (pegRNAs) to facilitate the targeted insertion of large DNA sequences without requiring an exogenous donor template (Wang *et al.*, 2022).

Some notable new techniques include Smart Nanocarrier Delivery and PE6c Prime Editing, known as Next-Gen CRISPR (Cao *et al.*, 2024; Doman *et al.*, 2023). "Prime editing" is often called "CRISPR 2.0" since, instead of making double-stranded DNA cuts, it uses a nickase enzyme complex (nCas9) to safely open one DNA strand and write new genetic code directly into the genome (Anzalone *et al.*, 2019). *Agrobacterium tumefaciens* delivers T-DNA encoding

PE6c a fusion of nCas9(H840A) and an evolved yeast Tf1 reverse transcriptase alongside a pegRNA (Cao *et al.*, 2024; Doman *et al.*, 2023). Following nuclear import, the complex identifies the target adjacent to an NGG protospacer adjacent motif (PAM) (Anzalone *et al.*, 2019). The nCas9 domain nicks the target strand, releasing a 3' DNA end that hybridizes to the 13-nt primer binding site (Lin *et al.*, 2020a). The RT domain then uses the 15-nt reverse transcriptase template to synthesize DNA, installing the designed C-to-T edit mechanism (Cao *et al.*, 2024). Finally, cellular mechanisms resolve the branched intermediate via gap repair, permanently incorporating the edited flap into the genome to develop crops with traits like herbicide resistance or yield boosts (Cao *et al.*, 2024; Lin *et al.*, 2020a) (Figure 3).



Schematic of PE6c-mediated prime editing in crops for precise genome modification without DSBs.

Fig. 3: *Agrobacterium tumefaciens* introduces PE6c and pegRNA into the nucleus. nCas9 creates a nick in the target DNA without DSBs. PE6c RT creates the precise edit, and natural cellular gap repair mechanism integrates this, resulting in crops that are resistant to herbicides and provide a yield boost. (Anzalone *et al.*, 2019; Cao *et al.*, 2024; Doman *et al.*, 2023; Lin *et al.*, 2020b)

The method of smart nanocarrier delivery involves inserting DNA into a plant cell using nanoparticles instead of using a bacterium (*Agrobacterium*) or a device that uses physical force (biolistics). Nanoparticles can precisely target plant cells and transport CRISPR components across both the plant cell wall and cell membrane using size and charge. (Demirer *et al.*, 2019). Also, other Cas protein families, including Cas12 and Cas14, have been discovered and investigated by researchers later in addition to Cas9. These Cas variants provide different mechanisms for genome editing as well as unique traits and functionalities that allow for the development of customized genetic engineering applications in a variety of organisms (L. B. Harrington *et al.*, 2018; Zetsche *et al.*, 2015).

Emerging concerns with the GM crops in agro-ecological contexts

Although significant evidence exists for a promising future, such as yield increases and lowered pesticide use as a result of GM crop adoption, a fair evaluation must also take into account known and emerging issues. Long-term studies show that while approved GM foods are deemed to be as safe as conventional foods based on current evidence, further research is needed to address ongoing scientific issues (Klümper & Qaim, 2014; Nicolai *et al.*, 2014). In economic terms, benefits have been mixed, with varying farm-level benefits depending on geographical location and size of farms, and technology costs affecting overall profitability (Qaim, 2020). From an agricultural point of view, the most important issues are those that relate to ecological and management dynamics, as the sustained soil health, ecological cycles maintained by various organisms, and other environmental factors are inevitable for the sustained profitability of Agriculture. Therefore, understanding the possible impacts on these aspects is essential.

Herbicide Resistance in weeds

The extensive cultivation of herbicide-tolerant crops has led to the rapid development of herbicide-resistant weeds, resulting in higher chemical use in some areas (Benbrook, 2012; Heap, 2014). The documented record on the evolutionary history of 512 different instances of herbicide-resistant weed evolution in 70 countries by the year 2020 is an exemplary demonstration of the selective pressures that are at play in modern agro-ecosystems. Though the rise of genetically engineered, herbicide-resistant monoculture has certainly contributed greatly to the acceleration of this process for specific herbicides, the global rise of resistance can ultimately be explained by the systemic over-reliance on repeated use of those chemicals with the same mode of action (Gaines *et al.*, 2020). (Heap, 2014; Bonny, 2016). It is known as treadmill phenomenon, as it commonly requires a return to the use of older, more toxic herbicides such as Dicamba or 2,4-D, which could counteract initial successes in environmental protection (Mortensen *et al.*, 2012). Also, the development of resistance in target insect populations poses a risk to the long-term stability of Bt crops when refuge strategies are not properly adopted (Pellegrino *et al.*, 2018).

Loss of genetic diversity

The diversity of genes in the natural world could be impacted by genetically modified crops. This happens when the modified genes meet the natural weeds or plants in the environment through pollen

(Rieger *et al.*, 2002; Snow *et al.*, 2005). Empirical evidence, that gene flow from domesticated to wild populations can occur (Ellstrand, 2003), exists in some cases, for example, in the case of the domesticated papaya (*Carica papaya*) and its wild relatives, where low but measurable gene flow were expected to negatively affect the genetic diversity of the wild populations in the Mesoamerican diversity area (Heredia-Pech *et al.*, 2022). In other cases, such as with transgenic soybean, actual instances of crop-to-wild gene flow have been demonstrated to produce hybrids that have altered fitness profiles, with environmental pressures favouring the persistence of these genes in the wild population, leading to unintended ecological consequences (Z.-J. Guan *et al.*, 2015; Liu *et al.*, 2021). A modified plant could become more dominant in the natural world through natural selection if it has a trait that gives it a better chance of survival, such as the ability to withstand stress or insects. In the natural world, this could lead to a lack of genetic diversity, which could become a bottleneck population for the wild species. Even some of the unique characteristics of plants in the natural world could be eliminated because of genetically modified crops (Haygood *et al.*, 2003; Snow *et al.*, 2003).

Public outrage and research efforts have also been triggered by concerns over transgene flow and possible genetic erosion during the past two decades. Mesoamerican biosafety monitoring and conservation efforts were intensified following the controversy over transgenic DNA in native maize landraces in Mexico, which generated heated debate among scientists and policymakers (Quist & Chapela, 2001). The distribution and magnitude of transgenes in Mexican maize were further investigated in subsequent reassessments (Piñeyro-Nelson *et al.*, 2009; Quist & Chapela, 2001). Large-scale research efforts were undertaken in response to the controversy, including a massive, multi-disciplinary investigation mobilized by the North American Free Trade Agreement (NAFTA) (McAfee, 2008). Current global biodiversity frameworks have recently given greater priority to the conservation of genetic diversity in agricultural landscapes, which has intensified in situ conservation of landraces and monitoring of crop-wild gene flow (Casacuberta & Puigdomènech, 2018), and Mexico has recently adopted a constitutional reform in March 2025 that prohibits the production of genetically modified corn (Singer & Michaud, 2025).

However, there is still little empirical data connecting the recent global decline in intraspecific genetic diversity to the cultivation of genetically modified crops. According to meta-analyses, these

trends are primarily caused by habitat destruction, land-use change, and population pressure, and they are indicative of a larger biodiversity crisis linked to agricultural expansion (Shaw *et al.*, 2025). Although gene flow and possible hybrid fitness effects necessitate wide-scale monitoring and biosafety evaluation in areas where crops have compatible wild relatives.

Effects on soil fertility

The possible disruption of soil ecology by genetically engineered crops has been raised due to the significant role that soil microorganisms play in soil fertility, nutrient cycling, organic matter decomposition, and nitrogen fixation (Dunfield & Germida, 2004). Soil microbial communities are very diverse and play a significant role in the biological processes that sustain plant growth. Any shift in the diversity of these microorganisms may impact soil function and plant growth, which may reduce soil fertility (Giovannetti *et al.*, 2005).

The early literature on biosafety considered that transgenic plants could impact microbial communities through the addition of root exudates, plant litter, or new proteins to the soil, which can alter the quantity or structure of important microbial populations participating in biogeochemical processes (Bruinsma *et al.*, 2003; Donegan *et al.*, 1995). Nevertheless, field experiments and reviews have indicated that genetically engineered (GE) plants have no significant adverse impacts on soil bacterial or fungal diversity relative to non-GE plants. Long-term experiments involving herbicide-tolerant soybean and herbicide-resistant maize using high-throughput sequencing demonstrated no significant differences in rhizosphere bacterial community structure or total soil microbiome diversity between GE crop plots and conventional controls (Dong *et al.*, 2024; Jang *et al.*, 2025; Shen *et al.*, 2025). In a recent study on semi-wild glyphosate-resistant soybean, there were no significant differences in the species diversity of rhizosphere bacteria between transgenic and non-transgenic lines at different growth stages. Some fungal species were found to be stable or even positively associated during flowering and maturation (Dong *et al.*, 2024). Likewise, in studies evaluating GE maize with a phosphinothricin N-acetyltransferase gene, there was no significant difference in bacterial diversity in the maize rhizosphere compared to non-GE varieties (Jang *et al.*, 2025). These results are in line with general reviews that found, despite the GM crop's ability to release new proteins or metabolites into the soil, the effect on the soil microbial community is often variable, transient, or masked by site-specific environmental

factors (Dunfield & Germida, 2004; Z. Guan *et al.*, 2016).

Although the evidence is generally encouraging, many specific issues still exist. The overall microbial community structure in Bt cotton systems expressing *Bacillus thuringiensis* insecticidal proteins expressed in plants frequently appears unchanged; however, under some circumstances, especially with long-term continuous cropping, subtle changes in nutrient cycling processes or gene expression pathways may occur. According to some research, soils under extensive Bt cultivation exhibit altered levels of functional genes of soil microbiomes linked to phosphorus cycling and nitrogen fixation (Fonseca de Souza *et al.*, 2025). Furthermore, the possible horizontal transfer of special genetic elements from GM crops to soil microbes could lead to a reduction in microbial genetic diversity. However, there is still limited evidence for horizontal gene transfer in the field (Dunfield & Germida, 2004; Guan *et al.*, 2016). Nevertheless, the functional implications of these subtle microbial changes could affect ecosystem processes, even in the absence of any significant losses in overall diversity.

Recent studies using high-resolution metagenomics to monitor the minute changes in microbial communities, functional gene copy numbers, and soil ecosystem processes, have shown that, although the overall species diversity in the rhizosphere zone may be similar for GM and non-GM varieties, there may be differences in the detailed patterns of community structure or metabolic gene expression, particularly in continuous monocultures and under particular environmental conditions (Dong *et al.*, 2024; Shen *et al.*, 2025). Such differences in the level of functional groups, such as nitrifiers and mycorrhizal associates, may influence the long-term availability of nutrients and soil texture. This may force farmers to apply more fertilizers to ensure NPK balance and optimal plant growth, thereby adding to their costs. This, in turn, indirectly affects developing and underdeveloped countries with small farmers who possess limited land and economic resources. Apart from microbial effects, some studies have shown that there may be alterations in the activities of soil enzymes such as dehydrogenase and urease in soils under some genetically engineered crops. Such alterations may influence the turnover of organic matter and nitrogen availability (Mandal *et al.*, 2020).

This underlines the importance of long-term, multi-factor research that is able to distinguish between the impact of GE traits and other agricultural practices, such as tillage, herbicide use, crop rotation, or soil management. In addition to ecological risk

assessments, researchers and other stakeholders are still debating the wider implications of the dominance of GM crops in global agriculture. According to some sources, the intensive cultivation of GE monocultures, in combination with reduced crop rotation and greater use of chemicals, may, in the long term, result in reduced complexity of soil microbial communities. This may, in turn, impact soil properties and stress

resistance (Pandey & Saharan, 2025). Nevertheless, proponents of GE crops claim that they have contributed to the adoption of conservation tillage and decreased pesticide use. These agricultural practices may improve soil health and decrease erosion, rather than degrade it (Brookes & Barfoot, 2018; Klümper & Qaim, 2014) (Figure 4).

SOIL FERTILITY REDUCTION PATHWAYS DUE TO GENETICALLY MODIFIED (GM) CROP CULTIVATION

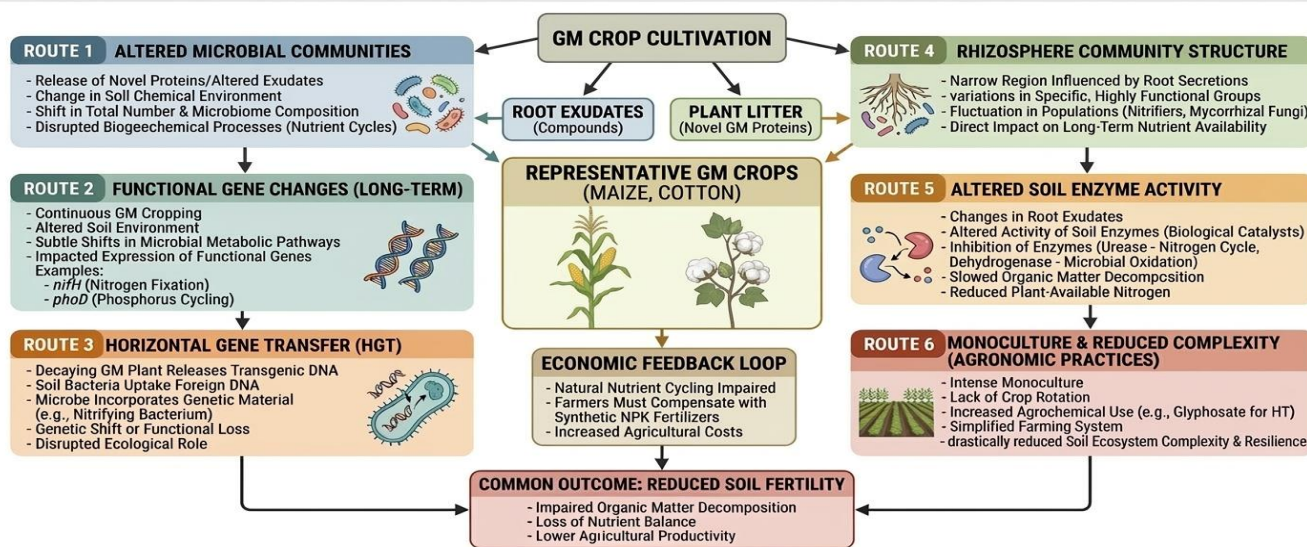


Fig. 4: GM crop cultivation leads to the formation of exudates and proteins, initiating six pathways of degradation: changes in microbe populations, functional gene shifts, gene transfer, rhizosphere shifts, and enzyme activity. Coupled with high monoculture, the result is a single outcome: poor soil fertility (Z. Guan *et al.*, 2016; P. Li *et al.*, 2023; Mandal *et al.*, 2020; Pandey & Saharan, 2025; Song *et al.*, 2021).

Probable effects on Non-Target Organisms (NTOs) other than soil biota

Besides the soil and soil biota, other ecological networks support agricultural productivity through the regulation of nutrient cycling, decomposition, water, and biological control of pests. Bees, birds, and other beneficial organisms play a direct role in fruit and seed production, pest biological control, and agroecosystem stability. Therefore, the environmental assessment of genetically modified (GM) crops is not only concerned with the impact of GM crops on soil microbial populations but also on non-target arthropods, pollinators, and vertebrates.

Since the mid-1990s, with commercialization of insect-resistant (IR) GM crops, a structured and science-based ERA (Environmental Risk Assessment) framework has been developed to assess potential effects on non-target organisms (NTOs). This ERA framework is mainly founded on a tiered toxicity testing strategy, for insecticidal proteins such as Bt Cry proteins (Romeis *et al.*, 2008). Testing usually starts in

controlled laboratory settings with highly purified transgene products at concentrations far exceeding the expected levels of environmental exposure. The initial tiers of testing are intended to assess intrinsic hazard potential by analysing sublethal endpoints such as survival, reproduction, development, and behaviour. However, if toxicological effects are found, the testing will move on to the next tier, which will involve more ecological realism, such as microcosm experiments, semi-field tests, and finally full-field experiments. The role of exposure assessment is pivotal in this process, where the data from the NTO species of choice is evaluated in the context of realistic environmental concentrations in the form of pollen, plant material, or soil (Raybould, 2007; Romeis *et al.*, 2011). The choice of test organisms is guided by certain criteria, such as ecological role (predators, decomposers, parasite etc.), abundance, phylogenetic relationship to the target species, and conservation significance (Romeis *et al.*, 2011).

Recent reviews highlight that risk characterization combines both hazard and exposure in such a way that

laboratory toxicity results are assessed in a field context (Roberts *et al.*, 2015; Sanvido *et al.*, 2012). Monitoring schemes after commercialization also evaluate long-term ecological impacts in a farm-scale cultivation setting. Over two decades of accumulated evidence have shown that approved Bt crops have had little consistent adverse impact on most NTOs when assessed using this tiered approach, although ongoing monitoring is still advised to account for context-specific ecological interactions (Romeis *et al.*, 2008; Roberts *et al.*, 2015).

On the other hand, the toxicity associated with pesticide and herbicide use remains a major environmental concern in modern agriculture, particularly in cropping systems dominated by herbicide-tolerant and insect-resistant genetically modified (GM) crops. While GM traits such as Bt (*Bacillus thuringiensis*) proteins were initially promoted as reducing the use of broad-spectrum insecticides, ecological debates persist regarding their direct and indirect effects on non-target organisms (Naranjo, 2009; Romeis *et al.*, 2008). The following points explain some of the probable effects of GM crops or cropping methods on several organisms important for maintaining the stability and sustainability of the agro-ecosystem.

Pollinators (Honey Bees and Bumble Bees)

Honey bees are considered as the best ones contributing to agricultural productivity. Even in self-pollinating crops, bee visitation can increase fruit and seed production. Agricultural habitats also support wild bees like bumble bees. Initial laboratory and field experiments, testing bees fed with purified Bt proteins or allowed to forage on Bt crops revealed no consistent lethal or sublethal effects, are consistent with regulatory assessments of low direct toxicity (Romeis *et al.*, 2008). Only serine protease inhibitors (PIs) expressed in some experimental GM plants were suggested to have potential effects at high laboratory exposure levels, influencing digestive proteases and survival (Malone & Pham-Delègue, 2001; O'Callaghan *et al.*, 2005).

Recent large-scale biotic syntheses have shown that Bt crops by themselves pose a low direct risk to honey bees, but there is a strong association between the decline of pollinators and the cumulative effects of stress factors such as pesticide exposure, habitat destruction, and nutritional stress. Herbicide-tolerant crops could have an indirect effect on reducing the diversity of wildflowers in agricultural landscapes, which could reduce foraging of the pollinators and the

strength of colonies, and thus can affect pollination of crop plants indirectly (Goulson *et al.*, 2015).

Monarch Butterflies

The monarch butterfly (*Danaus plexippus*) became symbol of GMO controversy when laboratory research indicated that Bt maize pollen was damaging to monarch larvae (Losey *et al.*, 1999). Subsequent risk assessments, taking into account field concentrations, determined that the risk of Bt pollen was low (Sears *et al.*, 2001).

However, monarch population declines in North America over the long term have been strongly linked to the loss of milkweed (*Asclepias* spp.), the only food source for monarch larvae. The increased use of glyphosate-resistant crop systems has been shown to cause a significant decrease in the amount of milkweed present in agricultural areas (Pleasant & Oberhauser, 2013). Habitat loss, rather than Bt toxicity, is thought to be a key factor in population decline. More recent assessments have indicated that habitat loss and herbicide-induced weed suppression may interact with climatic and migratory pressures, making this decline of the monarch butterfly population a landscape-level management problem rather than a GMO problem.

Earthworms

Earthworms are key ecosystem engineers that play important roles in litter breakdown, soil aeration, and nutrient turnover. In early toxicity assays, there was little evidence of direct toxicity of purified Bt toxins to *Eisenia fetida* at concentrations above expected field exposure levels (Romeis *et al.*, 2008). However, weight loss in *Lumbricus terrestris* fed Bt maize residues was reported (Zwahlen *et al.*, 2003), although nutritional deficits rather than toxin toxicity were proposed as the cause.

Recent meta-analyses have shown that Bt crops do not have a significant effect on the mortality or sublethal effects of earthworms in the field, although there could be an indirect effect on the soil macrofauna (Naranjo, 2009). Herbicide application in herbicide-tolerant crops could have an effect on earthworm reproduction and activity based on the type and intensity of the herbicide application. Therefore, soil ecological effects are dependent on management practices and not solely on GM traits of the cultivated crops.

Birds

Bird species in agricultural ecosystems could be indirectly impacted by GM crop technologies based on changes in the availability of insect prey, weed seeds, and habitat. Although Bt crops can reduce the need for

certain insecticides, herbicide-based crop technologies could reduce plant species diversity and associated invertebrate populations. Bird species declines in agricultural ecosystems across Europe have been attributed mainly to the intensification of pesticides and habitat simplification, rather than GM toxicity (Geiger *et al.*, 2010). Birds act as pollinators and biological control agents in agricultural ecosystems; therefore, habitat simplification could lower their ecological functions.

Unfair Practices by the corporates and socio-economic impacts

The advent of genetically modified (GM) crops occurred during a period when the global economy was more oriented towards financial returns. Investors, especially farmers, sought rapid returns from biotechnology. The first GM traits, such as herbicide tolerance, were relatively easier to develop and could be applied to different species of crops. This enabled faster expansion in the market and faster returns. Herbicide-tolerant soybean, maize, and cotton were widely adopted in large agricultural nations such as the United States, Brazil, and Argentina. This further strengthened the business model of seed and agrochemicals (Fernandez-Cornejo *et al.*, 2014; Schütte *et al.*, 2017).

During this period, large agrochemical corporations acquired seed companies, leading to a more consolidated industry. This led to greater ownership of intellectual property and market power by a few large multinational corporations (Howard, 2015), resulting in reduced competition in the seed industry, increased seed prices, and greater enforcement of patent rights. Farmers and social movements raised their concern about corporate influence over the agriculture sector as a result of these developments (Clapp, 2018; Howard, 2015). Financial factors have also influenced the strategies of corporations. The mega-mergers trend in the agri-food industry is noteworthy. Some critics suggest that when corporations are primarily concerned with generating profits and maximizing returns for their shareholders, other crucial sustainable development objectives such as promoting crop diversity, decreasing chemical use, and improving the independence of farmers may receive less attention than they deserve (Clapp, 2018).

Research indicates that the consolidation of agricultural biotechnology industries has been increasing steadily since the 1990s, particularly with regard to patented seed technologies (Howard, 2015). This trend has caused public concern in a number of regions, including India and Latin America. Farmers

and social movements have expressed concerns regarding seed prices, licensing agreements, and dependence on proprietary technologies. Although government agencies are generally concerned with biosafety and crop performance, other sustainable development objectives, such as equitable economic arrangements and cooperation among all stakeholders, are also important. In Africa, the discussion on GM crops has been informed by socio-economic considerations, in addition to biosafety, with civil society organizations demanding more transparency, respect for the rights of farmers, and risk assessments that are relevant to the region before commercialization. They argue that business agreements and intellectual property standards could compromise seed sovereignty and worsen inequalities in rural areas (Clapp, 2018). Public protests in various regions of Europe continue to focus on regulatory frameworks, risk assessments, and the right to choose non-GM agricultural practices, reflecting the underlying socio-political culture of food system governance.

Future Prospects

The trend of increasing cultivation area of GM crops in nations like US, Brazil, Argentina, India etc. was observed before but the recent trend is heralding future of GM crops beyond few larger agricultural nations and the current degree of performance. Such technologies are now evolving to address global nutritional and environmental challenges. Biofortification efforts, such as wheat strains developed at the John Innes Centre, have successfully doubled iron content to combat global anaemia (S. A. Harrington *et al.*, 2023). Productivity is also increasing; for example, US researchers increased corn yields by 10% through growth-regulating gene modifications that improve nitrogen and sunlight utilization. Beyond yield, genetic engineering has also resulted in health benefits: insect-resistant corn that reduces carcinogenic fungal toxins like fumonisins is claimed to decrease oesophageal cancer rates (Yoshizawa *et al.*, 1994). Sustainability has been a pivotal aim, with the SUSIBA2 rice variety containing barley plant gene, because of which they reduce methane emissions while boosting yield by 10%. Furthermore, the C4 Rice Project aims to integrate efficient photosynthetic pathways that could increase harvests by 50% in arid climates (Covshoff & Hibberd, 2012). Water conservation is being achieved by reducing stomatal density saving up to 60% of water (Phunthong *et al.*, 2024) and merging drought-resistant upland rice genes with traits of high-quality lowland varieties to create hardier, more resilient crops (H. Li *et*

al., 2026). There is huge potential of benefit from GM crop cultivation in the developing nations, beyond the aforesaid larger agricultural nations. Traits like draught resistance has opened new avenues for sustained profit from agriculture in tropical developing nations. There has been already increasing adoptions of GM crops in nations like Paraguay, South Africa and Pakistan (Ameer, 2024; Cheng *et al.*, 2024). If the existing questions related to GM crops are understood from the Government, Organisations and Public perspective and clarified to the respective stakeholders while providing framework of regulations and promotions, the adoption can be even more widespread in future.

Often the public scepticism developed around GMOs are due to ethical concerns over unnaturalness, economic fears regarding corporate seed monopolies, and fragmented international regulations (Hunt & Wald, 2020; Naveen & Sontakke, 2024). To bridge this gap, outreach strategies must prioritize science-based education and community engagement that respects local cultural and religious values (Fan *et al.*, 2021). Emphasizing genome editing specifically CRISPR Cas9 as a precise method that avoids foreign DNA can mitigate fears of unnatural tampering while streamlining regulatory paths (Javaid *et al.*, 2022). Furthermore, multi-sector collaborations and social media campaigns can demonstrate practical benefits for climate resilience and nutrition, shifting the public discourse from apprehension to optimism regarding biotechnology's role in global food security (Rahman *et al.*, 2025).

However, the global landscape of GM crops is expanding rapidly, with 65 transformants recently approved for food, feed, and cultivation. China leads this surge, accounting for 36.92% of approvals, followed by the EU (20%) and Australia/New Zealand (15.38%). By 2023, dominant crops like GM soybean and corn covered 100.9 and 69.3 million hectares, respectively, while 24.1 million hectares of GM cotton were planted globally (Cheng *li*). In 2024, China accelerated commercialization by approving 19 GM events and nine gene-edited varieties targeting yield, stress tolerance, and disease resistance. Brazil and Argentina also advanced, focusing on stacked traits like short stature and pest resistance in maize and soybeans (Li *et al.*, 2026).

This technological development has reshaped global trade, with major producers like the U.S., Brazil, and Argentina exporting to high-demand regions like Japan and China. While this trade effectively addresses irregular food distribution and enhances global food security, it presents challenges for local industries in importing countries due to price disparities created by

the low production costs and high returns of GM crops (Cheng *et al.*, 2024). These shifts underscore a move toward "new" features like drought tolerance, integrating biotech further into the global food cycle.

Conclusion

The development of genetic modification (GM) has been, for good reasons, to address major global challenges, including food security and climate change, by surmounting the limitations of traditional breeding. With the use of modern technologies such as CRISPR, or further advanced ones, like RNA interference and prime editing, biotechnology has progressed from the early transgenic approach to achieve a high degree of precision. Such traits include nutritionally improved varieties such as Golden Rice, stress-resistant crops, and insect-resistant crops. So, such a revolution in the field of science was inevitable, or in better words, was a necessity of time. But at the same time, the significant ecological and socio-economic hurdles remain, as explained in the review. The progress for the future will require a ground-level understanding of the situation and research that is comprehensive, long-term, and spatially explicit, and will need to integrate productivity trends, soil health, biodiversity, and rural economic resilience. To be precise, a comparative study based on productivity, other agricultural and socioeconomic parameters of a larger agricultural area over a longer time is necessary. Besides, a holistic approach is required to ensure that innovation is balanced with sustainability. Only then is the pragmatic cost-to-benefit analysis and aligning the efforts in the laboratory with the necessities of the farmlands will be possible.

Moving ahead, the implementation level future of GM crops will be determined not only by technological advancement but also by broad-scale ground-level research, governance, equity, prohibition of unfair practices, a stronger legal framework, ecological considerations, farmers' training for best practices, and management approaches that ensure agricultural productivity is aligned with environmental sustainability. Also, the development within a broader socio-economic context characterized by financialization, consolidation, and competition has affected public perception and raised ethical and policy debates. Assessment of these processes is essential. Besides these, the integration of crops that can sense the environment in real time and the democratization of gene-editing technology can be among such implementation-level solutions for sustainability, productivity, equity, and socioeconomic justice.

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