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REVIEW

Genetic modification strategies for enhancing plant resilience to abiotic stresses in the context of climate change

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Abstract

Enhancing the resilience of plants to abiotic stresses, such as drought, salinity, heat, and cold, is crucial for ensuring global food security challenge in the context of climate change. The adverse effects of climate change, characterized by rising temperatures, shifting rainfall patterns, and increased frequency of extreme weather events, pose significant threats to agricultural systems worldwide. Genetic modification strategies offer promising approaches to develop crops with improved abiotic stress tolerance. This review article provides a comprehensive overview of various genetic modification techniques employed to enhance plant resilience. These strategies include the introduction of stress-responsive genes, transcription factors, and regulatory elements to enhance stress signaling pathways. Additionally, the manipulation of hormone signaling pathways, osmoprotectant accumulation, and antioxidant defense mechanisms is discussed. The use of genome editing tools, such as CRISPR-Cas9, for precise modification of target genes related to stress tolerance is also explored. Furthermore, the challenges and future prospects of genetic modification for abiotic stress tolerance are highlighted. Understanding and harnessing the potential of genetic modification strategies can contribute to the development of resilient crop varieties capable of withstanding adverse environmental conditions caused by climate change, thereby ensuring sustainable agricultural productivity and food security.

Keywords Genome editing · Genetic engineering · Abiotic stress · Crop improvement · CRISPR/Cas9

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Introduction

Genetic modification in agriculture has emerged as a promising approach to address the challenges posed by climate change and enhance the resilience of crops (Jacobsen et al. 2013). The increasing global population and the impacts of climate change on agricultural productivity necessitate innovative strategies to sustainably increase food production and mitigate environmental stressors (R. Singh and Singh 2017). Scheelbeek et al. (2018) conducted a review that highlighted the anticipated impact of climate change on vegetable and legume yields. The findings revealed significant reductions in vegetable yields, with an average decrease of 34.7% projected for a 50% decline in water availability and a reduction of 31.5% for a temperature increase of 4°C above a baseline of 20°C (Scheelbeek et al. 2018).

These estimates demonstrate that the contemporary world is facing severe negative impacts from global warming and climate change, which pose significant threats to the environment (Shakoor et al. 2011). The global phenomenon of climate change, marked by escalating temperatures, shifting rainfall patterns, and more frequent occurrences of extreme weather events, presents substantial challenges to agricultural systems on a global scale (Duchenne-Moutien and Neetoo 2021). These changes disrupt the delicate balance between crops, pests, and diseases (Fand al. 2012; Patz et al. 2000), leading to reduced crop yields (Olesen and Bindi 2002), compromised nutritional quality (Louis and Hess 2008), and decreased overall food security (Schmidhuber and Tubiello 2007). In light of these challenging circumstances, genetic modification is often seen as a promising solution for addressing pressing issues such as food security and environmental sustainability (Joy 2000). Currently, approximately 525 different transgenic events across 32 crop species have been approved for cultivation in various regions around the world (Kumar et al. 2020), providing substantial evidence of the valuable contributions these crops make to the global economy.

The objective of genetic modification in agriculture is to incorporate favorable characteristics into crops by precisely modifying their genetic material (Gepts 2002). This technology enables scientists to enhance crop resilience by incorporating genes that confer tolerance to abiotic stresses such as drought, heat, salinity, and extreme temperatures (Bacha and Iqbal 2023(Lal et al. 2008). Additionally, genetic modification offers opportunities to improve nutritional content, increase yield potential, and enhance resistance to pests and diseases (Hall and Richards 2013; Uzogara 2000) (Parmar et al. 2017). One of the primary objectives of genetic modification in agriculture is to increase crop tolerance to abiotic stresses. By introducing specific genes into plant genomes, researchers have been successful in enhancing plants' ability to withstand adverse environmental conditions (Sedeek et al. 2019). Genetically modified crops display enhanced traits such as improved water-use efficiency (Flexas et al. 2013) and increased photosynthetic capacity (Ku et al. 2000) and superior nutrient uptake (Bouis et al. 2003), empowering them to flourish in demanding climatic conditions.

Furthermore, genetic modification allows for the enhancement of nutritional content in crops, addressing the growing concern of malnutrition and dietary deficiencies (Graham et al. 2001). Through the manipulation of genes involved in nutrient metabolism and biofortification strategies (Bhambhani et al. 2021), scientists can enrich crops with essential vitamins, minerals, and other beneficial compounds, thereby improving the nutritional value of the harvested produce (Zhao et al. 2020). A global meta-analysis on the impact of transgenic crop adoption has shown that, on average, the use of transgenic technology results in a 22% increase in crop yields, leading to a 68% estimated increase in farmer profits (Klümper and Qaim 2014).

Despite these significant successes, widespread public acceptance of transgenic crops has been challenging to achieve. Concerns about the insertion of foreign genes have led to negative attitudes and reluctance towards their adoption and use. In response to these concerns, two new techniques, intragenesis and cisgenesis, have been developed as alternative approaches that address some of the concerns associated with transgenesis (Rommens et al. 2007; Schouten et al. 2006). To gain widespread social acceptance of genetically modified crops, it is crucial to demonstrate their potential socioeconomic benefits, particularly in developing countries that are grappling with economic adversity and food insecurity due to climate change (Zetterberg and Edvardsson Björnberg 2017) (Séralini et al. 2011) (Dale, Clarke, and Fontes, 2002). Achieving this goal requires further research and the development of policies that address stakeholders' concerns and ensure that the benefits of genetically modified crops are accessible to those who need them most.

In conclusion, genetic modification in agriculture offers promising solutions to address the challenges posed by climate change and enhance crop resilience. By incorporating favorable traits into crops, such as tolerance to abiotic stresses and improved nutritional content, genetically modified crops have the potential to increase agricultural productivity, improve food security, and mitigate the negative impacts of environmental variations. However, addressing concerns related to safety, public acceptance, and equitable access to the benefits of genetic modification is crucial for the responsible deployment of these technologies.

This review aims to evaluate the effectiveness of genetic modification in enhancing crop tolerance to abiotic stress factors and its potential implications for sustainable agriculture.

Interplay of genetic modification and climate change: opportunities and challenges in enhancing plant resilience

Global warming and industrial pollution have a detrimental impact on plant life, affecting various aspects such as growth, physiology, metabolism, immunity, development, and biochemical pathways (Cao et al. 2023) (Al-Khayri et al. 2023; Sun et al. 2023; Kim et al. 2022; Liu et al. 2023; Ahammed et al. 2023; Sim et al. 2023). To counter these challenges and enable plants to withstand environmental stress, new genetic modification (GM) techniques have emerged, successfully developing novel species capable of tolerating climatic extremes (Zhang and Zhu 2023).

Studying the interplay of genetic modification and climate change is crucial in this review to identify opportunities and challenges in enhancing plant resilience. Understanding how genetic modification strategies can help plants withstand climate-related stressors is essential for ensuring food security and sustainable agriculture in a changing climate. Recent advancements in genomic research and molecular biology, particularly in the field of genome editing, offer promising prospects for enhancing crop yields, disease resistance, and tolerance to environmental stress (Yarra and Sahoo 2021; Molla et al. 2021; Liu et al. 2022a). The utilization of genetic modification holds potential for enlarging the medicinal and economic value of plants (Ghimire et al. 2023). However, the development and introduction of new GM techniques remain limited and controversial (Eckerstorfer et al. 2020).

Genetic modification can play a crucial role in mitigating the effects of climate change by reducing the carbon footprint of agriculture. Through the development of genetically modified crops that require fewer inputs like fertilizers and pesticides, greenhouse gas emissions contributing to climate change can be lowered (National Academies of Sciences and Medicine 2016; Zhou et al. 2021). Researchers are actively working on developing crops capable of withstanding water scarcity, pests, and diseases, enabling food production in areas prone to extreme weather events (Howell et al. 2018). The increasing interest and advantages of gene editing have stimulated global research in this field (Strobbe et al. 2023). While there is scientific consensus on the safety of GM crops for both human health and the environment, a significant portion of the US adult population still holds concerns regarding their potential negative impacts (Suldovsky and Akin 2023).

Different countries have varied responses to genetically modified (GM) crops. Some ASEAN countries, including the Philippines, Myanmar, Vietnam, and Indonesia, have approved the cultivation of GM crops such as maize, cotton, and sugarcane (Amirhusin 2023). In Korea, extensive research on GM plants, such as rice, pepper, lettuce, and grass, is underway alongside the importation of GM soybeans, corn, firewood, and canola (Choi et al. 2023). Conversely, Europe has strict regulations on genetically modified organisms (GMOs) due to negative consumer attitudes towards their use (Strobbe et al. 2023). China has made significant progress in adopting and commercializing Bt plants to address pest-related challenges, but a consumer survey revealed mixed views on GM foods (Chen et al. 2011; Cui and Shoemaker 2018). Russia prohibits the commercial cultivation of transgenic crops, despite having ample land available for cultivation (Chokheli et al. 2021). In Turkey, a pilot survey highlighted a lack of knowledge and confidence among adults regarding genetic modification, with a significant portion expressing concerns about GM foods (Basaran, Kilic, Soyyigit, and Sengun,

To recap, the interaction of genetic modification and climate change reveals potential opportunities and challenges in fortifying plant resilience. Genetic modification offers avenues for improving crop productivity, enhancing disease resistance, and increasing tolerance to environmental stresses. However, further research and consideration of public attitudes and international variations are necessary. By leveraging genetic modification, we can foster sustainable agriculture and confront the impacts of climate change head-on.

Mechanism of genetic modification in plants

Genetic diversity is a valuable asset for genetic research and the improvement of plant traits (Mao et al. 2019). Traditionally, plant breeders relied on natural variations to select the best genetic combinations (Mao et al. 2019). However, genetic modification, also known as genetic engineering, has provided a more effective method to expand the plant breeders' toolkit against pathogens and diseases (Van Esse et al. 2020). It involves introducing novel genetic variations into plants to develop new varieties. In the past, plant breeders used chemical compounds and irradiation to induce heritable mutations in plants, aiming to create new traits or variations (Hartwell et al. 2011). However, these random mutagenesis methods had limitations, and identifying specific mutations was labor-intensive (Novak and Brunner 1992; Oladosu et al. 2016).

With advancements in modern genetics, mutation practices have become more precise and less labor-intensive. Next-generation sequencing (NGS) has facilitated easy mapping and identification of causal mutations (Santosh Kumar et al. 2020). Induced mutagenesis techniques now aid in developing varieties that closely resemble their parents, with minor attribute differences and no environmental threats. Plant breeders currently employ various mutation techniques to improve plant phenotypic characteristics, including stress tolerance, nutritional value, quality traits, climate resilience, and herbicide resistance (Šamajová et al. 2013; Tien Lea et al. 2016; Lenaerts et al. 2019; Anderson and Song 2020; Mall et al. 2019). To fully comprehend the significance of genetically modified (GM) crops, it is crucial to understand the mechanism underlying genetic modification in plants. This knowledge helps evaluate the advantages, risks, and implications of GM crops, enabling informed decisions and progress in agricultural biotechnology.

The process of developing genetically modified crops involves several intricate steps to ensure that the desired traits are successfully introduced and properly evaluated before commercialization. Researchers begin by investigating genetic sequences, metabolic pathways, and biochemical processes to identify the specific genes of interest (Jankowicz-Cieslak et al. 2017). Induced mutagenesis is then utilized as an effective tool to locate and map these important genes within the plant's genome.

Once the target genes are identified, researchers employ recombinant DNA technology to insert the gene of interest into the plant's DNA at specific sites. This gene may originate from the same species or a different species, depending on the desired trait (Irwin 2001). The process of molecular characterization is then undertaken to analyze the transgene and determine its exact location and the nature of its insertion (Thole et al. 2009).

To confirm the successful genetic modification, researchers conduct laboratory tests using techniques like PCR, DNA sequencing, and Southern blotting. These tests validate the presence and accuracy of the inserted gene within the plant's DNA (Ahmed 2002). After laboratory testing, the next crucial step involves greenhouse testing. Here, researchers evaluate the growth, development, and expression of the introduced trait in the genetically modified plants. They observe how the plant behaves in response to various factors such as pests, herbicides, and different weather conditions. Additionally, they assess the yield and product quality to determine the potential of the genetically modified plant for future commercial cultivation (Veress et al. 2013).

Once all testing is completed, the genetically modified plant must undergo regulatory approval before it can be commercialized and released to the market. Data from laboratory, greenhouse, and field testing is compiled and submitted to regulatory agencies for thorough review (Nap et al. 2003; Fig. 1). These regulatory agencies assess the safety, environmental impact, and potential risks associated with the genetically modified crop to ensure its safety for human consumption and the environment.

Overall, the process of developing genetically modified crops involves meticulous scientific research, laboratory testing, greenhouse evaluation, and regulatory scrutiny. These steps are essential to ensure the successful and responsible use of genetically modified crops in agriculture, promoting food security and sustainable farming practices. In conclusion, genetic modification has revolutionized plant breeding, enabling the precise introduction of desirable traits. Advances in technology and rigorous testing ensure safety and efficacy. These advancements hold great potential for addressing agricultural challenges and promoting sustainable food production.

Gene editing and CPISPR-Cas9 technology

Advances in genome engineering have significantly transformed our ability to modify genomes with unprecedented accuracy, surpassing previous limitations (Voytas 2013). Genome engineering involves manipulating the genes of living organisms through various techniques, including deletion, substitution, and insertion. Among the cutting-edge tools available for genome engineering, the CRISPR-Cas9 system has emerged as the prevailing approach today. It relies on Clustered Regularly Interspaced Short Palindromic Repeats and associated protein 9 (El-Mounadi et al. 2020).

Compared to other genome editing tools like zinc finger nucleases (ZFNs) and transcriptional activator-like effector nucleases (TALENs), the CRISPR/Cas9 system offers distinct advantages, making it the method of choice for many researchers. Notably, CRISPR/Cas9 enables faster, cheaper, and highly efficient editing of genomes with greater precision (Shi et al. 1996; Voytas 2013).

Researchers have embraced CRISPR/Cas9 due to its versatility and ease of use, allowing for targeted modifications in various organisms across different scientific disciplines. Its wide adoption has accelerated progress in fields like agriculture, medicine, and biotechnology, opening new possibilities for disease treatment, gene therapy, and the development of genetically modified crops with improved traits.

By utilizing the CRISPR/Cas9 system, scientists can now manipulate specific genes with unprecedented precision, leading to a deeper understanding of genetic functions and unlocking new avenues for research and applications.

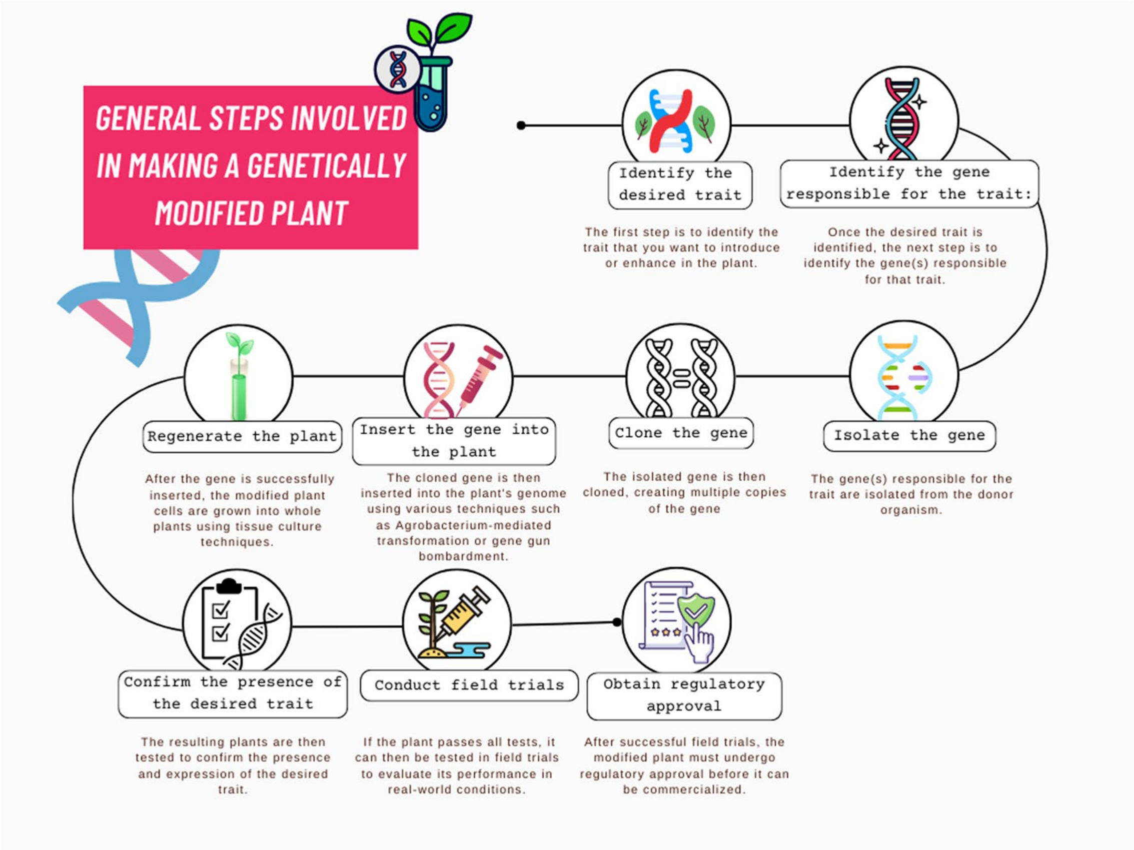


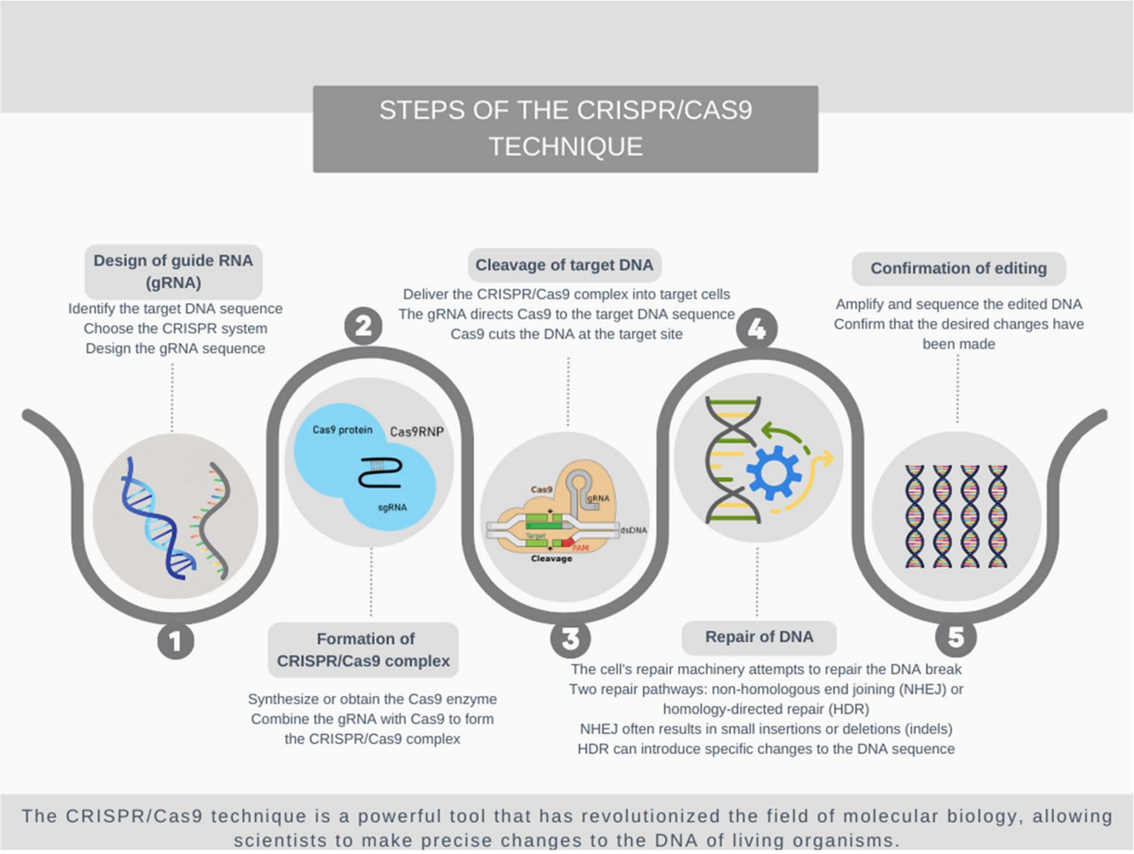
Fig. 1 General steps involved in making genetic modified crops

As a result, CRISPR/Cas9 has revolutionized genome engineering, propelling the scientific community into an era of unprecedented possibilities for genetic manipulation and gene editing (Shi et al. 1996).

Since its emergence in 2012, CRISPR/Cas9 has played an essential role in biological research, enabling precise manipulation of DNA sequences within cells and serving as a valuable tool for researchers. Despite not being a new concept or the first DNA editing technology, CRISPR/Cas9's unique properties of single effector enzymes make a critical difference in experimental (Capecchi 2005; Pyzocha and Chen 2018). The technique involves several steps: designing a guide RNA (gRNA) complementary to the target DNA sequence and combining the gRNA with the Cas9 enzyme to cut the DNA at the target site (Gao and Zhao 2014). This creates a double-strand break, which can be repaired using non-homologous end joining (NHEJ) or homology-directed repair (HDR) pathways (Chu et al. 2015; Feng et al. 2023; Su et al. 2016). NHEJ often leads to small insertions or deletions that disrupt the target gene's function, while HDR allows for specific changes in the DNA sequence (Malzahn et al. 2017). To confirm the desired changes, the edited DNA is amplified and sequenced (Jiang 2013). The accompanying Fig. 2 illustrates the steps involved in the CRISPR/Cas9 technique.

CRISPR/Cas9 has facilitated the development of transgenic crops through user-friendly tools and guides. These genetically modified plants efficiently address the harmful effects of climate change and ensure future food security (Haque et al. 2018).

In conclusion, advances in genome engineering, particularly with the CRISPR-Cas9 system, have revolutionized DNA modification, offering precise and efficient editing capabilities. This technology has been widely utilized in biological research, enabling targeted changes to DNA sequences. Additionally, it has facilitated the development of transgenic crops to address climate change and enhance food security. Genome engineering has opened up new opportunities for scientific exploration and practical applications.



Design of guide RNA (gRNA)
Identify the target DNA sequence
Choose the CRISPR system
Design the gRNA sequence

Formation of CRISPR/Cas9 complex
Synthesize or obtain the Cas9 enzyme
Combine the gRNA with Cas9 to form the CRISPR/Cas9 complex

Cleavage of target DNA
Deliver the CRISPR/Cas9 complex into target cells
The gRNA directs Cas9 to the target DNA sequence
Cas9 cuts the DNA at the target site

Repair of DNA
The cell's repair machinery attempts to repair the DNA break
Two repair pathways: non-homologous end joining (NHEJ) or homology-directed repair (HDR)
NHEJ often results in small insertions or deletions (indels)
HDR can introduce specific changes to the DNA sequence

Confirmation of editing
Amplify and sequence the edited DNA
Confirm that the desired changes have been made

The CRISPR/Cas9 technique is a powerful tool that has revolutionized the field of molecular biology, allowing scientists to make precise changes to the DNA of living organisms.

Fig. 2 CRISPR/Cas9 technique working principle and steps

Transgenic approaches

Given the compelling evidence of climate change and its anticipated impacts, it is crucial to adopt a comprehensive approach to agricultural adaptation (Howden et al. 2007). Adapting to climate variability is essential for both assessing the impacts and developing effective policies (Smit et al. 2000). Climate change poses a significant threat to agricultural production, emphasizing the need to enhance climate resilience in agriculture. Research suggests that genetic modification, in conjunction with other sustainable agricultural practices, can help mitigate the effects of climate change on agriculture (Akhtar et al. 2021; Zhou et al. 2021). Promoting genetic diversity in crops is also a valuable strategy for building resilience (Garland and Curry 2022). Advances in plant biotechnology, such as genetically modified (GM) crops, have contributed to improving the genetic diversity of crops and their ability to adapt to changing climatic conditions, thus safeguarding agricultural production in the face of a changing climate (Sainger et al. 2015; Garland and Curry 2022; Fig. 3).

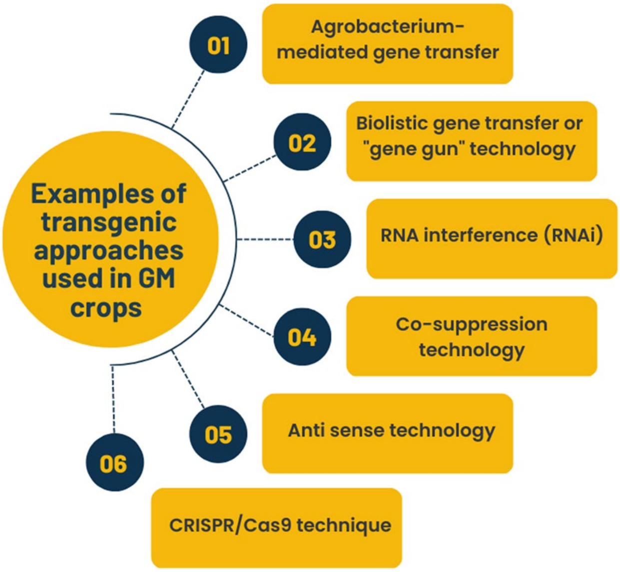


Fig. 3 Transgenic approaches used to develop genetically modified crops

Advantages of genetic modification in adapting to climate change

In light of the compelling evidence of climate change and its anticipated impacts, the adoption of a comprehensive approach to agricultural adaptation has become imperative (Howden et al. 2007). Adapting to climate variability is crucial for assessing impacts and developing effective policies (Smit et al. 2000). The increasing threat of climate change to agricultural production necessitates the implementation of strategies to enhance climate resilience. A study by Akhtar et al. (2021) suggests that genetic modification, in combination with other sustainable agricultural practices, should be employed to mitigate the effects of climate change on agriculture (Zhou et al. 2021). Another effective approach to enhancing resilience is the promotion of genetic diversity in crops (Garland and Curry 2022). Advancements in plant biotechnology, particularly genetically modified (GM) crops, have significantly contributed to improving the genetic diversity of crops (Sainger et al. 2015). This enhancement equips crops with the ability to adapt to changing climatic conditions and safeguards agricultural production in the face of a changing climate (Garland and Curry 2022; Fig. 4).

Increase tolerance to abiotic stress

Abiotic stress refers to the stress caused by non-living factors, negatively impacting plant development and growth. Examples of abiotic stress include drought, salinity, pollutants, and heavy metals (Hernández 2019; Ramadan et al. 2023; Shukla et al. 2016; Saeed et al. 2023; Choudhary et al. 2019; Zulfiqar and Ashraf 2022). These stresses disrupt metabolic and physiological processes in plants, such as respiration (Flexas et al. 2006; Zulfiqar 2021), water uptake (Abobatta 2020), and photosynthesis (Khan et al. 2010), leading to reduced yield (Wang et al. 2013), poor growth (Hasanuzzaman et al. 2018), and plant mortality (Nawaz et al. 2010). Mitigating abiotic stress is a significant challenge in agriculture, requiring an understanding of plant response mechanisms (Suzuki et al. 2014). Liu et al. (2022b) reported the molecular characterization of the isoflavone 2′-hydroxylase gene (*CtCYP81E8*) in safflower, revealing positive insights into flavonoid accumulation and abiotic stress tolerance in safflower plants (Liu et al. 2022b). Unfortunately, global warming exacerbates these stresses, making the situation worse. This highlights the urgent need for research and innovation in developing stress-tolerant crops to ensure food security and sustainability in the face of climate change (Kawakami et al. 2010).

To address global climatic stress, CRISPR/Cas-mediated gene editing can enhance crop plant tolerance to abiotic stresses such as temperature, drought, and salinity (Ahmad et al. 2021; Høyland-Kroghsbo et al. 2018; Santosh Kumar et al. 2020). The CRISPR/Cas system is highly efficient, specific, time-efficient, and cost-effective (Bhat et al. 2021). Recent studies indicate that CRISPR/Cas editing can target complex quantitative genes associated with abiotic stress

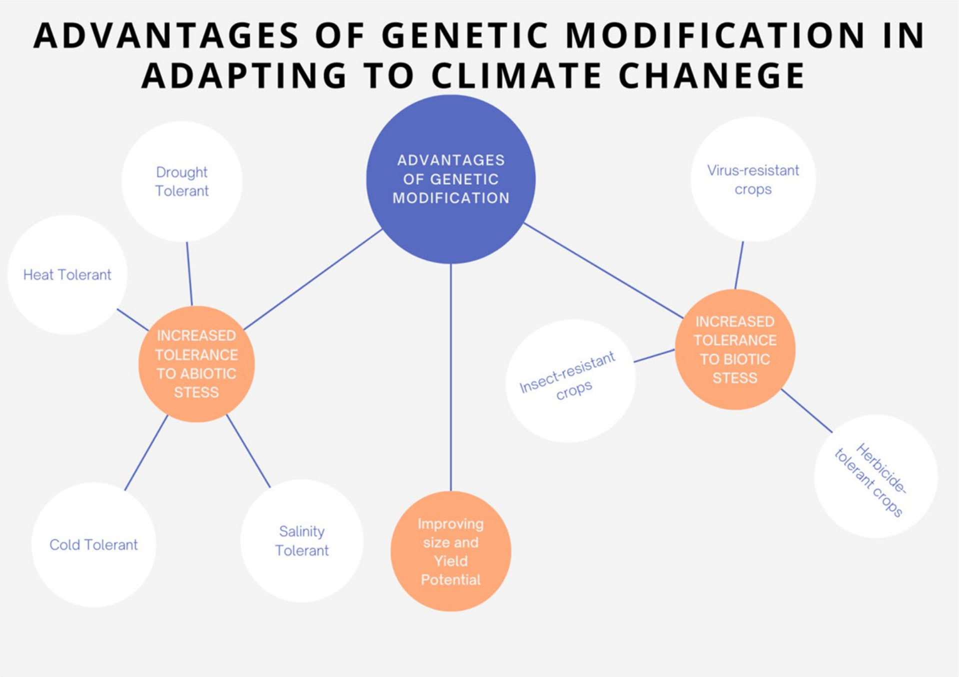


Fig. 4 The advantages of genetic modification in crop production

factors (Mushtaq et al. 2018). For instance, genes like phytoene desaturase (*OsPDS*), mitogen-activated protein kinase (*OsMPK2*), and betaine aldehyde dehydrogenase (*OsBADH2*) in rice can be edited, leading to improved abiotic stress tolerance (Kaur et al. 2018; Kumar et al. 2023; Ashokkumar et al. 2020). These findings highlight the potential of CRISPR/Cas-based editing to enhance crop resilience in challenging environments (Debbarma et al. 2019; Lin et al. 2020; Lou et al. 2017).

Notably, the manipulation of ethylene responsible factor (ERF) and stress/ABA-activated protein kinase 2 (*SAPK2*) genes through CRISPR/Cas editing has shown improved abiotic stress tolerance in rice (Debbarma et al. 2019; Lou et al. 2017). CRISPR/Cas technology has demonstrated its versatility in genome editing across various crops, including maize, rice, tomato, soybean, sorghum, flax, camelina, cotton, rapeseed, lettuce, potato, cucumber, watermelon, grapefruit, apple, and oranges (Chilcoat et al. 2017; Lin et al. 2020; Vu et al. 2020; Mao et al. 2016). This powerful tool offers new possibilities for crop improvement, enabling precise and efficient modifications in plant genomes (Chilcoat et al. 2017; Lin et al. 2020; Vu et al. 2020; Mao et al. 2016). Please refer to Table 1 for examples of successful genetic modification to improve abiotic stress tolerance in various crops.

Drought tolerance

Drought tolerance (DT) refers to the ability of plants to maintain a certain level of physiological activity even in severe drought conditions. This is achieved through the regulation of thousands of genes and metabolic pathways that help to reduce or repair the damage caused by drought stress (Fang and Xiong 2015). The International Service for the Acquisition of Agri-biotech Applications (ISAAA) released a report in 2019 which revealed that 29 countries had adopted biotech crops, including those with drought tolerance traits. The report indicates that 15.4 million farmers were planting these crops. Notably, countries such as the USA, Brazil, and South Africa have already commercialized drought-tolerant maize and soybean varieties (Clive 2008). Researchers demonstrated the potential of CRISPR/Cas9 technology in improving the resilience of rice to drought conditions, in 2016 by editing the *OsDREB* gene and in 2017 by editing the *ARGOS8* gene. The *OsDREB* gene editing resulted in the generation of inheritable mutations that improved the plant's tolerance to abiotic stress; in parallel, *ARGOS8* gene editing approach resulted in a significant increase in grain yield under drought conditions, without any loss of yield under optimal growth conditions (Hoang et al. 2016; Shi et al. 2017). Conversely, in 2018, scientists modify the *OsERF109* gene in rice. The resulting edited plants displayed enhanced tolerance to abiotic stress factors such as salt and drought (Mishra et al. 2018). Moreover, according to the recent work by Wang et al. (2023), research on cytochrome P450s in safflower unveils their vital role in regulating flavonoid accumulation, providing valuable insights for enhancing plant natural products (Wang et al. 2023). Similarly, scientists have successfully modified the *CBF4* gene in tomato plants, which plays a crucial role in the plant's response to drought stress. The edited plants exhibited improved drought tolerance and showed increased yields under water-limited conditions (Lin et al. 2020).

Correspondingly, drought-tolerant maize (*Zea mays*) has been genetically engineered to express the C_4 photosynthesis pathway enzyme pyruvate orthophosphate dikinase (PPDK). This modification enhances the plant's ability to conserve water and maintain photosynthesis under drought conditions, resulting in improved yield and productivity. On the same pattern, Liu et al. (2019) identified a gene in maize that controlled the plant's response to drought stress and used CRISPR-Cas9 gene editing technology to modify the gene. The resulting plants had improved drought tolerance and increased yield under water-limited conditions (Cummins et al. 2019; Gassmann et al. 2011; Koziel et al. 1993; Vaughn et al. 2005). Currently, researchers are identifying genes that control the plant's response to water stress and used CRISPR-Cas9 to modify that gene. The resulting plants have improved drought tolerance and increase yield under water-limited conditions; in this pattern, Ha et al. (2021) developed a genetically modified soybean plant with improved drought tolerance (Cai et al. 2021).

All these successful examples of GM crops highlight the potential of CRISPR/Cas9 technology to develop crops that can withstand environmental stressors such as drought, which could contribute to ensuring global food security in the face of climate change (Munaweera et al. 2022). While genetic modification can play an important role in developing such drought-tolerant crops, it is important to consider the potential environmental and social impacts of such crops and to ensure that they are developed and used responsibly and ethically (Cai et al. 2021).

Heat tolerance

Drought tolerance (DT) refers to a plant's ability to maintain physiological activity even in severe drought conditions. It involves the regulation of numerous genes and metabolic pathways that help mitigate the damage caused by drought stress (Fang and Xiong 2015). The adoption of biotech crops, including those with drought tolerance traits, has been observed in 29 countries, with

Table 1 Case studies of successful application of genetic modification in agriculture to tackle climate change impacts

Crops	Gene added	Effect or improved traits	Reference
Alfalfa	*AVP1* gene from *Arabidopsis thaliana*	Improved salt and drought tolerance and photosynthetic rate	Bao et al. (2009)
Rice	*AtHSP101* gene from *Arabidopsis thaliana*	Improved heat tolerance, better growth in recovery phase, no adverse effects on growth and development	Katiyar-Agarwal et al. (2003)
Soybean	*GmHSFA1* gene from *Glycine max*	Enhanced thermotolerance, no abnormality in the development and growth	Zhu et al. (2006)
Cotton	*AsHSP70* gene from *Agave sisalana*	Improved heat tolerance and boll production, higher chlorophyll, proline, and soluble sugar contents	Batcho et al. (2021)
Tomato	*LeAN2* gene from *Lycopersicum esculentum*	Improved heat tolerance, high photosynthetic rate, fresh weight and antioxidant activity, lower ROS	Meng et al. (2015)
Tobacco	*EcDREB2A* gene from *Eleusine coracana*	Enhanced thermotolerance, seed germination, fresh and dry weight, and increased stomatal conductance	Singh et al. (2021)
Creeping bentgrass	*OsSIZ1* gene from *Oryza sativa*	Enhanced thermotolerance, water retention and cell membrane integrity, photosynthesis, and growth	Shiferaw et al. (2013)
Wheat	*BADH* gene from *Atriplex hortensis*	Enhanced heat and drought tolerance, higher photosynthetic rates under heat and drought stress, increased membrane stability under heat stress	He et al. (2008)
Canola	*AtNHX1* gene from *Arabidopsis thaliana*	Improved salt tolerance up to 200 mM NaCl; seed yield and seed oil quality were not affected by salt stress	Zhang et al. (2001)
Eggplant	*TaNHX2* gene from *Triticum aestivum*	Improved salt tolerance and growth, higher RWC and chlorophyll content, reduced MDA and ROS	Yarra and Kirti (2019)
Apple	*MdNHX1* gene from *Malus* × *domestica Borkh*	Improved salt tolerance, high K+ /Na+ ratio in the leaves	Li et al. (2010)
Soybean	*GmCLC1* gene from *Glycine max*	Enhanced salt tolerance, lower relative electrolyte leakage	Wei et al. (2016)
Maize	*ZmbZIP4* gene from wild *Zea mays*	Enhanced salt, drought, and osmotic stress tolerance	Ma et al. (2018)
Potato	*P5Cs* gene from *Arabidopsis thaliana*	Increased salt tolerance and proline content, less altered tuber yield and weight	Hmida-Sayari et al. (2005)
Peanut	*AVP1* gene from *Arabidopsis thaliana*	Improved salt and drought tolerance, biomass, and photosynthetic rate and higher yields	Wijewardene et al. (2020)
Sugarcane	*AVP1* gene from *Arabidopsis thaliana*	Enhanced salt and drought stresses and robust root system	Kumar et al. (2020)
Grapevine	*VaNCED1* gene from *Vitis amurensis*	Improved drought tolerance, higher growth, lower leaf stomatal density, and lower photosynthesis rate	He et al. (2018)
Rapeseed	*NCED3/ABAR/CBF3/LOS5/ICE1*	Enhanced heat, salinity, osmotic stress, and cold tolerance, greater yield, biomass, spikelet number, and grain number	Wang et al. (2018)
Rice	*OVP1* gene from species of *Oryza sativa*	Enhanced salt tolerance and membrane stability and higher chlorophyll content	Kim et al. (2020)
Rice	*OsbZIP46CA1/SAPK6*	Improved drought, heat, and cold tolerance, higher yield, biomass, spikelet number, and grain number	Chang et al. (2017)

approximately 15.4 million farmers involved (ISAAA 2019). Notably, countries like the USA, Brazil, and South Africa have already commercialized drought-tolerant maize and soybean varieties (Clive 2008). CRISPR/Cas9 technology has demonstrated potential in enhancing drought resilience in crops. In rice, editing the *OsDREB* and *ARGOS8* genes resulted in inheritable mutations that improved drought tolerance and grain yield, respectively (Hoang et al. 2016; Shi et al. 2017). Similarly, editing the *OsERF109* gene in rice enhanced tolerance to salt and drought stress (Mishra et al. 2018). In tomato plants, modifying the *CBF4* gene through CRISPR/Cas9 editing improved drought tolerance and increased yields (Lin et al. 2020). Drought-tolerant maize has been genetically engineered to express the PPDK enzyme, which enhances water conservation and photosynthesis under drought conditions, leading to improved productivity (Cummins et al. 2019). Using CRISPR/Cas9, researchers identified a gene in maize that controls the plant's response to drought stress, resulting in improved drought tolerance and increased yield (Liu et al. 2019). The identification and modification of genes associated with water stress response are ongoing research efforts aimed at developing drought-tolerant crops (Ha et al. 2021; Cai et al. 2021).

These successful examples of genetically modified (GM) crops highlight the potential of CRISPR/Cas9 technology in developing drought-tolerant crops, which can contribute to global food security amidst climate change (Munaweera et al. 2022). However, it is crucial to consider the potential environmental and social impacts of GM crops and ensure their responsible and ethical development and use (Cai et al. 2021).

Cold tolerance

Cold stress refers to the detrimental effects of exposure to chilling temperatures below 20°C and freezing temperatures below 0°C on plant growth and development. It directly inhibits metabolic reactions and indirectly induces osmotic, oxidative, and other stresses, limiting the expression of plants' genetic potential (Chinnusamy et al. 2007). To enhance plants' ability to withstand freezing temperatures, researchers have introduced genes encoding antifreeze proteins or transcription factors involved in cold acclimation into plants (Hightower et al. 1991). Genetically modified (GM) plants with improved cold tolerance have been developed, including GM tobacco (Yang et al. 2022), GM tomato (Shah et al. 2016) and GM potato (Muringai et al. 2020).

In 2018, a study used CRISPR/Cas9 technology to create mutants of the C-repeat binding factor 1 (*CBF1*) gene in tomato plants. The study revealed the role of CBF1 in protecting against cold and chilling injuries. The *CBF1* mutants exhibited increased levels of indole acetic acid and hydrogen peroxide, resulting in improved cold tolerance. Additionally, *CBF1* was found to prevent electrolyte leakage, indicating its potential for enhancing cold tolerance in crops (Li et al. 2018). In rice, the modification of the *OsMYB30* gene in 2016 resulted in improved cold tolerance. The edited plants exhibited enhanced cold tolerance compared to the unedited plants (Zhu et al. 2016). Furthermore, in 2017, editing the *SAPK2* gene and modifying the *OsANN3* gene in rice improved cold tolerance. The *SAPK2*-edited plants showed enhanced resistance to cold stress, while modification of the *OsANN3* gene led to improved cold tolerance as indicated by reduced relative electrical conductivity. These advancements can contribute to food security in regions with low temperatures where traditional crops struggle to thrive (Lou et al. 2017; Shen et al. 2017).

Salinity tolerance

Salinity tolerance in plants refers to their ability to grow and survive in soils or water with high salt concentrations. This trait is crucial for crops cultivated in areas with saline soils or irrigation water, as it ensures yield stability and food security (Bressan et al. 2008). While there have been successful examples of genetically engineering plants for improved salt tolerance, there are still challenges to overcome before widespread adoption of this technology in agriculture (Fita et al. 2015). One notable application of CRISPR/Cas9 technology was demonstrated in a 2017 study where researchers generated mutants in *Arabidopsis thaliana* that overexpressed the *SOS1* gene, responsible for encoding a plasma membrane Na+/H+ antiporter. The mutants exhibited enhanced salt tolerance and increased biomass production under saline conditions (Wang et al. 2017). Another successful example is reported that *CtCYP82G24* overexpression plays a crucial regulatory role in polyethylene glycol-induced osmotic stress tolerance and enhancement of flavonoid accumulation in transgenic *Arabidopsis*, indicating its significance in plant growth, development, and response to abiotic stresses (Ahmad et al. 2019).

In 2018, scientists used genomic editing to modify genes in rice, including the OsNHX1 gene, which led to improved salt tolerance. Additionally, in 2020, they modified the *OsHKT1* gene, resulting in higher yields and enhanced salt tolerance under saline conditions (Wang et al. 2020; Zhang et al. 2018). These advancements contribute to the development of salt-tolerant crops, but further research is needed to address the remaining challenges in this field.

Increase tolerance to biotic *stress*

Disease-resistant crops and genetic modification for climate change adaptation

The impact of global warming on crop pests and diseases poses a significant threat to food security (Shrestha 2019; Skendžić et al. 2021). Rising temperatures can accelerate the growth and reproduction rates of pests like aphids and spider mites, leading to increased infestations and crop damage (Mafongoya et al. 2019; Reddy 2013). Longer growing seasons due to warmer temperatures provide more time for pests and diseases to spread, resulting in higher pressure on crops and increased yield losses. Changes in precipitation patterns associated with climate change can also create favorable conditions for pests and diseases, such as promoting the growth of fungal diseases in increased rainfall or humidity, or weakening plants in drought conditions (Walther et al. 2009; Peace 2020; Roos et al. 2011).

Climate change disrupts the ecological balance in agricultural systems by impacting interactions between pests, diseases, and their natural enemies (Chaplin-Kramer and Kremen 2012; Romo and Tylianakis 2013). The effectiveness of beneficial insects and predators that control pest populations can be reduced due to higher temperatures, leading to an increase in pests and crop damage (Lehmann et al. 2020). Additionally, climate change can cause mismatches in the timing of pest and natural enemy activity, further disturbing agricultural ecosystems (Skendžić et al. 2021). These changes in pest and disease dynamics already have significant impacts on crop production and global food systems. To address these challenges, one strategy is the development of pest and disease resistant crops. Genetic modification techniques can be employed to enhance the resistance of crops, thereby increasing their adaptability to climate change (Andualem and Seid 2021). One approach involves introducing genes from other organisms that possess natural resistance to certain diseases (Borrelli et al. 2018). For instance, genes from *Bacillus thuringiensis*, a soil bacterium producing a protein toxic to insect pests, have been incorporated into crops like cotton and corn through genetic modification techniques (Verma et al. 2011; Sanahuja et al. 2011). As a result, these genetically modified crops exhibit resistance to pests, reducing the reliance on pesticides and enhancing yields (Mathesius et al. 2020).

Another strategy to enhance disease resistance in crops is to augment the plant's natural defense mechanisms against pests and diseases. The gene editing technique CRISPR-Cas9 has been utilized by researchers to modify the expression of genes involved in the plant's defense response (Borrelli et al. 2018). By increasing the expression of these genes, the plant's immune response is strengthened, resulting in improved resistance to pests and diseases (Ahmad et al. 2012). The development of disease-resistant crops is particularly crucial in the context of climate change, as rising temperatures and changing weather patterns are expected to intensify pest and disease pressures (Chakraborty and Newton 2011; Juroszek and Von Tiedemann 2011). Cultivating crops that are resilient to these pressures can help farmers enhance their resilience to the impacts of climate change (Maffioli et al. 2017).

Improving nutritional content and yield potential

The impact of climate change on global food production is expected to be significant, and one potential solution is to develop crops that are nutritionally enhanced and of higher quality (Datta 2013). Scientists at Cold Spring Harbor Laboratory (CSHL) utilized CRISPR/Cas9 technology to precisely engineer genes in tomatoes. By modifying the promoter regions of genes responsible for controlling quantitative traits such as fruit shape, size, and flowering timing, they were able to manipulate plant architecture (Rodríguez-Leal et al. 2017). In rice, researchers mutated three genes (*GW2, GW5, TGW6*) responsible for negatively regulating seed size, resulting in a significant increase in seed size (up to 30% in triple mutants) (Xu et al. 2016). Enhancing the nutritional quality and yield potential of crops through genetic modification has the potential to promote a more sustainable and equitable food system. However, it is crucial to maintain a balance between the potential benefits of genetically modified crops and the necessity to ensure safety, transparency, and ethical practices.

Technical, social, and financial challenges and concerns

Genetically modified (GM) crops offer potential benefits such as mitigating global warming, increasing crop yield, improving nutrition, and providing resistance against pests and diseases. However, concerns have been raised regarding unintended impacts on non-target organisms, development of herbicide-resistant weeds, and the potential for gene flow to wild relatives (Kumar et al. 2020). Addressing these concerns, scientific evidence dispels urban myths related to GMOs, highlighting the difficulty in finding valid scientific reasons for the lack of universal acceptance of GM technology. Nonetheless, recent research articles have identified unintended impacts of GMOs. Public perception remains a challenge, despite refuting objections related to monarch butterflies, allergen introduction, and other perceived risks (Cui and Shoemaker 2018).

Another concern is the ecological impact and development of resistance in pests, even though first-generation commercially available transgenic plants have reduced crop yield loss and pesticide use (Fontes et al. 2002; Lu 2008). The potential environmental impact and human health risks associated with GM crops have been investigated extensively. Hybridization with wild relatives and subsequent invasiveness is a concern (Allison Ann Snow et al. 2005), as well as the long-term effects on human health that remain uncertain (Key et al. 2008; Domingo and Bordonaba 2011; Domingo 2016). Regulatory challenges further complicate the GM crop landscape, with varying regulations across countries. Some countries have strict regulations in place, while others have more relaxed policies (Liu and Zhang 2022). For example, Russia prohibits the commercial use of transgenic crops, while Korea imports genetically modified soybeans, corn, and canola, with ongoing research on other GM plants (Chokheli et al. 2021; Choi et al. 2023; B. Ghimire et al. 2020).

Globally, the discussion about the safety and regulation of GM crops continues to be a source of disagreement, leading to opposition and regulatory challenges in various nations. There are concerns related to the reduction of biodiversity and the technical complexities in genetic engineering, specifically in the creation of stable transgenicplants (Carpenter 2011; Fesenko and Edwards 2014; Espinoza Cancino et al. 2013; Wahid et al. 2007; Koźmińska et al. 2018). Scientific studies have highlighted the need for comprehensive risk assessments of GMOs, transparency in regulation, and public engagement in decision-making processes. Technical challenges, including identifying suitable target genes and optimizing gene expression, must also be overcome in developing stress-tolerant GMOs (De Santis et al. 2018; Pallis 2021).

In conclusion, while GM crops hold promise for addressing agricultural challenges, their adoption and acceptance require thorough consideration of scientific and social factors (Sustek-Sánchez et al. 2023). It is essential to address environmental, health, regulatory, and technical challenges to ensure the responsible development and utilization of genetically modified crops.

Ethical and social considerations in the use of genetic modification in agriculture

Alternative technologies, such as cisgenesis and genome editing, may address many issues related to genetically engineered crop varieties with multiple favorable traits. These technologies may help to reduce some of the ethical and social concerns associated with traditional genetic engineering methods. Some potential ethical and social considerations related to genetic modification in agriculture include concerns about the safety of genetically modified crops for human consumption (Delaney et al. 2018) and the environment (Ferry and Gatehouse 2009), potential impacts on biodiversity, (Tiedje et al. 1989), and access to technology by small-scale farmers (Azadi et al. 2016). These issues are complex and require careful consideration by stakeholders from various sectors, including scientists, policymakers, farmers, consumers, and civil society organizations (Bruetschy 2019).

Concerns about the safety of genetically modified crops for human consumption have been a subject of debate and scrutiny in recent years (Al Anouti 2014). To address these concerns and avoid readers losing the train of thought, it is essential to acknowledge some of the studies that have contributed to this apprehension. Several studies have examined the potential allergenicity and unintended effects of genetic modifications on crop plants (Huang and Huang 2017), while long-term studies assessing the impact of genetically modified organisms (GMOs) on human health are also vital (Dona and Arvanitoyannis 2009).

To further strengthen the discussion, it is important to consider additional concerns regarding potential environmental impacts. These impacts include unintended effects on non-target species (Devos et al. 2016) or the development of herbicide-resistant weeds (Kuiper et al. 2000) and development of antibiotic resistance (Goldstein et al. 2005) making potential health risks to humans or animals consuming GMOs (Bakshi 2003). Furthermore, there are concerns about corporate control over seed production (Walters 2004) and intellectual property rights (Wong and Chan 2016), which may limit access to these technologies for small-scale farmers or lead to increased dependence on agribusinesses (Azadi et al. 2016). The alarming rise in global temperatures is an undeniable testament to the urgent need for collective action against climate change (Huang and Huang 2017). As extreme weather events become more frequent and devastating, it is evident that the consequences of inaction will be dire for both the planet and its inhabitants (Buhaug et al. 2008). The time for complacency has long passed, and the responsibility to protect our environment for future generations falls upon all of us ((Giddens 1999). By adopting sustainable practices, transitioning to renewable energy sources (Paris et al. 2022), and implementing effective policies (Antle et al. 2003), we can still steer the course towards a more sustainable and resilient future, where the beauty and diversity of our natural world can thrive once more (Drost et al. 1996), (Crist 2013). On the other hand, proponents of GMOs argue that they have the potential to increase crop yields and productivity (Kavhiza et al. 2022), reduce pesticide use (Phipps and Park 2002), and improve nutritional content in crops (Yan and Kerr 2002). They also point out that genetic modification is just one tool in a larger toolbox of agricultural technologies that can be used to address global food security challenges (Kavhiza et al. 2022). Social considerations include issues related to food security, access to technology, and cultural practices (Maghari and Ardekani 2011). For example, some people may object to GM crops on religious or cultural grounds (Thompson 1997). Additionally, there are concerns that GM crops may exacerbate existing inequalities in access to resources and technology between developed and developing countries (Otsuka 2003). Overall, it is important to consider both the potential benefits and risks associated with genetic modification in agriculture and engage in open dialogue with stakeholders from diverse backgrounds to ensure that these technologies are used responsibly and ethically (Kennedy 1999). Consumer choice is also a big problem as there are concerns about the right of consumers to choose whether or not to consume GM foods and the need for clear labeling and information about the presence of GM ingredients in food products (Sleenhoff and Osseweijer 2013). Another ethical concern is the potential for genetic modification to exacerbate existing inequalities in access to food and resources. For example, if only large agribusinesses can afford to develop and patent genetically modified crops, this could lead to increased concentration of power in the food system and limit access to these crops for small farmers or developing countries (Pechlaner and Otero 2008).

Public concerns surrounding GMOs include worries about long-term health effects (Butler et al. 1999), environmental impact (e.g. cross-contamination and herbicide resistance), and ethical issues with corporate control over seed production and patents (Bawa and Anilakumar 2013), (Raman 2017), (Myskja and Myhr 2020). Understanding these specific concerns is essential for informed discussions on GMO safety and regulation (Irwin 2001). Mainly revolving around their safety for human consumption, potential environmental impact, and ethical considerations (Gaskell et al. 2004), public concerns about GMOs also involve skepticism and opposition due to safety and environmental impact worries (Krimsky 2019). This can create challenges for companies seeking regulatory approval or market acceptance for their products. Addressing these concerns requires transparent communication, rigorous safety assessments, and comprehensive regulations to promote greater acceptance of genetically modified organisms. Overall, it is important for stakeholders involved in genetic modification in agriculture to consider these ethical and social considerations and engage in transparent dialogue with consumers, regulators, and other stakeholders (Costa-Font et al. 2008; Doh and Guay 2006). This can help ensure that the benefits of genetic modification are realized while minimizing any potential negative impacts. However, it is important to note that the use of genetic modification in agriculture is a controversial topic that raises many ethical and social concerns.

Some people argue that genetically modified crops could have negative impacts on people's health and the ecosystem, while others believe that they are necessary to feed a growing population. It is important to consider the potential benefits and risks of genetic modification in agriculture, as well as the broader social and ethical implications of its use (Pellegrino et al. 2018). Policymakers, scientists, and the public should engage in open and transparent discussions about the potential benefits and risks of genetic modification in agriculture to make informed decisions. By fostering dialogue and understanding, we can navigate the complexities of GMOs and work towards responsible and sustainable practices in the field of genetic modification.

In crux, public concerns surrounding genetically modified organisms (GMOs) encompass worries about long-term health effects, environmental impact, and ethical considerations. Understanding these specific concerns is crucial for informed discussions on GMO safety and regulation. Policymakers, scientists, and the public should engage in open and transparent dialogue to address these complex issues responsibly and foster sustainable practices in the field of genetic modification. By considering the potential benefits and risks while being mindful of broader social and ethical implications, we can navigate the complexities of GMOs and work towards a more sustainable future in agriculture.

Conclusion

Considering the ever-increasing global warming and climate change concerns, it is imperative to prioritize the enhancement of plant resilience to abiotic stresses. The adverse effects of climate change on agricultural systems necessitate the development of crops with improved tolerance to drought, salinity, heat, and cold. Genetic modification techniques offer promising avenues for achieving this goal. Transgenic technology has been employed as a powerful tool to enhance plant resilience in the face of abiotic stresses. These strategies encompass the introduction of stress-responsive genes, transcription factors, and regulatory elements to enhance stress signaling pathways. Additionally, the manipulation of hormone signaling pathways, osmoprotectant accumulation, and antioxidant defense mechanisms is explored. Furthermore, the use of genome editing tools, particularly CRISPR-Cas9, for precise modification of target genes is associated with stress tolerance. This technology opens up new possibilities for improving crop resilience by facilitating targeted genetic modifications. The challenges associated with genetic modification for abiotic stress tolerance are acknowledged, and future prospects in this field are highlighted. It is crucial to address regulatory, safety, and ethical considerations while continuing to advance genetic modification strategies for crop improvement. Overall, understanding and harnessing the potential of genetic modification techniques can contribute significantly to the development of resilient crop varieties capable of withstanding adverse environmental conditions caused by climate change. By ensuring sustainable agricultural productivity and food security, these advancements can play a vital role in mitigating the challenges posed by climate change to global food systems.

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Data availability Not applicable

Declarations

Ethics approval The authors declare that all the permissions or licenses were obtained to collect the data and that all study complies with relevant institutional, national, and international guidelines and legislation for research ethics.

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