



Plant breeding for harmony between sustainable agriculture, the environment, and global food security: an era of genomics-assisted breeding

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Main conclusion Genomics-assisted breeding represents a crucial frontier in enhancing the balance between sustainable agriculture, environmental preservation, and global food security. Its precision and efficiency hold the promise of developing resilient crops, reducing resource utilization, and safeguarding biodiversity, ultimately fostering a more sustainable and secure food production system.

Abstract Agriculture has been seriously threatened over the last 40 years by climate changes that menace global nutrition and food security. Changes in environmental factors like drought, salt concentration, heavy rainfalls, and extremely low or high temperatures can have a detrimental effects on plant development, growth, and yield. Extreme poverty and increasing food demand necessitate the need to break the existing production barriers in several crops. The first decade of twenty-first century marks the rapid development in the discovery of new plant breeding technologies. In contrast, in the second decade, the focus turned to extracting information from massive genomic frameworks, speculating gene-to-phenotype associations, and producing resilient crops. In this review, we will encompass the causes, effects of abiotic stresses and how they can be addressed using plant breeding technologies. Both conventional and modern breeding technologies will be highlighted. Moreover, the challenges like the commercialization of biotechnological products faced by proponents and developers will also be accentuated. The crux of this review is to mention the available breeding technologies that can deliver crops with high nutrition and climate resilience for sustainable agriculture.

Keywords Abiotic stresses · Drought · Climate changes · Food security · Human population · Agriculture

Abiotic stress and its significance in agriculture

Abiotic stressors are a major impediment to crop production and have both qualitative and quantitative detrimental effects (Bashir et al. 2019; He et al. 2018). The majority of croplands are exposed to such unfavorable conditions (Cramer et al. 2011). Ahmad and Prasad (2011) stated that abiotic stressors, such as drought, heat, salinity, and cold, are common worldwide and affect up to 70% of the survival biomass and yield of most major food crops (Wang et al. 2003; Wani et al. 2016). Climate change and an increasing human

population are expected to exacerbate negative impacts of abiotic stresses on agriculture and the ecosystem (Kopecká et al. 2023). Currently, the world population has passed the 8 billion mark, and the projections are for an increase to about 8.5 billion by 2030 and 9.7 billion by 2050 (Afridi et al. 2022). Therefore, environmental changes pose a major challenge to the agricultural sector's efforts to meet rising global food demand (Kopecká et al. 2023). In addition, the presence of multiple or altered abiotic and biotic stressors can trigger a trade-off between plant responses that are suitable for adaptation to one stress but may increase vulnerability to other stressors. This dilemma, involving global increases in yield demands and increasing threats to yields due to environmental conditions, requires significant investment in research and development focused on improving crop stress resistance (Dresselhaus and Hüchelhoven 2018). Traditional breeding techniques have significantly increased crop production and yields, but new methods and techniques

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are needed to meet the growing demand for food (Anwar and Kim 2020; Mishra et al. 2017). As noted by Mishra et al. and Anwar et al., several approaches have been developed to improve the resilience of plants so that they can better survive and produce more efficiently. When plants are exposed to environmental stressors, overproduction of reactive oxygen species (ROS) occurs, negatively affecting enzyme activity, carbohydrate biosynthesis, DNA and protein synthesis, and other biochemical processes, leading to oxidative stress (Pandey et al. 2017; Zhu 2016). As a result of ROS, many genes associated with growth, cell cycle, programmed death, abiotic stress response, systemic signal transduction, pathogen response, and development are also impacted (Gill and Tuteja 2010). Plant breeding techniques that enhance resistance to a variety of abiotic stresses are imperative in order to meet the increasing demand for food and counteract the deleterious effects of abiotic stress on crop production (Ghadirnezhad Shiade et al. 2023; Noman et al. 2017; Talaat and Shawky 2016). In order to increase the production of stress-tolerant crops and facilitate drought management through identification of different parental combinations and improvement of selection efficiency, it is imperative to integrate advanced genomic technologies and data-driven approaches into the breeding process (Yadav et al. 2018). Genes that control important adaptation traits can be identified using genetic approaches, such as quantitative trait loci (QTL) mapping, marker-assisted breeding, and genomic selection. Breeders can select superior genotypes quickly and speed up the breeding cycle with them (Maphosa et al. 2020). In recent years, new tools have emerged that aim to identify genes associated with drought resistance in wild relatives and landraces of crops that can be transferred to breeding lines to facilitate the breeding process and produce drought-tolerant strains. These tools include three main categories, namely marker-assisted selection (MAS), genomic selection (GS), and targeted gene editing (CRISPR technology).

Causes of abiotic stress

Environmental factors, such as temperature, water availability, light, and soil properties, can lead to abiotic stress

In agriculture, stress is regarded as a deviation from normal physiological processes (Oshunsanya et al. 2019). The disruption from ideal plant functions could be caused either directly or indirectly by it (Hatfield and Prueger 2015). Physiology, growth, development, yield, and quality of crops are all affected by environmental stresses. In order to improve agricultural practices, it is extremely important to understand how environmental factors interact with physiological

processes (Rao et al. 2016). Stress affects crops on a molecular to morphological level. The responses at the whole crop level take into account all the underlying processes. The quantitative assessment of these studies is therefore not always straightforward. Moreover, climate change will exacerbate this problem (Calanca 2017). As a result of abiotic stress, plant water relations could be disrupted, water usage efficiency reduced, photosynthetic capacity disrupted, gas exchange reduced, nutrients acquired altered, protein synthesis reduced, and organic solutes formed and accumulated (Talaat 2019). Anjum et al. described drought conditions as characterized by either limited water supply to the roots or high water loss through transpiration. Water stress can affect plants in a variety of ways such as decreasing photosynthesis and inhibiting growth, closing stomata, reducing transpiration rates, and reducing the water potential of plant tissues (Ghadirnezhad Shiade et al. 2023). In many parts of the world, soil salinity represents a significant factor limiting agricultural productivity (Zhu et al. 2016). It has been shown that high salt levels result in ion toxicity (mainly Na^+), hyperosmotic stress, and secondary stresses such as oxidative damage (Zhu 2002). Physiological and metabolic processes in plant tissue are affected by salinity stress, but since most economic crop species are glycophytes, salinity inhibits crop productivity (Abobatta 2020). High temperature stress also results in morphological, biochemical, and physiological changes that affect plant growth and development (Wahid et al. 2007). As a result of high temperature stress, proteins may be damaged, their synthesis disturbed, major enzymes inactivated, and membranes ruptured (Fahad et al. 2017). For Earth's regions, the minimum temperature reaches zero degrees Celsius (Rihan et al. 2017). Many crops, such as rice, maize, tomato, soybean, corn, and cotton, do not acclimate to cold temperatures and require tropical or subtropical climates to thrive (Chinnusamy et al. 2007). Plant growth and development are adversely affected by cold stress, which also limits the geographical distribution of plant species and lowers crop yields worldwide (Ding et al. 2019; Pearce 2001). For plant growth and development, light is one of the most important environmental factors. Aside from regulating plant growth and productivity, it determines photosynthetic rate and accumulate–assimilation. Nevertheless, plants are frequently exposed to excess or inadequate light intensities, which, collectively referred to as light stress, can affect their agronomic traits by inhibiting their physiological metabolic processes, such as photosynthesis, antioxidants, and nitrogen and carbon fixation (Yang et al. 2019). Biomass production is directly influenced by symbiotic relationships and soil microbial biodiversity between soil microorganisms, which contribute to physiological processes and plant nutrient uptake. It has been reported that abiotic stressors like drought, extreme salinity, and other abiotic stressors can affect plant carbon metabolism adversely or favorably,

depending on the stress rate, the species of plant, and the type of plant tissue (Abdul Rahman et al. 2021). Soil properties, such as pH, carbon, nitrogen, and moisture content, are abiotic factors that influence bacterial communities (Gahan and Schmalenberger 2014; Kalayu 2019; Nadarajah 2019). It is thought, however, that fungal communities are more influenced by biotic factors, such as plant diversity (Wang et al. 2020a, b). The bacterial and fungal communities affect soil variables like pH, carbon, nitrogen, and moisture content in a similar way, but regional abiotic factors such as climate have a larger impact on bacterial community variation than fungal communities (Bahram et al. 2018; Wang et al. 2020a, b).

Impacts of abiotic stress

Physiological effects of abiotic stress on plants and crops

Plant metabolism is immensely involved in the defense responses, physiological regulation, and signaling under severe abiotic stresses which affect the transport, concentration, biosynthesis, and storage of primary and secondary metabolites. In plant tissues, phenolic levels are affected by the nutrient deficiency. Phenylpropanoids accumulate as result of phosphate and nitrogen deficiency (Fritz et al. 2006). Phenolic concentrations are also regulated by low levels of magnesium, sulfur, and potassium. Excess phenolic acid is released from roots under low iron levels (Chen et al. 2018). Bryant et al. suggested that an exchange occurs between the carbon to biomass production or production of defensive secondary elements. Dramatic accumulation of phenyl amides and polyamines has been evident in tobacco and bean under abiotic stress conditions suggesting their antioxidant roles (Gupta et al. 2016). Similarly, drought, nutrient deficiency, sugar, light intensity, and UV also stimulate the accumulation of anthocyanin (Winkel-Shirley 2001).

Increasing the temperature above the threshold levels of plants disrupts their cellular homeostasis, metabolism and eventually growth. Plants possess photosynthetic apparatus which responds to the cellular energy imbalance but is very sensitive to heat and serves as first site of disruption before cellular disruptions (Ashraf and Hafeez 2004). Plants respond to the changes in temperature by adjusting their optimum photosynthetic rate to some extent, but extreme ups and downs in temperature limit the photosynthetic function as well as metabolic activities. Photosynthetic components, i.e., thylakoid electron transport, carbon reduction cycle, transpiration rate, and stomatal conductance are all disrupted by chilling stress (Mathur et al. 2014). Several studies have been performed to study the effects of temperature on the photosynthetic rates of plants. For example, high temperature enhances the photosynthesis rate, quantum

yield of PSII, electron transport, carboxylation rate, and mesophyll and stomatal conductance in *Glycine max* (G. Xu et al. 2016a, b), reduces stomatal conductance and CO₂ assimilation in *Pisum sativum* (Abdulmajeed et al. 2017), decreases the photochemical quenching coefficient, actual photochemical efficiency, starch content, and net photosynthetic rate in *Cucumis sativus* (Ding et al. 2016), and reduces the photochemical activity of PSII and chlorophyll content in *T. aestivum* (X. Chen et al. 2017). Chilling temperature reduces photosynthetic rate in *Lycopersicon esculentum* (Liu et al. 2017), lowers chlorophyll content in *Oryza sativa* (Han et al. 2017), and maximizes the photochemical efficiency of PSII in *Camellia sinensis* (Li et al. 2018a, b).

Fluctuations in light intensity serve as a major stress factor that have an enormous effect on the physiological and biochemical properties of the plants. For instance, limited light supply alters photosynthesis such that leaves become etiolated. High light intensity causes photo-inhibition while low light intensity results in insufficient energy for plant growth (Pascual et al. 2017). The cells of *Dunaliella salina* were damaged by high light intensity of 1000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Xu et al. 2016a, b). Photodynamic reactions, photolability, solarization, photo-inactivation, photo-oxidation, and photo-inhibition are the process which are affected by the reduction in photosynthesis under strong visible light (Powles 1984). The functions of the PSII are halted by the photo-inhibition process (Gururani et al. 2015). Moreover, reduction in photochemical efficiency and mitochondrial activity along with high emission of heat or fluorescence serves as a disaster for PSI and PSII under high light intensity (Faseela and Puthur 2018). High light intensity also affects the photosynthesis processes like chlorophyll/carotenoid ratio, electron transport flux, photochemical efficiency, and quantum efficiency of PSII (Carvalho et al. 2016). PSII also got affected under low light when pioneer plants were grown in shade or in plants with late succession while performance of PSI remained same (Krause et al. 2004).

The extent of changes in metabolic activities in plants depends on the type of the heavy metal accumulation. Metals like As, Hg, Cd, and Pb which have no valuable part in growth of plants, a small concentration of them can have adverse effects. The height of rice was reduced significantly with only 1 mg Hg/kg (Kibra 2008). Only a 5 mg/L of Cd was enough to reduce the root and shoot growth of wheat plants (Ahmad et al. 2012). These reductions may be attributed to the reduction in enzymes, plant nutrition, and less photosynthetic activities (Kabata-Pendias 2000). Heavy metals cause inhibition of protochlorophyllide reductase, porphobilinogen deaminase, and δ -aminolevulinic acid dehydratase (ALAD) activity which block the chlorophyll biosynthetic pathways resulting in reduced chlorophyll content and ultimately lead to photosynthesis inhibit. The chlorophyll content can also be reduced by chlorophyll

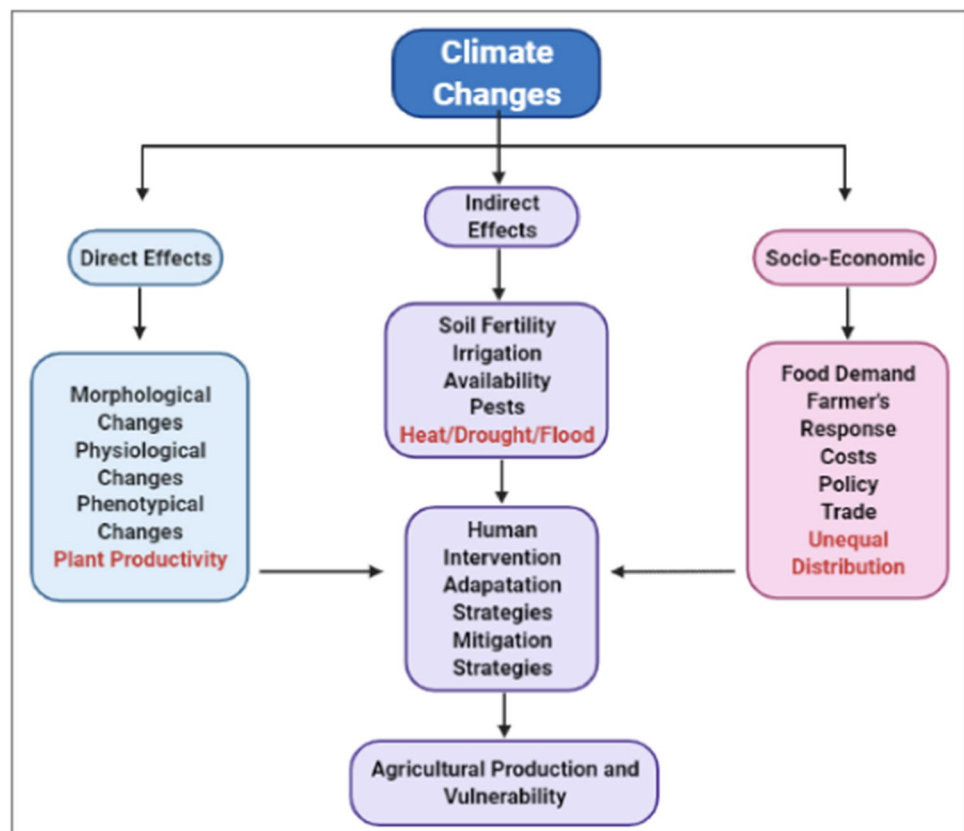
degradation by enhanced chlorophyllase activity under heavy metal stress (Sharma et al. 2020). Paunov et al. (Paunov et al. 2018) observed that 600 μM of Zn causes decline in efficiency of PSII and disturbs the process of photosynthetic electron transport in *Triticum durum*. In *Spinacia oleracea*, 150–300 mg/kg of Ni causes reduction in carotenoid and chlorophyll contents (Boostani et al. 2019). The content of photosynthetic pigments reduces in the presence of 5–15 μM Cd in *Cucumis sativus* (Dresler et al. 2019) while photosynthetic apparatus of *Lactuca sativa* got destroyed in 20 μM concentration of Cd (Wang et al. 2019). 3 mM of Pb caused reduction in transpiration, stomatal conductance, and CO_2 assimilation in *Populus canescens* (Shi et al. 2019).

Economic impacts of reduced yields and decreased crop quality

Agricultural production is primarily constrained by environmental stresses (Francini and Sebastiani 2019). Among these stressors, abiotic factors such as adverse environmental conditions have a significant impact and result in yield losses of 50 to 70% (Francini and Sebastiani 2019). Plants in

natural environments often experience multiple stressors at once rather than one stressor alone (Slama et al. 2015; Wani et al. 2016). According to Zhu (2016), agricultural crops are consistently grown under dynamic, changing and often adverse environmental conditions. The agricultural sector increasingly recognizes climate change as a significant future challenge. This global phenomenon requires the adoption of sustainable water resource management practices to mitigate its negative impacts. Although, in several agricultural regions, excessive rainfall can lead to flooding, which negatively affects crop growth and productivity. Therefore, the selection of appropriate crops and the implementation of effective agronomic management strategies in such areas are crucial to regulate soil water content (Francini and Sebastiani 2019). Climate change can have various direct, indirect, and socioeconomic impacts on the ecosystem, particularly with respect to abiotic stress conditions. Figure 1 illustrates the effects of climate change on abiotic stress conditions. The significant increase in average temperatures observed over the last century has had a major impact on soil degradation, caused soil salinization through increased evaporation rates, destabilized soil moisture through floods or droughts,

Fig. 1 Effects of climatic changes on crop production



and led to erratic precipitation patterns, significantly affecting global food security (Mafakheri et al. 2021).

Strategies for abiotic stress management

Cultural practices

Cultural practices, such as irrigation and nutrient management, are crucial for the survival of plants in abiotic stress environments. Irrigation practices can help alleviate drought stress by providing plants with the necessary water. For example, in dry areas, drip irrigation can deliver water directly to the roots of plants, reducing water loss through evaporation and ensuring that the water reaches the plants where it is needed most (Laxman et al. 2020). Under salt stress, excess salts can be leached from the soil using irrigation techniques. In areas with high salinity levels, flood irrigation can flush the salts out of the soil, reducing their impact on the plants (Machado and Serralheiro 2017). Similarly, in hot environments, overhead sprinkler irrigation can be used to cool the air around the plants, reducing heat stress, or mulching with biodegradable films or plastic can be done to minimize evaporation (Verma et al. 2020). In nutrient-scarce areas and areas with poor soil fertility, fertigation can be used to deliver nutrients to the plants through the irrigation system (Jayakumar et al. 2014). Poor soil structure, such as compaction or poor drainage, can stress plants by limiting root growth and water uptake. Irrigation practices can help alleviate soil structure stress by improving soil structure. For instance, in areas with compacted soil, deep-root watering can be used to promote more profound root growth and improve soil structure (Zegada-Lizarazu and

Iijima 2005). The type of irrigation practice used depends on the specific needs of the plants and the environmental conditions. Proper irrigation management is critical for successful stress mitigation, avoiding other problems such as overwatering, nutrient loss, or disease outbreaks.

Application of several nutrients, i.e., primary nutrients (potassium, nitrogen, and phosphorus), secondary nutrients (sulfur, magnesium, and calcium), micronutrients (copper, iron, boron, and zinc), and beneficial nutrients (silicon, selenium, and cobalt) alleviates the abiotic stress from plants. Exogenous application of N enhances the enzymatic activity, chloroplast fluorescence, photosynthesis, and strengthens the root system in rice (Tran et al. 2014), and enhances the accumulation of proline, and improves the plant water status of rapeseed (Abid et al. 2016). Similarly, leaf water status in cotton (Singh et al. 2006) and water use efficacy and nutrients uptake in wheat are improved by phosphorus (Ahmed et al. 2018) (Fig. 2). Potassium induces an antioxidant defense system and stimulates nitrogen metabolism in oat (Fig. 2) (Ahanger et al. 2015). Among secondary nutrients, sulfur enhances the nutrient uptake and photosynthesis status in oilseed rape (Lee et al. 2016), and magnesium increases root proliferation and the efficacy of sugar partitioning in rice (Ding and Guohua 2011). In tobacco plants, ROS reduction, stomatal conductance, and photosynthetic activity are regulated by calcium (Tan et al. 2011). Calcium also reduces hydrogen peroxide toxicity and ROS accumulation and mitigates aluminum toxicity in barley (Guo et al. 2006). Under abiotic stress conditions, exogenous application of copper (improves Na^+/K^+ ratio, glutathione, vitamin C, and antioxidant activity in tomato) (Pérez-Labrada et al. 2019), iron (enhances the activity

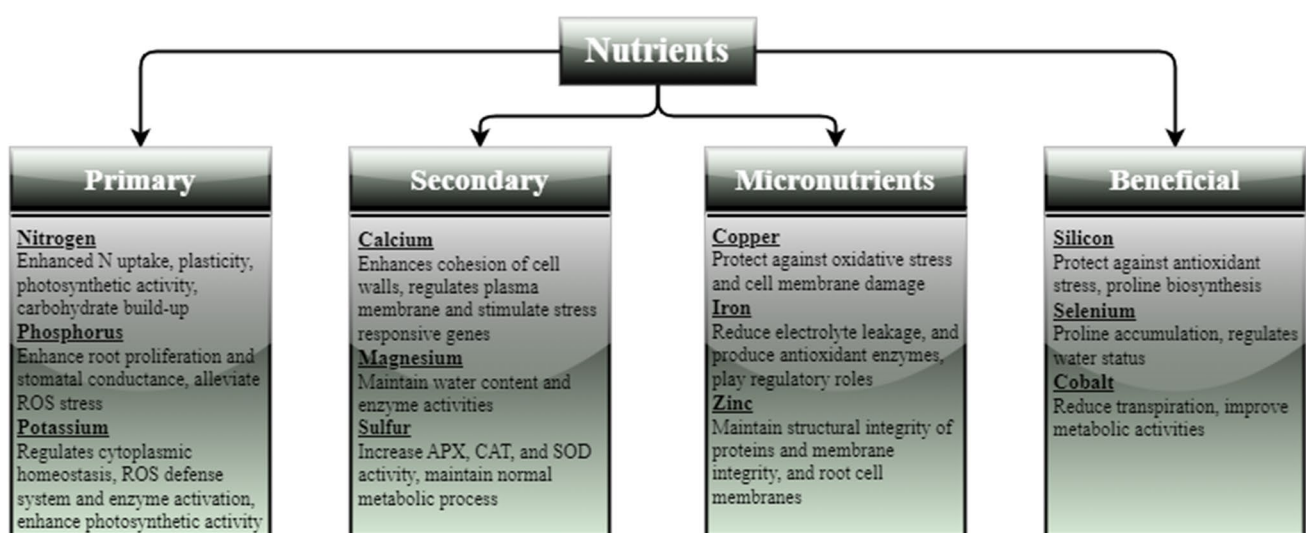


Fig. 2 Mechanism of nutrients in alleviating abiotic stresses

of ascorbate peroxidase, catalase, peroxidase, and superoxide dismutase in sunflower and improves shoot weight, transpiration rate, intercellular CO₂ concentration, and stomatal conductance in soybean) (Alidoust and Isoda 2013; Mohammadi et al. 2020), and zinc (improves chlorophyll content and stomatal aperture in tomato and increases SOD activity, proline accumulation, and chlorophyll content in sunflower) (Sakya et al. 2018; Zafar et al. 2014) also proves to be a beneficial practice for alleviating abiotic stresses from plants. Moreover, silicon, selenium, and cobalt could also be applied to plants to alleviate abiotic stresses (Abdel Latef and Tran 2016; Hasanuzzaman et al. 2011; Sarma et al. 2014).

Development of abiotic stress-tolerant crops through breeding technology

Plant breeding technology refers to the use of various techniques and methods to improve the genetic makeup of plants for desirable traits such as disease resistance, yield, tolerance, and quality. Plant breeding aims to develop new varieties that are better suited for specific environments and can meet the needs of farmers, consumers, and the food industry. Several breeding technologies are used to improve crops' abiotic stress tolerance. One approach is the use of traditional breeding techniques to identify and select plants with desirable traits such as drought tolerance, salt tolerance, and heat tolerance. These traits can be inherited by subsequent generations, developing new varieties with improved stress tolerance. This method has been used for centuries and has resulted in the development of wide crop varieties that are widely grown today (Palareti et al. 2016). For example, durum wheat is sensitive to saline conditions because of the lack of *HKT1;5* allele that excludes Na⁺ from root xylem. As this allele is present in bread wheat, the two species can be cross-bred so that the genome version of *HKT1;5* can be transferred to durum wheat. Under saline stress, grain yield was found to be 25% higher in the durum lines containing *HKT1;5* allele (Munns et al. 2012). Another approach is the use of genetic engineering technologies to introduce specific genes into plants that help them tolerate abiotic stress. For example, genes that encode enzymes responsible for the biosynthesis of osmoprotectants such as proline, glycine betaine, and trehalose have been introduced into crops to improve their drought and salt tolerance. Similarly, genes encoding heat-shock proteins and antioxidants have been introduced to help crops cope with high-temperature stress (Rani et al. 2021; Roy et al. 2011). Recent advances in genome editing technologies such as CRISPR/Cas9 have also enabled precise and targeted modifications to plant

genomes, allowing breeders to develop crops with specific traits more quickly and efficiently. Genome editing can be used to introduce or modify genes responsible for abiotic stress tolerance (Jinek et al. 2012). For instance, fruit development under cold or heat stress declines the fruit development in *S. lycopersicum* as sexual reproduction in them is highly temperature-sensitive. Sexual reproduction can be uncoupled with fruit development by halting the expression of *SIAGL6* to produce seedless fruit under extreme temperature conditions (Klap et al. 2017). Similarly, the *ARGOS8* gene can be over-expressed by the insertion of an alternative promotor by a CRISPR-mediated technique to increase the yield of *Zea mays* under water-scarce conditions (Shi et al. 2017).

Use of agrochemicals to alleviate abiotic stress

Agrochemicals, such as plant growth regulators and bio-stimulants, are utilized to ameliorate stress in plants. Plant growth regulators such as abscisic acid (ABA) and gibberellins can help regulate plant growth and development in response to environmental stress. Bio-stimulants, such as humic and fulvic acids, can enhance plant growth by increasing nutrient uptake and improving soil structure.

Phytohormones

Phytohormones bring about variegate biochemical and physiological processes in plants under stress conditions. They trigger signaling pathways which make them crucial for plants' survival under stressful conditions. The active role of phytohormones in the physiological processes makes them a promising candidate for exogenous application to boost tolerance in plants. The exogenous application of phytohormones is a well-known crop management approach under environmental stress conditions, as some examples are highlighted in Table 1.

Phytohormones regulation

Phytohormones are the critical modulators of plant growth, development, and physiology. They also induce environmental stimuli in regulatory systems in response to environmental stress. Therefore, intervening in the hormone signaling and metabolic processes offer an encouraging route in favor of stress tolerance. However, mitigation of adverse effects on development and growth requires tight spatiotemporal regulation. ABA plays an eminent role in plant acclimation under drought stress. Previously discussed strategies relying on the over-expression of ABA genes effectively imparted drought stress, but even with the use of inducible promoters,

Table 1 Effect of exogenous phytohormones on plants development under stressful environment

Phytohormone	Plant Species	Stress	Effect	References
Salicylic acid	<i>Torreyia grandis</i>	Oxidative and salinity	Enhances chlorophyll content and stimulates the photosynthetic process	Li et al. (2014)
	<i>Solanum lycopersicum</i>	Salinity	Changes the expression pattern of the GST-gene family (<i>SIGSTT2</i> , <i>SIGSTT3</i> , and <i>SIGSTT4</i>)	Csiszár et al. (2014)
	<i>T. aestivum</i>	Heat	Enhances pro-production and halts the formation of ethylene	Khan et al. (2014)
	<i>H. vulgare</i>	Drought	Enhances plant fry mass by increasing stomatal conductance and CO ₂ assimilation	Habibi (2012)
Jasmonates	<i>Oryza sativa</i>	Drought	Increases efficacy of photosystem-II (PSII) eventually improves photosynthesis	Sheteiwy et al. (2018)
	<i>Triticum aestivum</i>	Drought	Improves shoot growth, carbohydrate accumulation, and germination percentage	Ilyas et al. (2017)
	<i>Thymus vulgaris</i>	Drought	Increases antioxidant activities	Sheteiwy et al. (2018)
Auxin	<i>Triticum aestivum</i>	Heat	The grain number and yield increased by 6–8%	Abeyasingha et al. (2021)
	<i>Oryza sativa</i>	Heat	Increased the spikelet fertility	Zhang et al. (2018a, b)
ABA	<i>Zea mays</i>	Drought and oxidative	Stimulates the antioxidant enzymes to increase endogenous ABA levels and modulate <i>ASR1</i> expression	Yao et al. (2019)
	<i>Oryza sativa</i>	Salinity	Preserve ionic balance to avoid chloride toxicity and maintain the K ⁺ /Na ⁺ ratio	Gurmani et al. (2013)
	Bermuda grass	Cold	Modify the expression of cold-related genes like <i>LEA</i> , <i>CBF</i> , and <i>ABF1</i> , maintain cell membrane integrity, increase chlorophyll content, enhance the efficacy of photosystem-II	Huang et al. (2017)
Cytokinins	<i>Solanum melongena</i>	Salt	Enhance proline levels	Wu et al. (2013)
	Waxy corn	Water logging	Decline in ROS accumulation and incline in activities of enzymes (monodehydroascorbate reductase, dehydroascorbate reductase, glutathione reductase, ascorbate peroxidase)	Wang et al. (2021a, b, c)
Ethylene	Grapevine	Cold	Exogenous application of ethylene (1-aminocyclopropane-1-carboxylate) is associated with over-expression of the <i>VaERF057</i> gene, which imparts tolerance against cold	Sun et al. (2016)

the pleiotropic effect led to the down-regulation of growth (Govind et al. 2011; Hwang et al. 2010). CRK45, i.e., a stress-inducible kinase that plays its role in ABA signaling, can be over-expressed to gain a tighter control on levels of ABA and ABA signaling and induce drought tolerance. This indicated that endogenous ABA levels could be fine-tuned by CRK45 (Zhang et al. 2013). Similarly, the grain yield, ROS scavenging, cytokinin content, and root growth in crops can be enhanced by controlled expression of IPT (isopen-tenyl transferase), i.e., modulates rate-limiting step in the biosynthesis of cytokinins in the presence of stress-inducible promoters (Kuppu et al. 2013). A similar stratagem could be employed for other stress-related hormones such as ethylene,

brassinosteroids, jasmonic acid, and salicylic acid (Gepstein and Glick 2013).

Biostimulants

The organic or inorganic compounds and/or microorganisms that modulate several processes and enhance the development and growth of plants are termed biostimulants. They are exogenously applied near the root area as foliar sprays or in the soil as they are available in the form of liquids, powder, and granular forms. The demand for biostimulants is expected to reach 5.6 billion dollars by 2026, with an annual growth rate of 12% because of their low or no toxicity and long-term effects (Bulgari et al. 2019). Seaweed, humic substances, protein

Table 2 Use of biostimulants to mitigate abiotic stress

Biostimulant	Plant species	Stress	Effect	References
Seaweed	<i>Saccharum</i> spp.	Drought	Seaweed extract from <i>A. nodosum</i> activated the enzymatic processes and increased the production of sugar	Jacomassi et al. (2022)
	<i>Solanum lycopersicum</i>	Salinity	Extracts from <i>Zostera marina</i> induced the over-expression of <i>CcWRKY</i> , i.e., stress-responsive genes	Campobenedetto et al. (2020)
Protein hydrosylates	<i>S. lycopersicum</i>	Drought	Mediated the ROS-mediated oxidative imbalance by inducing radical scavengers and reducing tetrapyrrole coproporphyrins biosynthesis	Paul et al. (2019)
	<i>A. thaliana</i>	Salinity	Declined the levels of phytohormones (gibberellins, auxins, cytokinins) and stress-related molecules (terpenoids and flavonoids)	Sorrentino et al. (2022)
	<i>Lolium perenne</i>	Heat	Improved the levels of carotenoids, chlorophyll, photosynthesis, and stomatal conductance	Botta (2012)
Humic substances	<i>Zea mays</i>	Acidity	Stimulated plant acclimation and induced weak acid stress response in cells	Baía et al. (2020)
	<i>Oryza sativa</i>	Drought	Modified the expression of <i>OsTIP</i> and induced antioxidant enzymes	García et al. (2014)
Microorganisms	<i>Cajanus cajan</i>	Salinity	Application of <i>Pseudomonas fluorescens</i> enhanced the expression of <i>CcWRKY</i> genes	Kumar et al. (2019a, b)
	<i>S. lycopersicum</i>	Heat	Application of PBPB along with humic acid improved nutrient uptake, salicylic acid, and chlorophyll content and declined the expression of <i>SIATG5</i> and <i>SIWRKY33b</i>	Khan et al. (2020)

hydrosylates, arbuscular mycorrhizal fungi, and PGPB are examples of biostimulants, and their impact on plants are discussed in Table 2.

Plant breeding technology and its importance in agriculture

Plant breeding technology refers to the use of various scientific techniques and methods to create new plant varieties with desirable traits. In this technique, two species with the best qualities are crossed in order to produce progeny with ideal characteristics. The procedure comprises three main steps, usually referred to as a collection of germplasm, superior phenotypes identification, and better cultivars, resulting from their hybridization (Al-Khayri et al. 2016). In germplasm collection, the genetic makeup of plants is conserved for research and breeding purposes. It serves as a critical resource for improving agricultural productivity, food security, and biodiversity conservation (He and Li 2020). In contrast, superior phenotypes identification refers to the breeding of plants with desirable characteristics to get efficient future generation (Chawade et al. 2019). Plants are selected from the assorted population, followed by many years of their stabilization. The resulting plants are subjected to the test under diverse conditions for their improved traits. In 1996, Rajaram reported wheat crossed 3170 times by using 51 crops collected from 21 different countries (Rajaram

et al. 1996). This was one of the earliest successful experiments of plant breeding. Since now, rice (Chu et al. 2023), corn (Alcántara et al. 2023), soybeans (Rahman et al. 2023), tomato (Rajaram et al. 2023), apples (Mignard et al. 2023), roses, and grapes (Battaglene 2023) have been produced by the services of this technique.

Moreover, plant breeding technology proves very helpful in agriculture as it also involves the use of traditional breeding methods, such as cross-pollination and hybridization, and modern molecular techniques, such as genetic engineering and gene editing. Scientists use these techniques to select and transfer desirable genes from one plant to another, resulting in plants with improved traits. It is well known for its increased crop productivity as it helps in developing new crop varieties with improved yield potential. This, in turn, increases the overall productivity of the agricultural system, which is essential for meeting the growing food demand of the world's population (Unkovich et al. 2023). As mentioned above, plant breeding is capable of developing crops with improved quality traits, such as better taste, aroma, texture, and nutrient content (Schaart et al. 2016). This helps to enhance the nutritional value and marketability of crops. Using plant breeding technology, scientists can develop crops resistant to pests and diseases (Ceccarelli et al. 2010). This can reduce the use of chemical pesticides and other harmful chemicals, leading to a more sustainable agricultural system. Furthermore, this technology can help in developing crops that can withstand environmental stresses, such

as drought, heat, and salinity. This is essential for ensuring food security in areas that are vulnerable to climate change. Scientists can conserve the genetic diversity of crops with the help of this technique, ensuring that important traits are not lost and can be used for future breeding programs.

Methods of plant breeding

Traditional breeding methods

Hybridization

The crossing of two or more plants with desirable traits to produce offspring with a combination of those traits is called hybridization. Hybridization aims to create plants with improved characteristics, such as disease resistance, higher yield, improved quality, or environmental adaptation. Reproductive barriers like male/female sterility or sexual incompatibility that are encountered during sexual breeding can be overcome by hybridization (Mwangangi et al. 2019). The hybridization process begins with selecting parent plants with desirable traits. These parent plants can be from the same species (intraspecific hybridization) or from different species (interspecific hybridization) that are closely related. The selected plants are then crossed through controlled pollination, which can be achieved by manually transferring pollen from the male flower to the female flower or by using specialized breeding techniques such as emasculation or hand pollination (Mukasa et al. 2007). The resulting offspring from the cross are called hybrids, and they possess a unique combination of the traits of the parent plants. The hybrids are evaluated for desirable traits, and those with the desired characteristics are selected for further breeding. This process is repeated over several generations until the desired plant variety is achieved. Hybridization is a time-consuming process that requires careful selection and evaluation of parent plants and offspring. However, it remains a popular method for traditional plant breeding because it allows for the creation of new plant varieties with desirable traits, while maintaining the genetic diversity of the original plant species.

Selection

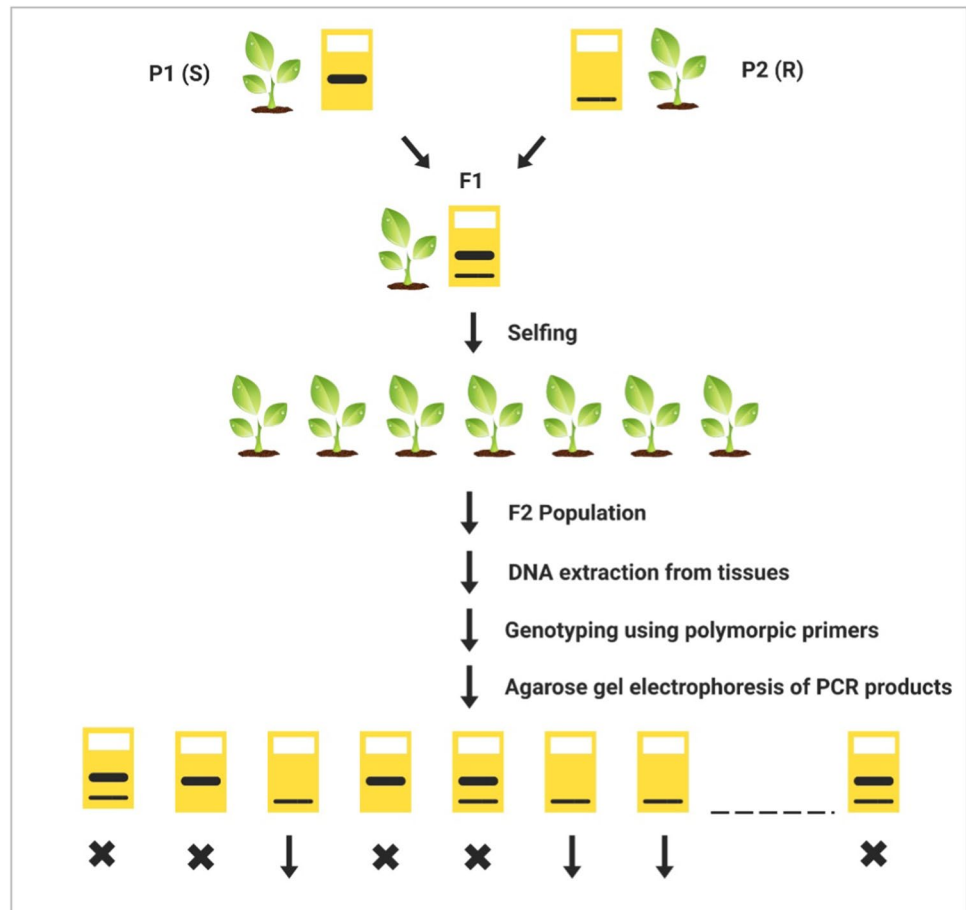
Pure line selection and mass selection are two conventional breeding techniques that have been used to improve plant traits. The choice of technique to use depends on the

specific crop and the desired outcome. Pure line selection involves selecting individual plants with desirable traits and self-pollinating them over several generations to create a pure line with the consistent expression of those traits. This technique is used for self-pollinated crops, such as wheat, rice, and soybeans, where genetic stability is important for consistent yields and quality (Brescaglio and Coelho 2013). In contrast, mass selection involves selecting a group of plants with desirable traits and breeding them to produce offspring with a combination of them. This technique is used for cross-pollinated crops, such as corn, where genetic diversity is important for adaptation to changing environmental conditions (Joshi 2017). Moreover, pure line selection is time-consuming and results in a population of plants with uniform genetic makeup and consistent expression of desirable traits (Begna 2021). In contrast, mass selection can be done more quickly and can result in a population with greater genetic diversity, which can be beneficial for adaptation to changing environmental conditions. However, mass selection can also result in plants with undesirable traits, making it important to carefully evaluate and select the parent plants (Acquaah 2015).

Backcross breeding

It is a conventional breeding technology used to transfer a desirable trait from a donor parent to an elite cultivar or variety while retaining the desired characteristics of the elite cultivar (Aleksoski 2018). A donor parent with the desired trait is selected and crossed with the elite cultivar. The donor parent can be a wild relative or a previously developed cultivar that possesses a desired trait, such as disease resistance, tolerance to abiotic stress, or higher yield potential. The hybrid progeny resulting from the initial cross is backcrossed with the elite cultivar to recover the genetic background of the elite cultivar while retaining the desired trait. The backcrossing process is repeated 5–6 times until the progeny have a genetic makeup similar to that of the elite cultivar but also possess the desired trait (Vogel 2009). The progeny are evaluated for the presence of the desired trait and for other traits of interest. The selected plants with the desired trait are then self-pollinated to create a pure line with the desired trait. Backcross breeding has several advantages over other breeding methods. It allows breeders to transfer a desirable trait from a donor parent to an elite cultivar while retaining the genetic makeup of the elite cultivar. It also enables the rapid incorporation of a desirable trait into a cultivar without sacrificing its desirable agronomic traits. In addition, it

Fig. 3 Schematic representation of MAS



reduces the time and resources required for the development of new cultivars (Lafitte et al. 2006).

Modern breeding techniques

Marker-assisted selection

Marker-assisted selection (MAS) is a modern breeding technology used to enhance the selection process in plant breeding. It involves identifying and selecting desirable traits in plants based on the presence or absence of specific DNA markers associated with these traits (Das et al. 2017). To use MAS, breeders first need to identify the specific DNA markers associated with the trait they want to select. Once the markers are identified, breeders can test plants to determine if they have the desired marker(s) and select those that do. The steps involved in MAS are shown in Fig. 3. MAS can help reduce the time and cost associated with traditional plant breeding and also increase the precision and accuracy of selection. It is particularly useful for traits that are difficult to evaluate visually or have low heritability, such as tolerance to environmental stresses or resistance to pests and diseases. Moreover, it is useful in selecting traits of the late reproductive stage, like seed characteristics, flower color,

grain yield, etc. (Madhusudhana 2019). MAS could also be implied for simultaneous genotyping by combining the molecular markers of interest for high-throughput applications in breeding programs. This can be achieved by following several steps of research, like mapping quantitative trait loci (QTL), fine mapping, and positional cloning. After the identification of causative agents on the basis of contrasting allele pairs, the range of trait variation in germplasm can be expanded by novel alleles to deal with specific abiotic stresses (Bhullar et al. 2010).

Overall, MAS is a powerful tool in modern plant breeding that allows breeders to select plants with desirable traits more efficiently and accurately. It has the potential to improve crop yields, enhance food security, and contribute to sustainable agriculture. Under drought stress, yield production of the rice lines could be stabilized by mapping three QTLs (*RM8085*, *II2S*, and *RM6836*) on chromosomes 1, 4, and 6 (Prince et al. 2015). Similarly, ten QTLs for productivity and physiology-related traits were identified by Sangodele et al. (2014) in backcross inbred lines (BILs) of a cross between WAB 450 and Swarna. The positive alleles from WAB 450 provided grain yield stability under drought stress. Zhao et al. (2016a, b) discovered three novel QTLs, i.e., *qPSLht10.2*, *qPSLht7*, and *qPSLht4.1*, in the breed

produced by a cross between Habataki (heat-tolerant) and Sasanishiki (heat-susceptible) when 11 QTLs on the chromosomes 1, 2, 3, 4, 5, 7, 8, 10, and 11 by SSR markers. Among QTLs, qPSLht4.1 was found to be responsible for heat tolerance and was implied in rice lines for better pollen growth under heat stress. Barakat et al. (2015) found that the F_4 population produced by a cross between Pavon 76 (drought tolerant) and Yecora Rojo (drought-sensitive) wheat lines contain 13 QTLs for abscisic acid when mapped by different markers (SSR, TRAP, and SRAP) and drought-tolerant cultivars could be produced from QTLs mapped in chromosomes 3B (Barc164), 4A (Wmc96), and 5A (Trap9). The cross between CML311-2-1-3 (waterlogging-sensitive but elite) and CAWL-46-3-1 (tolerant) maize lines produced recombinant inbred lines (RILs), in which 18 QTLs were found to be responsible for waterlogging-tolerance along with improved chlorophyll content, and % root and stem lodging traits (Zaidi et al. 2015).

Genomic selection

It is a type of modern breeding that uses information from the entire genome of an organism to select individuals with desirable traits. In plant breeding, this involves analyzing the DNA of plants to identify genetic markers associated with important traits, such as disease resistance or yield. At first, a reference population of plants is genotyped and phenotyped for the traits of interest. This allows breeders to identify genetic markers associated with these traits. Next, the genetic markers are used to predict the performance of new individuals that may not have been phenotyped yet (Voss-Fels et al. 2019). This makes the genomic selection superior to MAS as it uses genome-wide markers to predict the outcome of quantitative gene loci, thereby calculating estimated breeding value (Wang et al. 2018). To make these speculations, statistical models are used to estimate the effect of each marker on the trait of interest. Some of these models include reproductive kernel Hilbert space (RKHS) (Gianola et al. 2006), variants of best linear unbiased prediction (BLUP), i.e., genomic best linear unbiased prediction (GBLUP), genomic best linear unbiased prediction with linear ridge kernel regression (rrGBLUP), ridge regression best linear unbiased prediction (RRBLUP), and single-step genomic best linear unbiased prediction (ssGBLUP) (Meuwissen et al. 2001) and variegates of Bayesian models, i.e., Bayes A, Bayes B, Bayes C π , Bayes D π , Bayesian ridge regression (BRR), and Bayesian LASSO (Habier et al. 2009). These models can also take into account environmental factors that may affect the expression of the trait. The models are then used to calculate a genomic estimated breeding value (GEBV) for each individual, which is a prediction of its performance for the trait of interest. In contrast to other methods, the purpose of this method is not to locate

the Quantitative trait loci (QTL) but to make speculations on the performance of future offspring based on the DNA information (Rabier et al. 2016), as some of the examples are given in Table 4. It has successfully mapped small effect genes with multiple QTL, which are crucial agronomically and economically (Robertson et al. 2019). This method can be particularly useful for traits that are difficult to measure directly or have low heritability, such as tolerance to environmental stresses or disease resistance. It also has the potential to accelerate the breeding process by allowing breeders to predict the performance of individuals before they are even grown in the field.

Horticultural crops

Horticultural crops, such as vegetables, refer to plants that are grown for either food or esthetic purposes within the realm of horticulture. Horticulture encompasses the cultivation of various plants, including those that bear fruits, vegetables, flowers, ornamental plants, and herbs. In this specific context, the phrase emphasizes the category of horticultural crops that includes vegetables. Vegetables, as a subset of horticultural crops, are plants cultivated primarily for human consumption. They are known for their nutritional value, providing essential vitamins, minerals, and dietary fiber. Examples of vegetables include carrots, tomatoes, lettuce, bell peppers, and cucumbers. These plants are typically grown in gardens, farms, greenhouses, or other controlled environments, with the edible portions often being roots, leaves, stems, flowers, or fruits (Kader 2002). Genomic research can lead to the development of improved varieties of horticultural crops through methods like marker-assisted selection and genetic modification. By identifying specific genes associated with desirable traits, researchers can develop crops with enhanced characteristics. For example, scientists might identify genes responsible for disease resistance in vegetables and use this knowledge to breed or engineer crops that are more resilient to pests and pathogens (Kalloo and Bergh 2012) (Table 3, Fig. 4).

CRISPR-Cas9

CRISPR or clustered regularly interspaced short palindromic repeats of DNA sequence endow the adaptive, heritable immunity against pathogens and viruses. It is composed of 25–50 bp sequences that are separated by unique sequence spacer of similar length. The CRISPR-associated (Cas) protein is the vital protein associated with this system. CRISPR-Cas is a powerful tool for genetic engineering that has revolutionized the way scientists can modify the genomes of plants. This technology allows precise changes to be made to an organism's DNA, enabling the modification of specific genes, and creating desirable traits. The Cas9 proteins bind

Table 3 Genomic prediction of traits in crops

Crops	Population type	Trait	Model	Prediction accuracy (PA)	References
Maize	Test cross progenies and inbred lines	Drought-resistance	BLUP	0.42–0.65	Badu-Apraku et al. (2019)
	Breeding lines	Waterlogging-tolerance	GBLUP	0.37–0.38	Beyene et al. (2015)
	African and Asian inbred lines	Drought- resistance	BLUP	0.71–0.75	Vivek et al. (2017)
Wheat	Breeding lines	Grain yield (GY)	Bayesian LASSO	0.50–0.60	Burgueño et al. (2012)
	Breeding lines	GY	GBLUP	0.12–0.34	Sun et al. (2019)
Rice	Germplasm	Drought-resistance	GBLUP RKHS	0.23–0.80	Bhandari et al. (2019)
	128 Japanese rice varieties	Field grain weight	GBLUP	0.28	Yabe et al. (2018)
Apple	Biparental families and germplasm	Firmness	RRBLUP	0.81	Roth et al. (2020)
Apricot	F1 pseudo-testcross population	Glucose content	RRBLUP	0.31	Nsibi et al. (2020)
			GBLUP		
Barley	Breeding lines	GY	RRBLUP	0.57	Sallam and Smith (2016)
<i>Brassica napus</i>	Test cross F1s	Lodging resistance	RRBLUP	0.39	Jan et al. (2016)
Chickpea	Breeding lines	Drought	RRBLUP	0.56–0.61	Li et al. (2018a, b)
			BRR		
			Bayesian LASSO		
Common bean	Germplasm	Cooking time	GBLUP	0.22–0.55	Diaz et al. (2021)
			Bayes A		
			Bayes B		
			Bayes C π		
Ground nut	Breeding lines	Yield	Bayesian generalized linear regression	0.49–0.60	Pandey et al. (2020)
Lentil	RIL	Maturity duration	GBLUP	0.58–0.84	Haile et al. (2020)
			Bayes A		
			Bayes B		
			Bayes C π		
			Bayesian LASSO		
			BRR RKHS		
Pear	Full sib families	Crispness	GBLUP	0.32	Kumar et al. (2019a, b)
Soy bean	RILs	Yield	RRBLUP	0.68	Beche et al. (2021)
Sun flower	F1s from factorial mating design	Oil content	BLUP	0.783	Mangin et al. (2017)
Tomato	Germplasm	Biochemical profile	RRBLUP	0.13–0.70	Duangjit et al. (2016)

with DNA template and cleave the target site using crRNA (CRISPR RNA) and tracrRNA (transactivating crRNA), which fuses to form sgRNA (single guide RNA) (Ghosh and Dey 2022). Cas9 has a HNH-like nuclease domain which is used to cut target DNA strand complementary to guide RNA sequence and a RuvC-like nuclease domain to cut non-target strand complementary to DNA sequence. Strand incision and R-loop formation are formed simultaneously with complementary base pairing between target DNA and sgRNA. Cas9–DNA interactions and several conformational changes follow thereafter. The damage DNA undergoes two different pathways, i.e., high-fidelity homology directed pair (HDR) pathway or error-prone non-homologous end joining (NHEJ) pathway as shown in Fig. 5 (Jiang and Doudna 2017). In plant breeding, CRISPR-Cas9 can be used to create new crop

varieties with improved yield, resistance to disease, and tolerance to environmental stresses. By targeting specific genes and making precise modifications to the plant's DNA, plants with desired traits can be introduced. In crops like tobacco and rice, molecular breeding with CRISPR started in 2013. Recently, this technology has been used to alleviate abiotic stresses from various plant species as listed in Table 4.

This is a complex process and can be done in three ways. (i) Agrobacterium-mediated CRISPR-Cas9: In this technique, the CRISPR-Cas9 system is designed to target specific genes in the plant genome. The CRISPR RNA (crRNA) is designed to recognize and bind to the target gene, while the Cas9 protein cleaves the DNA at the target site. Then the CRISPR-Cas9 construct is introduced into Agrobacterium, which then acts as a delivery system for the CRISPR-Cas9

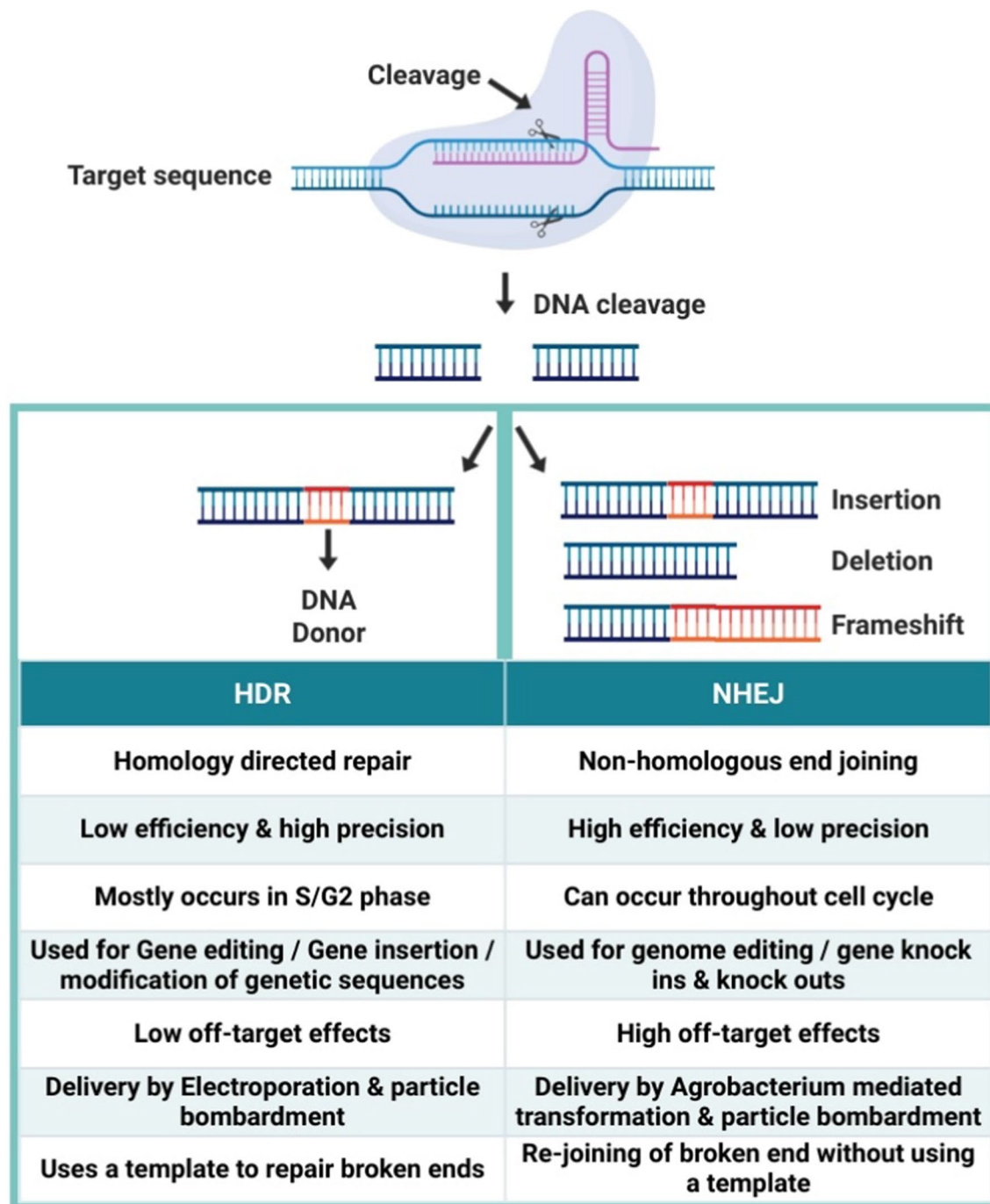


Fig. 4 Genome editing by CRISPR/Cas9-mediated technology

system into plant cells. The *Agrobacterium* is used to infect plant cells, which then take up the CRISPR-Cas9 construct. Once inside the plant cell, the CRISPR-Cas9 system can be used to edit the plant genome by targeting specific genes and introducing precise modifications. This allows the targeting of multiple genes simultaneously, resulting in plants with multiple traits of interest. Several plant species, including *A. thaliana*, Banana, *Glycine max*, *Oryza sativum*, *S.*

lycopersicum, *S. tuberosum*, and *Zea mays*, have been successfully transformed using this method (Bari et al. 2019; Butler et al. 2015; Char et al. 2017; Jacobs et al. 2015; Kaur et al. 2018; Li et al. 2013; Shufen et al. 2019). (ii) PEG method: This method is particularly useful for plants that are difficult to transform using other methods, such as cereal crops. The CRISPR-Cas9 construct is prepared as previously mentioned, and then plant tissue is treated with enzymes to

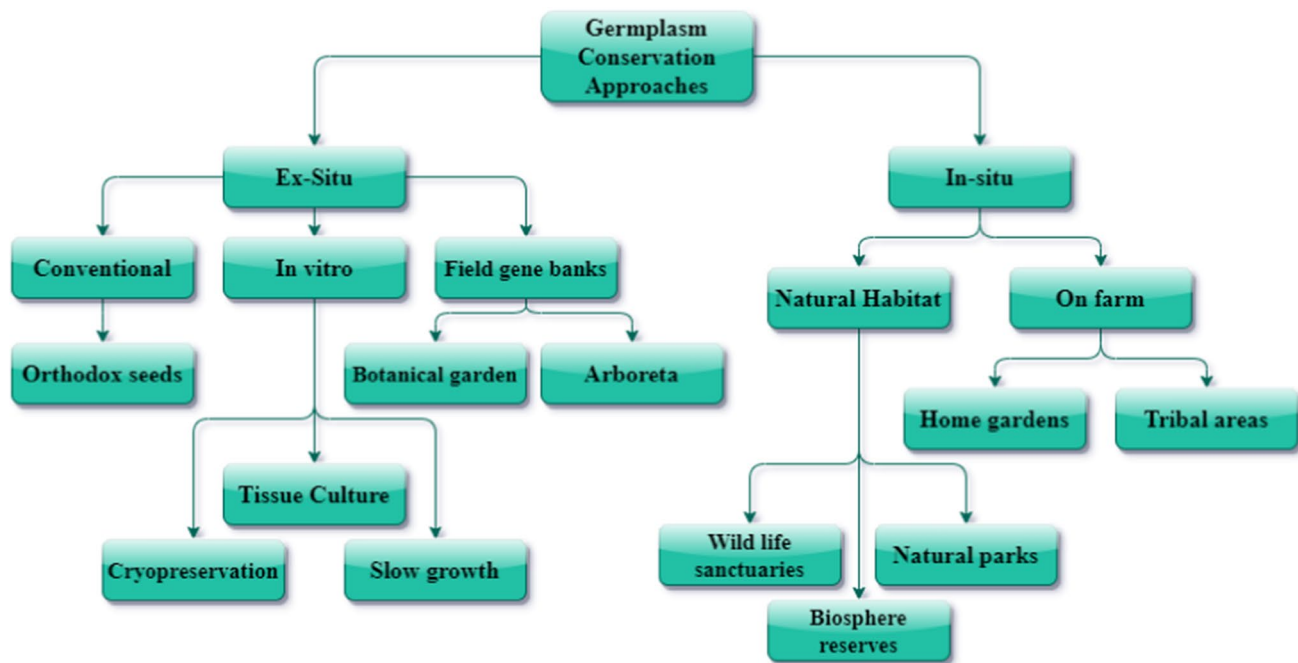


Fig. 5 Approaches devised for germplasm conservations

break down the cell walls and release the protoplasts. The CRISPR-Cas9 construct is mixed with the protoplasts in the presence of PEG (polyethylene glycols), which facilitates the plant cells' uptake of the CRISPR-Cas9 system. The transformed protoplasts are cultured under specific conditions to induce the formation of new plant tissue and regenerate whole plants. This method also allows the easy insertion of plasmids, proteins, and RNPs. This method has successfully been used for plants such as wheat, rice, tobacco, *A. thaliana*, soybean, lettuce, and maize (Sandhya et al. 2020). The lettuce mutants had an editing frequency of up to 46%. This method was also used for transgenic free editing of six *polyphenyl oxidase* mushrooms, and 30% reduced enzyme activity for browning was shown by mutant mushrooms (Waltz 2016). (iii) Particle gun method: This method involves the physical delivery of DNA-coated particles into plant cells using a high-velocity particle accelerator, typically a helium-driven gun. The CRISPR-Cas9 construct is coated onto microscopic gold or tungsten particles, which will be propelled into the plant cells. The DNA-coated particles are shot into plant tissues using a helium-driven gun. The particles penetrate the cell wall and cell membrane of the plant cells and deliver the CRISPR-Cas9 system into the plant cell's nucleus. This method has usually been used for genome editing of wheat, soybeans, and maize. Successful delivery of the CRISPR-Cas9 system has been reported in

brassica, potato, and maize (Andersson et al. 2018; Murovec et al. 2018; Svitashhev et al. 2015).

Conservation of crop genetic resources through germplasm collection and storage

Many scientists chronicled that aggrandizing behavior of modern breeding technologies has shrunk crop diversity (Rocha et al. 2008; Ruiz et al. 2002). Moreover, the changing agriculture systems, population pressure, disease/weed/pest infestation, policy/legislation change, indirect land clearing, reduced fallow, over-exploitation of species, direct replacement of local varieties, and climate change have contributed to the genetic erosion (Brodie et al. 2014). This situation has concerned scientists about the eroding genetic diversity. Germplasm global conservation programs like Millennium Seed Bank Partnership (MSBP) have been developed to address the conservation of native plants, including crop wild relatives (CWRs) (SCBD 2009). Germplasm can be conserved away from natural habitat (ex situ) or within the natural habitats (in situ).

Ex situ conservation

Ex situ conservation of germplasm involves the storage of plant genetic resources outside their natural habitat in

Table 4 Abiotic stress mitigation in plants by CRISPR-Cas9 technology

Plant species	Abiotic stress	Target gene	Gene function	References
<i>Arabidopsis</i>	Cold	<i>CBFs</i>	Transcription factor	Zhao et al. (2016a, b)
	Drought/Salt	<i>AtAITR family</i>	Transcription repressors induced by ABA	Chen et al. (2021a, b)
	Drought	<i>AtOST2</i>	Regulator for stomatal opening	Osakabe et al. (2016)
	Drought	<i>AREB1</i>	ABA-binding protein	Roca Paixão et al. (2019)
	Salt	<i>ACQOS</i>	Toll-interleukin1 receptor-nucleotide-binding leucine-rich repeat class protein	Kim et al. (2021)
<i>Zea mays</i>	Drought	<i>ARGOS8</i>	Down-regulator of ethylene	Shi et al. (2017)
<i>Oryza sativa</i>	Cold	<i>OSPRP1</i>	Proline rich protein	Nawaz et al. (2019)
	Cold	<i>OsMYB30</i>	Transcription factor	Zeng et al. (2020)
	Cold	<i>OsAnn5</i>	Annexin	Que et al. (2020)
	Cold	<i>OsAnn3</i>	Annexin	Shen et al. (2017)
	Heat	<i>OsHSA1</i>	Fructokinase-like protein	Qiu et al. (2018)
	Heat	<i>OsNAC006</i>	NAC TF	Wang et al. (2020a, b)
	Drought	<i>OsERA1</i>	ABA-signaling	Ogata et al. (2020)
	Drought	<i>OsSRL1,2</i>	Leaf rolling regulator	Liao et al. (2019)
	Salt	<i>OsRR22</i>	Cytokinin signaling	Zhang et al. (2019)
	Salt	<i>OsVDE</i>	Induces xanthophyll cycle	Wang et al. (2021a, b, c)
	Drought/Salt	<i>OsDST</i>	Drought-salt tolerance gene	Santosh Kumar et al. (2020)
	Salt	<i>OsNAC041</i>	NAC TF	Bo et al. (2019)
<i>Solanum tuberosum</i>	Salt	<i>Coilin</i>	Cajal regulating proteins	Makhotenko et al. (2019)
<i>Solanum lycopersicum</i>	Heat/ROS	<i>SIMAPK3</i>	MAP kinase un-regulating the gene expression of HSPs/HSEs'	Yu et al. (2019)
	Heat	<i>SIBZR1</i>	TF for brassinosteroid response	Yin et al. (2018)
	Parthenocarp	<i>SIHAA9</i>	TF for auxin response	Ueta et al. (2017)
	Heat/Parthenocarp	<i>SIAGL6</i>	MADS-box	Klap et al. (2017)
	Drought	<i>SILBD40</i>	Plant-specific TFs	Liu et al. (2020)
	Drought	<i>SIARF4</i>	Auxin response factors	Chen et al. (2021a, b)
	Drought	<i>SINPR1</i>	Salicylic acid receptor	Li et al. (2019)
	Salt	<i>SIHyPRP1</i>	Plant cell wall glycoproteins	Tran et al. (2021)
	Salt	<i>SIARF4</i>	Auxin response factor	Bouzroud et al. (2020)
<i>Glycine max</i>	Salt	<i>GmAIR</i>	Transcription repressors induced by ABA	Wang et al. (2021a, b, c)
<i>Triticum aestivum</i>	Salt	<i>TaHAG1</i>	Histone acetyltransferase	Zheng et al. (2021)

controlled conditions such as seed banks, field gene banks, or in vitro culture facilities. It is a crucial strategy for preserving the genetic diversity of plant species, particularly for those that are threatened by habitat destruction, climate change, or other environmental factors (ISTA 2018). Seed banks are facilities that store seeds in cold and dry conditions, such as refrigerators or freezers, to preserve their viability and genetic integrity. Seeds can be stored for several years, and in some cases, even for decades or centuries, depending on the species and the storage conditions (ISTA 2018; SCBD 2009). On the basis of storage capability, seeds can be divided into orthodox seeds (can tolerate freezing and drying, e.g., legumes, grains, cashews, citrus, etc.) and recalcitrant seeds (cannot survive > 0 °C temperature or 30–50% moisture drop, e.g., Jackfruit, mango, oil palm, etc.) (Nagendra et al. 2013). Seed banks are suitable

for conserving a wide range of plant species, including both wild and cultivated plants. On the other hand, in vitro culture involves the propagation of plants in sterile conditions using tissue culture techniques (Ding et al. 2008). It is a useful method for conserving plant species that are difficult to store as seeds, such as orchids or other rare plants, or species that do not produce viable seeds, such as bananas (Engelmann 2011). In vitro culture can also be used to regenerate plants from seeds or tissues that have lost their viability or genetic diversity. In vitro conservation involves techniques like in vitro conservation under slow growth (IVAG), cryopreservation, slow growth cultures, DNA storage, cold storage, and low-oxygen and low-pressure storage (Priyanka et al. 2021). The third type of ex situ germplasm conservation is field gene banks, which are living collections of plants that are maintained in their natural environment in the form of

crop plots or botanical gardens. They are suitable for conserving crop species and other plants that require specific environmental conditions to grow and reproduce. Field gene banks often include diverse collections of landraces, wild relatives, and other crop varieties, which can also be used for breeding programs and genetic research (O'Donnell and Sharrock 2018).

In situ conservation

It involves the conservation of plant genetic resources in their natural habitat or *in situ*, where they have evolved and adapted to their local environment. This approach aims to protect the natural ecosystems, species, and genetic diversity of plants and to support sustainable use and management of the resources (Cruz-Cruz et al. 2013). Protected areas, such as national parks, wildlife reserves, and biosphere reserves, are designated areas where natural ecosystems and their biodiversity are conserved and protected. These areas can serve as habitats for plant species and can provide opportunities for research, monitoring, and education (Nagendra et al. 2013). Moreover, the active involvement of local communities in the management and conservation of natural resources, including plant genetic resources, is also crucial. This approach to community conservation recognizes local communities' traditional knowledge and practices and seeks to promote their participation and ownership in conservation efforts. Another method is agroecosystem conservation, which involves the conservation and sustainable use of plant genetic resources in traditional agricultural systems, such as agroforestry, home gardens, and mixed-crop systems. These systems can support the genetic diversity of crops and wild relatives and can provide ecosystem services, such as soil conservation and water management; however, it is disadvantageous if the farmers switch to modern cultivars (Swaminathan 2002). One advantage of *in situ* conservation is that it allows species continuity while evolving new recombinant types, but the cost associated with retaining a high number of germplasm, environmental factors that contribute to contamination of germplasm, and the requirement of management surveillance are the factors that put *in situ* conservation to disadvantage (Huang et al. 2017).

Challenges and limitations

Breeding programs are evolving with the advent of science and technology. Plant breeding started with the direct selection of visual characters. However, it was not efficient as various environmental factors affect visual characters. Since then, modern breeding technologies have overcome the traditional ones because they are accurate and are not affected by environmental factors. However, the implementation of modern breeding technologies is not easier either. Most of

the developing countries lack the infrastructure needed and require cost operations. Although breeding has alleviated the environmental stresses from crops, it has also endangered the wide-type plants and local landraces. Moreover, inbreeding and genetic drifts eliminate species' favorable alleles, variation, and adaptability (Klap et al. 2017). Culturally important crops have lost their importance because biotechnology only favors agricultural products that are exclusively market-oriented (Ueta et al. 2017). Wild types and local plants are genetic reservoirs, and losing them also affects future improvement programs. The selection of limited traits decreases the variance and serves as a bottleneck for breeding programs. The number of cultivated crops is declining each decade. For instance, 10% of the area was cultivated by high yielding rice in 1970s, while in 1998, 70% of the area was covered by it, replacing the local varieties in Asia with genetically identical modern cultivars (Van de Wouw et al. 2010).

Modern breeding techniques have revolutionized plant breeding, but some limitations still need to be addressed. For instance, effective genomic selection requires a large amount of genetic diversity. It relies on identifying genetic markers that are associated with desirable traits and using those markers to select plants with those traits for further breeding. However, suppose the crop has been heavily bred for specific traits. In that case, there may be limited genetic diversity, making it more difficult to find markers that are associated with new and desirable traits (Heslot et al. 2015). This is particularly true for crops that have been bred for yield or other agronomic traits, where the focus has been on a narrow set of traits rather than overall genetic diversity. To address this limitation, plant breeders can use a variety of approaches to increase genetic diversity, including the use of wild relatives, landraces, and heirloom varieties (Smith et al. 2015). These approaches can help bring new genetic material into the crop and improve the effectiveness of genomic selection and other breeding techniques. However, these methods can also be time-consuming and labor-intensive and may not always be successful in achieving the desired results. The plant genome can be highly complex, with many duplicated and repetitive sequences. This can make it difficult to identify and manipulate specific genes using CRISPR, as the duplicated sequences can cause unintended mutations or affect the regulation of other genes. In addition, the plant genome can be much larger than the genomes of other organisms, which can make CRISPR more challenging to use in plants than in other organisms. Furthermore, the CRISPR system can sometimes have off-target effects, where it makes unintended cuts in non-target genes. These off-target effects can potentially have negative consequences for the plant, such as reducing yield or affecting the nutritional value of the crop (Cho et al. 2014). Moreover, modern breeding technologies can be expensive, especially for

small farmers and researchers with limited resources. This can limit the widespread adoption of these techniques (Smith et al. 2021).

Economic and regulatory barriers to the development and commercialization of new crop varieties

People are concerned about the effects of genetically engineered (GE) crops on the environment and consumers. For instance, health and environmental concerns are related to gene transfer to non-target proteins. The antibiotic-resistance genes are inserted into the plants as markers so that selection of plant cells with successful gene transfers can be made possible. There are chances that GE crops can transfer antibiotic resistance genes to the gut of the consumer (human, insect, or animal). Farmers have raised serious concerns regarding the resistance development in pests and insects that feed on BT cotton (Wolter et al. 2019). Many countries have developed strict regulations to address the issues regarding cultivating and commercializing genetically modified organisms (GMOs). The regulatory framework of GMOs follows two main approaches across the globe: (i) Product-based regulation of GM plants, where the focus is on the final product and not on the process used for production. This system sticks with the idea that the technique used for production does not pose any threat to health. So the risk is only associated with the final product regardless of the technology used for genetic engineering. The countries like Chile, Australia, Russia, Argentina, and US follow this system as it is reliable, simple, and compatible with World Trade Organization (WTO) free trade agreements. This also alleviates the restrictions regarding the regulation of GE crops (Ahmad et al. 2021). (ii) Process-based regulation of GM plants where the technique differentiates between GM and non-GM crops. This system works on the idea that the process used for the production of GE crops also influences the potential risks. This assumes that there is no natural transfer of genes across species, and any deviation denotes that crops have been produced using genetic engineering. In European Union (EU), GMOs are controlled by this system using EC regulation 258-97 (1997) and EU directive 2001-18-EC (2001) (Zhang et al. 2018a, b). This could be explained by an ongoing debate on the classification of genome-edited organisms produced using CRISPR technology, be regarded as GMOs or not. In some countries like India, New Zealand, and European Union, they are dealt as GMOs, while in the USA, Japan, Chile, Brazil, Australia, and Argentina, they are regarded as non-GMOs. Different countries make different regulations regarding

genome-edited crops, hindering their mass commercialization. A more realistic regulatory framework is required to bring the world under the safety regulation of one umbrella (Biswas et al. 2021).

One of the major demarcating factors in the cultivation and commercialization of GE crops is the high cost associated with their safety assessment and the complexity of the regulatory approval process. The average cost of safety assessment, gaining global registration, and authorization was estimated to be US\$ 35.01 million, and it took ~ 13 years to complete the process from project development to commercialized product (Kumar et al. 2020). Developing GE product seems easy compared to the complexity of safety assessment and regulatory approval. The mean approval time for the commercialization of GE crops is five years in the US and 7 years in the EU, which makes it unaffordable for public institutions and small companies (Smart et al. 2017). This serves as a bottle for small biotechnology companies to enter this sector.

Ethical and social concerns associated with the use of genetic engineering in agriculture

Studies have been conducted on the perception of people toward the application of genetic modification (GM) in food that differs in certain socio-demographic attributes, e.g., income, age, education, and gender (Christoph et al. 2008; Ganiere et al. 2006; Jurkiewicz et al. 2014; Kimenju and De Groote 2008; Todua and Gogitidze 2017). In the United States, men perceive fewer risks and are more involved in gaining benefits juxtaposed to women (Finucane et al. 2013). In some cases, gender and educational level had an insignificant effect on the public attitude toward GM. For instance, the attitudinal difference was found negligible when both genders were presented with tangible benefits of GMs (Frewer et al. 1996). Moreover, food disgust sensitivity, food technology neophobia, food neophobia, cultural values, religious affiliations, interpersonal networks, reporting, and press media also shape the social behavior of the public in response to new technology (Jin et al. 2023).

The proponents and developers of GE crops claim that these plants (like the ones produced by CRISPR) do not contain any foreign DNA. However, their opponents deem them as GMOs and want them to be dealt with by GMO regulations. Ethically, public concerns must be addressed by new plant breeding technologies (NPBTs) and the benefit associated with them. In the case of CRISPR, the final product does not contain a transgene, but in the EU, all NPBTs are regarded as GMOs regardless of the presence or absence of transgene (Eckerstorfer et al. 2019). Moreover, ethical, religious, and social beliefs like whether gene scientists are playing God and interfering with Mother Nature. People believe that GE crops pose unknown environmental threats, and these beliefs can

be attributed to poor communication between developers and consumers, lack of scientific knowledge, inadequate regulation, and lack of trust in developers. Despite the approval of legislation on the use of GE crops, people still reject them in China, Argentina, the US, Brazil, Canada, and India. In the context of public concern, countries like New Zealand and Japan have prohibited the cultivation of GE crops. In addition, people are also concerned about risk transgenes. Though the CRISPR product is transgene-free, it is not risk-free. In the case of multiplex CRISPR, off-target mutations must be carefully investigated for better safety assessments. The fear of the emergence of new diseases from GE crops is also there. It could cause poor development, early death, and tumor formation, as in cases of rodent experiments (Marshall 2007; Romeis et al. 2013). However, in many studies, it has also been reported safe, but the criticism of the methodologies employed during these experiments has also suggested that monitoring of the risks will remain unabated for some time (Bartholomaeus et al. 2013; Paul et al. 2010; Zdziarski et al. 2014).

If governments and developers believe that their products can improve production and alleviate world hunger, they should engage the public in a more agreeable manner to bridge the gap between the biotechnological sector and public distress. This emphasizes the need for mutually respectful dialog between legislatures and the public, more research on potential hazards of product, transparent regulatory processes, genuine community consultation, and public education influencing local knowledge of genetic engineering and gene cloning. Apparently, there is no food with zero health risks, be it natural or transgenic. For instance, glycoalkaloids like α -solanine and α -chaconine can be present in potatoes at harmful levels (Friedman and Rasooly 2013).

Conclusion

Plant breeding technologies have evolved significantly in recent years, allowing more precise and efficient manipulation of the genetic makeup of crops. This has resulted in the development of crop varieties that exhibit desirable traits, such as higher yield potential, better quality, and resistance, to pests and diseases. In the case of abiotic stress mitigation, the focus is on breeding crops that can withstand a range of environmental stresses, including drought, salinity, heat, and cold. These technologies have allowed breeders to develop crop varieties that are more resilient to a range of environmental stresses, including drought, salinity, heat, and cold. Through the use of tools such as molecular markers, genetic engineering, and genomic selection, breeders can select for specific traits that confer stress tolerance, resulting in crops that are better able to withstand adverse growing conditions. Moreover, the development of stress-tolerant crop varieties has the potential to improve global food security by increasing

the productivity and resilience of agriculture in areas that are prone to abiotic stress. This can help farmers to produce more food and improve their livelihoods, while also helping to meet the growing demand for food as the world's population continues to increase. Therefore, the continued development and implementation of plant breeding technologies is essential for achieving sustainable food production in the face of climate change and other environmental challenges. By leveraging these tools and techniques, we can help to ensure a stable and secure food supply for future generations.

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