



Advancements in Plant Breeding: New Techniques and Future Directions

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ABSTRACT

This review describes the advances in plant breeding-from traditional to state-of-the-art molecular methods emphasizing the role of innovation in MAS, QTL mapping, and genomic selection to bring about changes in a transformative manner through CRISPR/Cas9 gene editing technologies. Such innovative approaches have impressively increased the rate of precision with which crop varieties are produced to possess desirable attributes for resistance to diseases, abiotic stress tolerance, and improved nutritional levels. The present pace of progress in crop improvement has been further accelerated by the integration of omics technologies, high-throughput phenotyping, and precision agriculture. However, this review also discusses some of the ongoing challenges with respect to ethical issues, intellectual property rights, and ecological effects. While emerging technologies like artificial intelligence, machine learning, and synthetic biology could probably underpin the future of plant breeding, this needs to be pursued with due consideration for ethical and socio-economic consequences to ensure global food security.

Keywords: Sustainable Food Systems, Engineering Technology, Food Processing Innovations, Artificial Intelligence in Agriculture, Digitalization in Agri-Food.

INTRODUCTION

10,000 BC marks the beginning of modern human civilization when people still relied on hunting and gathering for subsistence. After 2300 years, primitive people began

domesticating sheep and other kinds of livestock. Potatoes, maize, and wheat were successively planted in different areas. The plough and systems of irrigation were invented about 2900 BC.

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Following this, the breeding of other crops accelerated (Agronomy P & Agriculture, 2021). During the Neolithic period, cultivated wheat and emmer wheat were discovered to be the first crops to exist in South-West Asia (Zohary et al., 2012). All of the basic grains and cereals that humans eat today were cultivated by Neolithic man around 20 or 30 millennia ago (Borlaug, 1983). There are now 2500 varieties of plants that have been domesticated (Dirzo & Raven, 2003) and 250 of them have done so completely (Harlan & Gepts, 2012).

The process of domesticating plants may be classified into the following phases: "collecting", "farming", and "breeding". At first, individuals began gathering plants from their natural habitats. Subsequently, they proceeded to grow the plants in their planting area and ultimately engaged in the process of visually selecting those plants that had desirable features. During the process of domestication, individuals deliberately chose certain crops in order to acquire advantageous traits from their wild counterparts. The breeding of seed crops was driven by specific characteristics such as bigger seed size, thinner seed coats, absence of dormancy, greater production, and a fixed development pattern. Species possessing these advantageous traits were the only ones selected for domestication (Meyer & Purugganan, 2013). The process of domesticating species took place in many regions rather than in just one (Meyer et al., 2012). Selection, being the earliest stage of plant breeding, is thought to have been unconsciously conducted by early humans throughout the early phases of crop domestication.

Plant breeding is fundamentally a fusion of crop genetics in plants to develop crops based on plant ideotypes. It is a continual process of selecting parent plants and their offspring for preferred traits. The practical idea of plant breeding began only with Mendel's principles of inheritance in 1865. As Mendel researched sweet-pea to create his ideas, it motivated others to use his

theory in practical plant genetics. Prior to the 1800s, big growers developed plants by selecting seeds from plants that had aesthetically pleasing characteristics and cultivating such plants. Following the restoration of Mendel's law in the 1900s, individuals started fusing superior kinds to create hybrids with the required features (Hickey et al., 2017). The significance of plant breeding is considerable in today's world. In 1965, Norman E. Borlaug initiated the "Green Revolution" by harnessing plant genetics to cultivate compact, fertilizer-dependent, and disease-resistant wheat breeds. The International Rice Research Institute likewise introduced a rice specie that is resistant to lodging and insensitive to photoperiod (Lee et al., 2015). The use of genetics and plant breeding may be the biggest developments in agriculture.

Agriculture, which started approximately 12,000 years ago, originally witnessed increasing output via expansion of land rather than yield increases, resulting in widespread famine until the 19th century (Fogel, 2004). Malthus forecasted famine due to rising populations surpassing the food supply (Malthus & Winch, 1992). Scientific improvements in late in the 1800s, notably in plant genetics and fertilizers, dramatically enhanced crop yields in the United States and Europe by the mid-20th century (Qaim, 2016). The Green Revolution of the 1960s, which brought high production crop types to Asia and Latin America and doubled or tripled yields while lowering poverty and hunger, caused the poorest nations to fall behind (Evenson & Gollin, 2003), (Qaim, 2017). Africa, however, did not gain as much owing to sluggish productivity development and significant population expansions, resulting in ongoing high hunger rates (Food & Nations, 2019). Figures demonstrate higher crop production and decreased undernutrition internationally during the 1960s, except in Africa where hunger remains persistent (Fan et al., 2005), (Qaim, 2017).

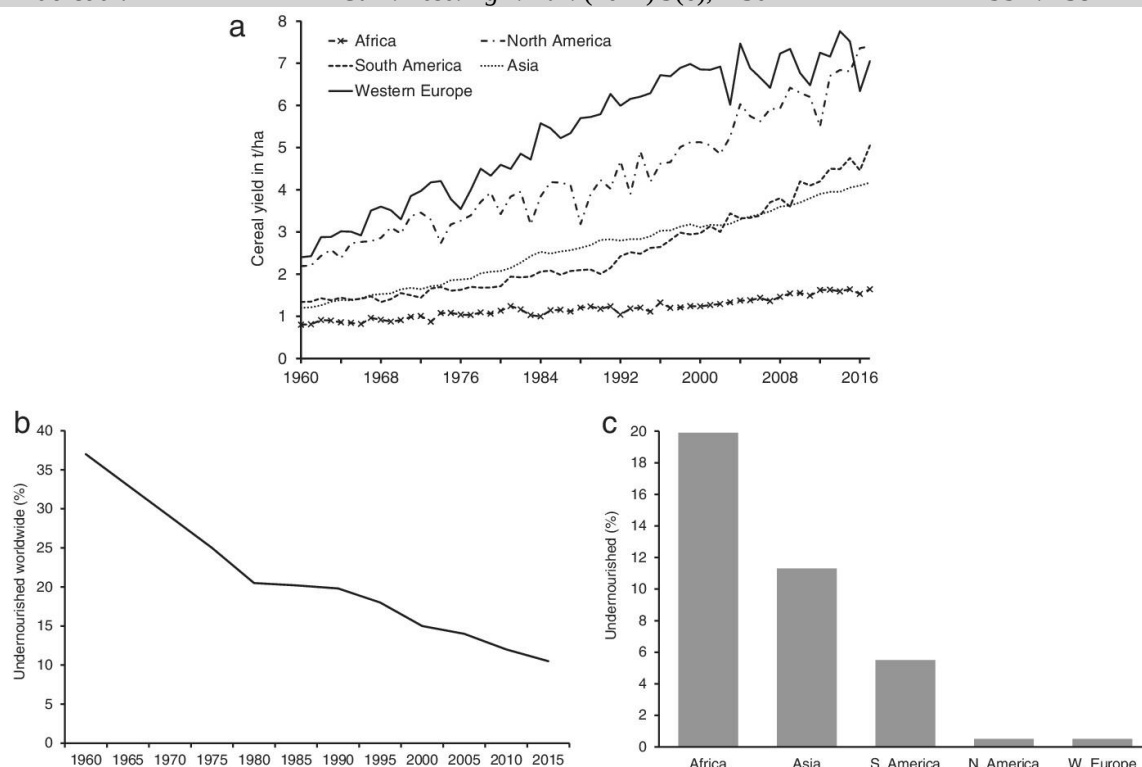


Figure 1 Worldwide Patterns in Agricultural Output and Food Insecurity. (a) Average grain yields by area, 1960–2017. (b) Rate of food deficiency globally, 1960–2015. (c) Rate of food deficiency by area, 2018. Source: Based on data from FAO (Food & Nations, 2019)

Over 800 million individuals experience prolonged hunger, and two billion people are undernourished, both of which have detrimental effects on their health (Development Initiatives, 2018; Food & Nations, 2019). Beyond band-aid solutions, "zero hunger" requires significant adjustments to the world's food systems (Meemken & Qaim, 2018), (Food & Nations, 2019; Springmann et al., 2018). Over the last century, there has been a tremendous improvement in agricultural output, yet hunger still exists, particularly in emerging nations. Future agricultural output is at risk of environmental harm and global warming brought on by innovations in plant breeding and increasing use of chemical inputs, which have improved food production (Masson-Delmotte et al., 2019; Wheeler & Von Braun, 2013).

Through increasing production, reducing reliance on chemicals, and enhancing climate adaptation, Emerging Plant Breeding Innovations (EPBIs), which include genetically modified organisms and gene-edited crops, provide viable answers. These

advancements could lead to higher agricultural yields, reduced reliance on synthetic pesticides and soil enhancers, improved crop resilience to environmental stresses, decreased post-harvest wastage, and the production of more nutrient-dense foods (Bailey-Serres et al., 2019; Eshed & Lippman, 2019; Zaidi et al., 2019). Nevertheless, because of worries about the environment, economy, and health, these technologies are met with strict controls and public distrust (Sciences et al., 2016; Shew et al., 2018; Stone, 2010). Particularly, transgenic GMOs are often viewed with great skepticism. There are still a lot of people worried about potential harm to their health and the environment, despite the fact that 30 years of study and commercial uses indicate that genetically modified crops are not any riskier than traditionally cultivated crops (EASAC., 2013; Leopoldina, 2019; Sciences et al., 2016). Since GMOs are more closely regulated in terms of safety than any other technology used in agriculture, these worries have led to significantly harsher rules overall (Qaim, 2016). Concerns about market dominance and uneven benefit distribution are both social and

economic, as the majority of genetically modified organisms (GMOs) that have been marketed to far have been created by big, multinational corporations (Stone, 2010). Concerns about the more modern crops that have undergone gene editing have also been raised (A. M. Shew et al., 2018).

Conventional Plant Breeding Techniques

New plant cultivars are created by conventional breeding, which does not use cutting-edge molecular breeding techniques. The law of inheritance is not broken by conventional breeding. According to the better performance of chosen characteristics, plants are chosen via a selective breeding process known as conventional breeding. Through hybridization, new cultivars are created by combining the necessary traits that are obtained from closely related individuals (Lamichhane & Thapa, 2022). Hybridization is the process by which conventional breeding achieves variability. The most significant genotype is found by phenotypic selection. Following evaluation, the chosen cultivars are issued as varieties. Similar parents do not create diversity in traditional breeding because there is no gamete segregation (Acquaah, 2009). To release a new cultivar, conventional breeding is a more time-consuming method that often takes more than ten years (Bharti & Chimata, 2019). The phenotypic manifestations of crops are too relied upon in conventional breeding to distinguish better ones. Because genotype by environment interactions greatly impact phenotypes, well-chosen cultivars are thus not error-free (Lema, 2018). Conventional breeding relies on the experiences, findings, and judgmental abilities of breeders since it is an applied science (Allard, 1961). For example, Burbank, the potato that is produced most widely in America, was found by chance assessments of producers using traditional breeding techniques (Smith & Fehr, 1987). The primary cause of conventional breeding's uneven results is an over-reliance on subjective analysis. Whereas modern plant breeding is particularly objective and scientific in character. Consequently, contemporary

breeding methods are more effective and prolific (Jiang, 2013b).

Pure-line selection:

One of the oldest techniques in plant breeding is screening within the same population. In certain self-pollinating plants, such as wheat and rice, pure line selection is often seen (Bresghehlo & Coelho, 2013). Progenies generated by self-pollination from only one homozygous parent are known as pure lines. Pure line selection cannot produce novel genotypes since the genetic makeup of progenies is identical to that of their parents. Following Johannsen's presentation of pure-line theory in 1903, pure-line selection became operational (Poehlman JM, 2012). Studies on wheat yield heterosis increased by 15–25% compared to the parental line with greater performance via pure line selection (Lane, 1981). Pure lines are frequently used in situations where product homogeneity is highly valued in the market because of their even genetic makeup. Pure line phenotypic variations are solely caused by environmental factors. Because of this poor heritability, selection in pure lines is thus ineffectual (Begna, 2021).

Better homozygous parental genotypes are picked using this procedure, and the plants self-pollinate. Each parental genotype's progenies are grown and evaluated separately. Uniformity and desirable features are assessed in plants. Progenies of the second generation with better kinds are subjected to first yield testing. Then, with check varieties from chosen persons present, multi-location testing are carried out. After several years of testing across multiple locations, high-performing strains are eventually released as a novel cultivar. The entire process typically takes about six to seven years to complete (Lamichhane & Thapa, 2022).

Mass selection:

Both self- and cross-pollinated crops are subjected to mass selection (Allard, 1999). By raising the frequency of desired features, mass selection is used to increase base population productivity. over mass selection, the landraces that have been passed down over the

millennia are enhanced. Desired plants are chosen to undergo further breeding and research initiatives, while off-type plants are eliminated from the farmed population. Phenotypic expression is the basis for those plants' selection. If the chosen qualities are highly heritable, this kind of selection will be more successful (Brown & Caligari, 2011). The occurrence of diversity attributed to additive genetic factors renders mass selection highly effective (de Wolff, 1972). This process can be executed. This process can be performed through single-parent selection (with control over one type of gamete) or dual-parent selection (with the regulation of both male and female gametes). Nevertheless, when both male and female gametes are managed, dual-parent mass selection is highly efficient, as both parents are chosen (Chao-Ying et al., 2010).

Using this strategy, a landrace is chosen based on how well it exhibits characteristics like as height, resistance to disease, and maturity timing. When the chosen person reaches maturity, they are harvested from the field. The collected seeds are combined and passed on to the next generation. The crops are produced in large quantities from mixed seeds in their second year and contrasted with a control variety. A first yield experiment is conducted. The varieties are evaluated over the next three to four years at many places with a check variety present. The chosen plant is marketed and issued as a variety in the seventh year of selection (Lamichhane & Thapa, 2022).

Hybridization:

Hybridization is the process that produces hybrids through the combination of genetically distinct parents. This might include individuals belonging to the same species, individuals with distinct genetic backgrounds, or a blend of man-made and natural phenomena. In order to create genetically superior kids, characteristics from many parents are combined. In 1760, German botanist Joseph Koerauter was the first to use hybridization to improve crops (Begna, 2021). Although hybridization produces recombinant genes with potentially beneficial traits, it leaves the

plant's genetic composition unchanged. Additionally, this procedure is utilized to get beyond many reproductive obstacles that come up during typical sexual crossings, such as male or female infertility, sexual incompatibility, etc. (Mwangangi et al., 2019). These two hybridizations occur most frequently:

a. Interspecific hybridization:

It involves the breeding of two different types that are typically not sexually compatible with each other. Another name for this technique is broad crossing. This technique is often used to combine advantageous features from two distinct species or to transfer characteristics from wild relatives (Lidder & Sonnino, 2012). When a particular group of characters is not accessible, this technique is often used. Due to pre- and post-fertilization restrictions to interspecific hybridization, not all species are capable of hybridization. Barriers to pre- and post-fertilization stop the development of embryos and decrease the vitality of existing embryos. Pre-fertilization hurdles include pollen incompatibility and failure to germinate, whereas post-fertilization barriers include inadequate vigor, hybrid sterility, seed mortality, and seed abortion (Murray BG, 2016).

b. Intraspecific hybridization:

Commercial plant breeding uses it extensively since it is one of the most effective hybridization techniques. There are no impediments to hybridization since the mating population is of the same species. When combining favorable features from multiple plants in the same species, this strategy is often used to create variants for selection (Murray BG, 2016). Intraspecific hybridization can lead to either a Basic or Advanced Cross depending on how many parents are participating. A basic cross occurs when two parents are crossed to produce F1 hybrids, which are subsequently backcrossed or self-pollinated to generate F2. In contrast, an advanced cross involves the combination of more than two parents to create F1 hybrids. An advanced cross is employed to integrate desirable traits from multiple parents into a single hybrid offspring (Lamichhane & Thapa, 2022). **Table 1.**

Feature	Conventional Plant Breeding	Modern Plant Breeding
Basis	Phenotype (appearance)	Genotype (genes)
Accuracy of Gene Line Determination	Unreliable	More accurate
Time to Release New Variety	More time consuming	Less time consuming
Variability Creation	Hybridization	Genomic selection, enviromics, High Throughput Phenotyping (HTP)
Gene Selection	Primarily dominant genes; recessive alleles require lengthy procedures	Recessive alleles can be selected using markers and gene site identification
Effectiveness	Less effective, relying on breeder skills and subjective analysis	More effective and reliable, based on scientific research
Technical Skills Required	Less technical skills and genetic knowledge	Demands greater technical expertise and understanding of genetic science
Cost	Less expensive, using local techniques and tools	Extremely costly, demanding advanced equipment and techniques

Molecular Breeding Techniques

Marker-Assisted Selection (MAS):

With the introduction of marker-assisted selection (MAS), a new chapter in the history of molecular selection has started (Gupta et al., 2010), which involves the alteration of genomic areas implicated in desirable characteristics by DNA markers (Ribaut & Hoisington, 1998). The advantage of MAS over visible phenotypic selection is that it increases the targeted trait's selection effectiveness by linking the trait that is important to a molecular marker (Jiang, 2013a).

Any crop improvement program's primary goal is to identify productive plants with the necessary features. Conventional plant breeding involves longer development times for new cultivars and a greater likelihood of omitting the desired characteristic. On the other hand, by decreasing the impact of the

environment and boosting selection efficiency, MAS enhances a number of characteristics in agricultural plants (Tester & Langridge, 2010). However, a number of issues, including genetic background (Charcosset & Moreau, 2004), QTL precision, reliability (Melchinger et al., 1998), low marker-gene linkage, as well as high costs of input, may hinder the efficacy of MAS.

Nevertheless, numerous factors may limit the efficiency of MAS, including genetic background, QTL precision, and dependability, the low linkage between QTLs and markers, (Sharp et al., 2001), costly inputs (Brennan et al., 2005), (Brumlop & Finckh, 2011), a limited number of molecular markers and their constrained fury of polymorphism, as well as the lack of knowledge between molecular biologists and plant breeders (Collard & Mackill, 2008).

Plant breeding has employed various indicators, including structural (characteristic-specific), protein-based (isozyme), cellular (chromosome-targeted), and DNA markers. However, DNA-based markers are predominantly used by plant breeders in marker-assisted selection (MAS) for a range of traits and crops (Madina et al., 2013). Efficient MAS in plant breeding necessitates dependable DNA markers, qualitative and quantitative verification of genetic material (DNA), suitable marker analysis methods, comprehensive genomic marker coverage, high degrees of polymorphism, and the genetic characteristics of markers such as co-dominance (Collard & Mackill, 2008), (Mackill & Ni, 2001), (Mohler & Singrün, 2004), (Bohar et al., 2020).

Crop improvement projects throughout the globe have made substantial use of recent developments in molecular breeding, including single nucleotide repeats (SNPs), insertion/deletion mutations (Indels), genomic sequencing (GS), genotype-by-sequencing (GBS), and PCR-based approaches (Platten et al., 2019), (Bohar et al., 2020).

Advantages of Marker-Assisted Breeding:

There are several benefits related to using DNA markers to screen and choose plants in breeding programs, which attracts plant breeders.

- 1) Plants may be screened as seedlings or even as seedlings thanks to the availability of DNA marker-based genotypes that can be acquired from virtually any plant tissue. This makes it easier to select for features (such as grain or fruit quality, male sterility, and photoperiod sensitivity) that are only expressed in mature plants early on. MAS enables controlled pollination, as in marker-assisted recurrent selection, using preflowering genotypic information.
- 2) With the use of markers, traits that are expensive, lengthy, or difficult to assess phenotypically might be chosen. Because DNA markers are mostly insensitive to environmental variation, selection is carried out more effectively.

- 3) Single-plant selection is feasible, while phenotypic selection is not always feasible. If marker information is used for selection, poor heritability is not an issue.
- 4) Each individual genetic component that contributes to a characteristic that has a complicated inheritance pattern may be chosen independently. It is possible to sustain and eventually repair many characteristics that typically only exhibit good or bad effects when combined.
- 5) Recessive genes may be kept eliminating the need of testing for offspring in every generation since co-dominant markers can be utilized to distinguish between homozygous and heterozygous plants. In backcrossing, DNA markers may reduce linkage drag surrounding the gene of interest and decrease the number of generations required to reconstruct a recurrent parent's reproductive history.
- 6) Parents might be selected for crossing programs using markers. They may aid in minimizing diversity to protect gene complexes accumulated in superior inbred germplasm or increasing variety to take advantage of heterosis (Dale Young, 1999; Edwards & McCouch, 2007; Hospital & Charcosset, 1997; Koebner, 2004; Koebner & Summers, 2003).

Genomic Selection:

Genomic selection (GS), a different marker-based selection method, makes the use of widely distributed, genome-wide molecular markers to more successfully enhance complex traits (Meuwissen et al., 2001). Every marker helps predict phenotypic values in GS, so there are not any important tests involved. This includes the main and minor QTL for the complicated attributes (Bernardo & Yu, 2007). A training population (TP) along with one or more breeding populations (BP) are needed for GS (Bernardo, 2008). Breeding schemes are frequently structured to include fewer repetitions in the initial, segregating generations and increased repetitions in the subsequent generations, incorporating larger plot sizes and multi-site evaluations (Bernardo, 2002). Breeders should take into account the

cost of implementation and the impact on the genetic gain of the tiered system used in the breeding program when planning the integration of GS. Genomic selection in the early generation causes a greater reduction in the breeding cycle through the elimination of a few selfing cycles (Hickey et al., 2014). The breeding cycle is shortened by cycling a select group of people with high GEBVs back into the breeding pipeline as parents. The breeding cycle would not be shortened by integrating GS at later generations to evaluate the efficiency of the lines as a whole, but selection precision may be improved. The use of GS attracts breeders in later generations due to genotyping cost decreases; yet, in later stages, phenotypic selection outperforms GS in terms of advantages. (Endelman et al., 2014) discovered a 5% boost over phenotypic selection when he used GS to inbred lines. To maximize genetic gain, several GS systems in active breeding programs should be assessed to determine the trade-offs between cycle time and selection precision (Rutkoski et al., 2017). (Bassi et al., 2016) examined the effects of genomic and phenotypic selection in F2, F3, F4, and F7 of different wheat breeding programs. An initial segregating generation, such the F2, had the most genetic gain through GS at 0.47 per year, which was six times greater than from traditional mating. However, the expense of genotyping was highest in the early generations since there were many individuals to genotype. They also assessed schemes for middle and subsequent generations, and they discovered that, in terms of expenses and genetic gain advantages, using GS in the F3 and F4 generations was preferable to applying it in the F7 generation. When GS accuracy in forecasting is unreasonably high, several cycles of GS are beneficial. As a result, in scenarios with poor prediction accuracy, GS might contribute to negative selection by eliminating underachievers (Longin et al., 2015). To attain equilibrium between genomic and phenotypic selection concerning the genetic advantages and costs related to the breeding program, it is recommended to conduct one or two rounds of

GS followed by a single round of PS (Rutkoski et al., 2015).

Using 5568 SNPs, the GEBVs of 206 landraces from 32 nations were assessed for wheat rust resistance breeding using the GBLUP and BayesR techniques. The three rusts resistance had prediction accuracies ranging from 0.27 to 0.44 with GBLUP and 0.30 to 0.38 with BayesR, in that order. Prediction accuracy was increased by using PCR-based genotyping, which uses diagnostic markers for known rust-resistance genes. The results of this GS investigation in wheat indicated that the forecast accuracy was encouraging for breeding wheat to resist rust (Daetwyler et al., 2014).

Genomic selection (GS) in lentil breeding was assessed with the use of one genotype $\times$ environment interaction (GEI) model, two multiple-trait models, and nine single-trait (ST) models. When comparing single-trait models to GS models with GEI and multiple traits, the former demonstrated better prediction accuracy for traits with low heritability. The range of prediction accuracies was 0.19 to 0.89 across settings and 0.36 to 0.85 among populations. Accuracy levels, however, varied widely across groups (Haile et al., 2020). For soybean, the genomic selection (GS) evaluation of protein, oil, and yield in 483 top-tier lines utilizing 5403 single nucleotide polymorphisms (SNPs) produced forecast accuracies of 0.81, 0.71, and 0.26 for protein, oil, and yield, respectively, throughout the dataset. Among bi-parental recombinant inbred lines (RILs), the accuracies were 0.55, 0.30, and 0.12, whereas across bi-parental RILs, the values were 0.60, 0.52, and 0.13. The density of markers had a less significant impact on the reliability of prediction in contrast to the size of the training population (Stewart-Brown et al., 2019). For variables including seed production and days to flowering, genomic forecasting in chickpeas employing 3000 DArTseq markers revealed forecast accuracies ranging from 0.138 to 0.912. Among the six GS models that were evaluated, no discernible differences were discovered (Roorkiwal et al., 2016). When

genotype $\times$ environment interaction (GEI) was analyzed in chickpeas, DArTseq prediction accuracy was greater than that of genotyping-by-sequencing (GBS) (Roorkiwal et al., 2018). A 16% improvement in mean yield for chosen hybrids over all possible hybrids was achieved in rice hybrid breeding as a consequence of GS using 278 hybrids from 210 RILs to forecast GEBVs [180]. Compared to other hybrids, maize "AQUAmax" hybrids that were created using precise phenotyping demonstrated greater yield stability under tension from the water (Gaffney et al., 2015). In sorghum, phenotypic selection yielded lower genetic gains than genetic selection (GS), particularly for massive populations and polygenic characteristics. Annual GS model updates increased genetic gain and forecast accuracy (Muleta et al., 2019).

Challenges for GS in Crop Improvement:

A major obstacle to genomic selection (GS) is genotype-environment interactions (GEI), wherein genotype scores might vary across settings and impact environmental-conditioned phenotypes (Boer et al., 2007), (Cooper, 1999). In multi-environment trials (METs), in particular, this variability may decrease heredity and prediction accuracy (Belamkar et al., 2018). By assembling comparable settings, traditional approaches lessen this, which is advantageous for creating GS training datasets (Van Eeuwijk et al., 2019). Additionally, it's critical to handle testing environments effectively (Xu, 2016).

Non-additive genetic influences, such as dominance and epistatic interactions, add complexity to genomic selection (GS). Including these influences can enhance predictive accuracy, but may decrease narrow-sense heritability (Su et al., 2012), (Sun et al., 2014), (Bouvet et al., 2016). For instance, including dominance effects enhanced forecasts in hybrids of maize (Dos Santos et al., 2016), and epistasis has proven critical for characteristics like rice blooming time and corn nutritional content (Wang et al., 2015), (Ahsan et al., 2019). Dominance variance, on the other hand, is a crucial emphasis since epistatic variance typically decreases with

more loci (Wang et al., 2012), (Mäki-Tanila & Hill, 2014), (Denis & Bouvet, 2013), (Hill & Mäki-Tanila, 2015).

However, cost-effective genomic selection (GS) depends on how trait heritability, training number of individuals, and phenotyping and genotyping expenses are balanced. When there are numerous functional chromosomal segments and a large training population, GS is especially beneficial for characteristics with poor heritability (Rajacic et al., 2016), (Heffner et al., 2010), (Wong & Bernardo, 2008). GS success may be limited by high early-stage genotyping costs and the inclusion of unrelated families, but economic performance may be enhanced by lowering genotyping costs and using predictions from several generations (Hickey et al., 2014), (Rajacic et al., 2016). To further improve applicability and cost-effectiveness, open-source GS networks for high-throughput genotyping and phenotyping might be established (Hickey et al., 2014).

Gene Editing Technologies:

Molecular breeding and molecular biology have been considerably influenced by the emergence of gene-editing technologies. These innovations have been primarily propelled by site-specific nucleases (SSNs), which encompass CRISPR/Cas9, zinc finger nucleases (ZFNs), homing endonucleases (HEs), meganucleases (MNs), and transcription activator-like effector nucleases (TALENs) (Gaj et al., 2013), (Adli, 2018). Rare endonucleases called HEs and MNs have a restricted number of target sites but may detect vast DNA lengths (Cohen-Tannoudji et al., 1998), (Rasheed et al., 2021). Conversely, ZFNs and TALENs provide increased specificity by assembling numerous zinc fingers or TALE modules, respectively (Klug & Rhodes, 1987), (Kim et al., 1996), (Christian et al., 2010). While CRISPR/Cas9 only requires the redesign of short guide RNAs (sgRNAs), these methods, while efficient, have the drawback of requiring the redesign of proteins for distinct genomic targets (Adli, 2018).

The CRISPR/Cas9 system, originally identified in *Escherichia coli* (Ishino et al., 1987) and later characterized by Horvath's group (Barrangou et al., 2007), is an affordable and accessible technique for gene disruption. This technique was further simplified by substituting sgRNAs for crRNA and tracrRNA, which are used by this system to aim for particular patterns of DNA (Jinek et al., 2012). A breakthrough in gene editing has been seen with its ability to modify genes in live cells (Cong et al., 2013), (Jinek et al., 2013), (Mali et al., 2013).

CRISPR/Cas9 involves actions including choosing the target place, single guide RNA (sgRNA) design, transformation vector delivery, and screening in plant genetic alteration. This method uses a CRISPR-based toolkit to enable the simultaneous modification of many genes (Puchta, 2017). CRISPR/Cas9 has been extensively used to increase agricultural quality and quantity of output, and stress tolerance (Ricroch et al., 2017) since it was first used in plants in 2013 (Shan et al., 2013).

CRISPR/Cas9 and Other Gene-Editing Tools:

Molecular breeding has been transformed by CRISPR/Cas9 and other gene-editing technologies that enable accurate alterations to plant genomes. With the use of these instruments, crops with superior qualities like increased nutritive power, disease defense, and increased ability to withstand abiotic stress can be developed (Guo et al., 2023). Among other gene-editing techniques, CRISPR/Cas9 works by directing the Cas9 nuclease to a particular DNA sequence where it creates double-strand breaks using a guide RNA. Targeted mutations or insertions are made easier by this process, which modifies the way genes operate. Crops with characteristics like pathogen resilience, environmental stress adaptation, and nutrient density may be improved thanks to this level of editing accuracy (Wang et al., 2021).

CRISPR/Cas9 has been effective in the development of disease-resistant crop kinds. To enhance resilience against the bacterial blight pathogen *Xanthomonas oryzae*,

rice has undergone modification of the *OsSWEET14* gene. When compared to unedited controls, this alteration significantly reduced the severity of the illness and reduced the incidence of pathogen infection by as much as 80% (Wang et al., 2021). Similarly, wheat with a 60% decrease in disease symptoms after the TaMLO gene was altered to provide resistance to powdery mildew (Gaikwad et al., 2020).

Crops' increased nutritional value is another benefit of CRISPR/Cas9. Targeted alterations in the *OsPDCD5* gene, for example, enhanced grain production and nutritional content in rice, including greater amounts of zinc and iron (Dong et al., 2021). In a different research, rice that has had its *GW2*, *GW5*, and *GW6* genes edited showed a significant rise in both the amount of protein and critical minerals, with the amount of protein rising by up to 30% and zinc content rising by 40% (Xu et al., 2016), (Achary & Reddy, 2021). Furthermore, by altering the genes for phytoene synthase (*PSY*) and phytoene desaturase (*CRTI*), CRISPR/Cas9 was able to boost the number of carotenoids in rice by 50% (Dong et al., 2020). CRISPR/Cas9 editing has been utilized to enhance the amount of amylose in wheat, which has led to increased amounts of resistant starch (RS), which is good for human health. The RS content increased by 25% as a result of this adjustment (Qin et al., 2023). Moreover, the method has been used to lower the gluten level, resulting in wheat cultivars with lower gluten content. These types are more suited for those who are sensitive to gluten since they have been shown to have a 50% lower gluten level (Sánchez-León et al., 2018). Abiotic factors that may have a major impact on agricultural yields include salt, drought, and high temperatures. Utilizing CRISPR/Cas9 has increased crop resilience to various stressors. For instance, transgenic plants exhibiting a 40% increase in survival rates under drought circumstances have been produced by altering the *DREB1A* gene in *Arabidopsis* and rice, conferring increased drought resilience (Zhang et al. 2020). In a different research, the *SOS1*

gene in rice was altered using CRISPR/Cas9, increasing the plant's resilience to salt stress and enhancing growth and yield by 30% in salinized environments (Ma et al., 2017).

Though there are many potential advantages to gene-editing technology, there are also moral and legal questions. Genetically modified organisms (GMOs) are seen and accepted differently by the general public, and certain stakeholders have expressed worries regarding the safety and long-term effects of gene editing. Globally, different nations have adopted different regulatory frameworks for crops that have undergone genetic engineering, with some enacting stricter laws than others. While other areas, including the US, have more lax rules that concentrate on the final product rather than the technology used to make it, the European Union, for instance, has strict restrictions on gene-edited crops that require thorough risk evaluations and labeling (GRIN, 2023).

To address these concerns and guarantee that the advantages of gene-editing technologies are achieved in a responsible and ethical way, it is imperative that scientists, politicians, and the general public have continuous communication as these technologies continue to progress.

CRISPR/Cas9-Mediated Molecular Breeding Improves Crop Quality:

CRISPR/Cas9 may be utilized to enhance the effectiveness of the primary food crops. For instance, the GS3 gene, that controls grain length in rice, was altered to create longer grains with a higher market value. Moreover, OsAGAP and OsPDCD5 genes were chosen to enhance grain production and plant structure (Fan et al., 2006), (Shen et al., 2018). Additionally, CRISPR/Cas9 has been used to increase the amount of important dietary vitamins and minerals in rice, improving its nutritional quality (Achary & Reddy, 2021). Genome editing with CRISPR/Cas9 has greatly enhanced rice grain quality. Researchers have improved the aroma of rice, making it more enticing to customers, by focusing on genes such as BADH2. In addition, to enhance the quality of food and

cooking, genes controlling the amount of amylose and protein in grains were altered (Yang et al., 2022), (Fu et al., 2022). By deleting genes like TaGW7 and TaGW2, CRISPR/Cas9 has been used in wheat to improve grain shape and boost 1000-grain weight. Furthermore, technology has facilitated the creation of low-gluten wheat varieties, resolving the issue of human gluten sensitivity (Wei Wang et al., 2018), (Wang et al., 2019), (Sánchez-León et al., 2018).

Through the production of waxy corn types, CRISPR/Cas9 has increased the amylopectin concentration in maize, improving its quality. The technique targets genes involved in protein and oligosaccharide production in soybeans to improve taste and nutritional quality. Similarly, gene editing has added aromatic qualities to sorghum, increasing the crop's value (Gao et al., 2020), (Le et al., 2020), (Zhang et al., 2022). Additionally, CRISPR/Cas9 has been used to enhance the nutritional value of industrial crops such as peanuts, cotton, and rape. For example, cotton seed with a higher oil content has been produced by modifying the GhFAD2 gene. FAD2 and FAE1 gene alterations have been linked to increased oleic acid and decreased erucic acid concentrations in rape, respectively. Furthermore, gene editing in peanuts has resulted in a decrease in saturated fatty acids and a rise in oleic acid, both of which improve health outcomes (Chen et al., 2021), (Huang et al., 2020), (Tang et al., 2022).

Omics Technologies in Plant Breeding

Genomics:

The study of genes and genomes, with an emphasis on their structure, function, evolution, mapping, epigenomics, mutagenomics, and genome editing, is referred to as genomics (Muthamilarasan et al., 2019). Understanding genetic diversity is essential to improving crop species and breeding efficiency. This field of study plays a key role in this. By examining chromosomal organization and sequence variation, structural genomics makes it easier to create physical and genetic maps that show relevant features.

An knowledge of gene functions and how they regulate phenotypes is made possible by functional genomics. The study of epigenetic changes, comprising DNA methylation and histone modifications, is known as epigenomics. While pangenomics refers to the whole genome of every member of a species, including a dispensable genome that is either partly shared or unique to each person, metagenomics studies genetic alterations in mutant features (Tettelin et al., 2005). In agricultural sciences, mutagenesis and the pangenome are highlighted by recent omics techniques called mutagenomics and pangenomics (Golicz et al., 2016, {Goh, 2018 #157), (Muthamilarasan et al., 2019).

Structural Genomics:

For crop breeding programs, structural genomics maps and tags genes of interest using genetic markers. Single nucleotide polymorphisms (SNPs), amplified fragment length polymorphisms (AFLP), random amplified polymorphic DNA (RAPD), and other PCR-based methods are examples of marker techniques that fall into the non-PCR-based category. DNA polymorphism is detected by non-PCR-based RFLP by hybridizing labeled DNA probes to a Southern blot of DNA that has been digested by restriction enzymes (Agarwal et al., 2008). AFLP involves selectively amplifying restriction fragments from a genomic DNA digest using PCR (Rabouam et al., 1999), while PCR-based RAPD amplifies random DNA segments using single primers with random sequences (Vos et al., 1995). Single nucleotide variants (SNPs) in a genome are found by sequencing genomic PCR results from several subjects (Appleby et al., 2009). Microarray hybridization-based diversity array technology (DArT), a high-throughput method, genotyping a large number of polymorphism loci across the genome (Jaccoud et al., 2001).

Crop characteristics are studied using genome-wide association studies (GWAS) and quantitative trait loci (QTL) research. Using molecular markers such as amplified fragment length polymorphisms (AFLPs) and single

nucleotide polymorphisms (SNPs), QTL analysis connects specific genotypes to complex phenotypes (Kearsey, 1998), (Challa & Neelapu, 2018). GWAS uses SNPs mainly to identify genetic variations associated with characteristics and investigate the links between these variants and phenotypes within populations (Challa & Neelapu, 2018). Genome-wide association studies (GWAS) have improved crop resilience to abiotic stress by pinpointing quantitative trait loci (QTLs) connected to yield in maize under thermal and hydric stress (Millet et al., 2016), single nucleotide polymorphisms (SNPs) related to arid conditions in sorghum (Lasky et al., 2015), (Spindel et al., 2018), and loci associated with drought resistance in rice (Guo et al., 2018). Agronomically significant features in crops are also greatly influenced by structural variations (SVs), as shown by the GWAS of soybean and *B. napus* (Gabur et al., 2018), (Luo, 2015), (Zhou et al., 2015). Utilizing genotyping-by-sequencing (GBS) in conjunction with marker-assisted selection (MAS) has improved hybrid breeding for increased agricultural output and quality (He et al., 2014). Phenotypic variety in model plants and crops is shown by multiparent mapping, which includes nested association mapping (NAM) and multiparent advanced generation intercrosses (MAGIC) (Kover et al., 2009). With genotype-phenotype connection investigations discovering QTLs confirmed using functional genomics techniques, MAGIC populations are perfect for breeding enhancement.

Functional Genomics and Mutagenomics:

Gene functions are evaluated by functional genomics using knowledge from structural genomics (Grabowski et al., 2016). With the use of biotechnological instruments, genes may be found, isolated, cloned, characterized, and overexpressed or knocked out lines can be produced for functional transgenic studies (Muthamilarasan et al., 2019). Suppression subtractive hybridization (SSH), expressed sequence tag (EST), and cDNA-AFLP sequencing were used to identify candidate genes prior to genome sequencing; however,

next-generation sequencing (NGS) made these methods less laborious (Muthamilarasan et al., 2019). Genes associated with disease resistance, stress tolerance, and yield prediction have been identified in crops through genome sequencing. Tools for genome editing, such as transcription activator-like effector nuclease (TALEN) and CRISPR/Cas9, enable the enhancement of crops without requiring the introduction of foreign DNA.

Significant crops like soybean, rice, maize, and sorghum have all been engineered with CRISPR/Cas9 technology (Jiang et al., 2013; Lawrenson et al., 2015; Li et al., 2015), (Svitashev et al., 2015). It has also been used to alter bread wheat (Wang et al., 2014) and tomato (Nekrasov et al., 2017). A backward genetic method called virus-induced gene silencing (VIGS) is used to examine how genes in tomatoes respond to biological and environmental stress (Saand et al., 2015). Mutants pertaining to rice, maize, wheat, barley, and crop development and stress tolerance have been found using comparative genomics (Talukdar & Sinjushin, 2015). For instance, mutations in soybeans affect the transcriptome profile of rhizobia-independent nodulation by the jasmonate pathway and GmNARK (Glycine max leucine-rich repeat receptor kinase) (Pathan & Sleper, 2008).

Mutagenomics is a cutting-edge omics approach that uses high-throughput genomic technologies like microarray analysis, high-resolution melt (HRM), targeted induced local lesions IN genomes (TILLING), and serial analysis of gene expression (SAGE) to search for genetic changes in mutant characteristics caused by mutation occurrences (Penna & Jain, 2017). TILLING, which began as a functional genomics approach, has developed into a effective technique for crop breeding. It is now used for soybean, wheat, rice, tomatoes, rapeseed, and sunflower, among other crops (Kurowska et al., 2011), (Witzel et al., 2015). Through genetic reverse methods like RNA interference (RNAi) and VIGS, it is possible to mute or disrupt potential genes in order to learn more about their functions.

Screening mutations in crops such as wheat, rice, corn, barley, tomato, sunflower, cotton, chickpea, pea, and soybean has been done using these approaches (Dwivedi et al., 2008), (Gupta et al., 2008), (Toorchi et al., 2009).

Transcriptomics:

Within a particular cell or tissue, transcriptomics examines the whole range of RNA transcripts produced by an organism's genome (Raza et al., 2021). Transcriptome analysis looks at how genes respond to stimuli over a period of time (Duque et al., 2013), (El-Metwally et al., 2014). There was little resolution available with traditional profiling methods such cDNAs-AFLP, differential display-PCR (DD-PCR), and SSH (Nataraja et al., 2017). RNA expression profiling has been improved by modern techniques such as digital gene expression analysis, RNAseq, NGS, microarrays, and SAGE (De Cremer et al., 2013; Duque et al., 2013; Kawahara et al., 2012).

Microarray studies using the Affymetrix GeneChip array have revealed variations in gene expression in both soybean and barley under drought conditions, as well as in soybean during dehydration stress (Guo et al., 2009; Khan et al., 2017; Le et al., 2012). In Arabidopsis, soybean, and rice, changes in gene expression influence a variety of transcription factors (TFs) in response to environmental stresses (Wohlbach et al., 2008; Xiong et al., 2002). For example, in rice, the Cys-2/His-2-type zinc finger (C2H2-ZF) transcription factor and drought and salt tolerance (DST) play roles in regulating stomatal opening in response to salt and drought stress (Huang et al., 2009). WRKY transcription factors also respond to abiotic stress in wheat (Okay et al., 2014). Gene expression is further regulated by phytohormones, non-coding RNAs, and small peptides, which are key components in abiotic stress responses in Arabidopsis and model crops like rice, tomato, and wheat (Bashir et al., 2019; Chekanova, 2015; Matsui et al., 2008). Several transcription factors, such as DRE-/CRT-binding protein 2 (DREB2) and dehydration-responsive element/C-repeat

(DRE/CRT), are involved in controlling abiotic stress responses in rice (Todaka et al., 2015).

Widely expressed genes in sorghum have been discovered by transcriptome analyses in response to osmotic stress, heat, drought, and hormone therapy (Dugas et al., 2011; Johnson et al., 2014). When rice was growing under dry stress, different patterns of OsMADS gene activity were seen (Jin et al., 2013). Functional studies of crop growth and stress responses may benefit from these analyses. In situ RNA-seq, a breakthrough in transcriptomics, is a technique that reads RNA in live cells or tissues (Ke et al., 2013; Wensheng Wang et al., 2018), to provide a biological understanding of single-cell biology. RNAseq data from single cells in model crops have shown different expression levels during growth and in reaction to stress (Yang et al., 2021).

Proteomics:

roteomics encompasses various categories, including sequence, structural, functional, and expression proteomics, all essential for profiling the full range of proteins expressed in plants (Aizat & Hassan, 2018; Mosa et al., 2017). In sequence proteomics, high-performance liquid chromatography (HPLC) is utilized to ascertain the amino acid sequences of proteins (Twyman, 2004). Protein structures are examined by structural proteomics, which makes use of techniques including computer modeling, NMR, and X-ray diffraction (Sali et al., 2003; Woolfson, 2018). Using methods like protein microarrays and yeast hybrids, functional proteomics investigates the roles of proteins (Lueong et al., 2013).

Plant proteome research has been improved by developments in the extraction of proteins and methods for separation (Nakagami et al., 2012). Conventional procedures include chromatography-based approaches such as affinity chromatography, SEC, and IEC as well as selective protein analysis techniques like ELISA and western blotting. SDS-PAGE, 2-DE, and 2D-DIGE are examples of advanced techniques that enhance protein separation. Moreover, quantitative

proteomic analysis is made easier by protein microarrays, SILAC, ICAT labeling, and iTRAQ (Aslam et al., 2016).

Three-dimensional protein structures are determined using high-throughput methods like as NMR spectroscopy and X-ray crystallography (Aslam et al., 2016). While peptide molecular masses are analyzed by MS, IT-MS, and LC, protein identification and quantification are critical tasks for techniques such as 2-DE and SDS-PAGE (Eldakak et al., 2013; Fournier et al., 2007). Molecular weights are identified using techniques such as ESI and MALDI-TOF (McLuckey & Stephenson, 1998; Tanaka et al., 1988), (Baggerman et al., 2005).

Important stress-response proteins in crops including tomato, sunflower, wheat, and sugarcane have been found via functional proteomics (Di Baccio et al., 2004; Mittova et al., 2004; Shalata et al., 2001), (Demirevska et al., 2008), (Jangpromma et al., 2010). Extensive research has identified rice varieties that are both drought-tolerant and sensitive (Maksup et al., 2014; Muthurajan et al., 2011; Rabello et al., 2008; Salekdeh et al., 2002). The iTRAQ technique has shown differences in protein expression under abiotic stress in crops such as coconut and potatoes (Li et al., 2015; Yang et al., 2020), and has also shed light on somatic embryogenesis in cotton (Zhu et al., 2018).

Pathogen responses in crops like Vitis species have been studied using proteomic methods (Basha et al., 2010). Protein phosphorylation analysis known as phosphoproteomics has been utilized to recognize proteins linked to drought stress in wheat and the crops' responses to diseases, including grapevine and wheat (Margaria et al., 2013; Zhang et al., 2014), (Yang et al., 2013). The combination of functional genomics, proteomics, and metabolomics has led to an advance in our understanding of stress biology. This has been achieved by the development of molecular markers, which are used in breeding projects (Ramalingam et al., 2015).

Differentially expressed proteins (DEPs) implicated in stress responses in different crops have been found by studies employing LC-MS/MS (Arefian et al., 2019; Subba et al., 2013), (Larrainzar et al., 2009; Larrainzar et al., 2007; Ramalingam et al., 2015). Crops such as rapeseed, soybean, wheat, sugarcane, and cotton have had their stress-response pathways studied using techniques such as MALDI-TOF, SDS-PAGE, MS, 2-DE, and PMF (Demirevska et al., 2008; Jangpromma et al., 2010; Nouri & Komatsu, 2010; Toorchi et al., 2009). Reviews of proteomics methods in drought-stressed cereal crops emphasize how important they are for comprehending how crops react to abiotic stress (Ghatak et al., 2017).

To sum up, proteomics is essential for comprehending functional pathways in agricultural research, especially when paired with other omics techniques. By enhancing crop yields and tolerance to various pressures, this integrated method holds great promise for future developments in plant breeding.

Future Directions and Challenges

Plant breeding is faced with a number of problems and ethical issues as it develops and grows in importance in the context of food security and environmentally friendly farming. As biotechnology and molecular breeding methods become more widely used, the question of intellectual property rights (IPRs) over genetic material from plants becomes more important. Certain genes or features may be patented by private businesses or academic institutions, restricting the accessibility and utilization of these genetic resources by other parties, such as public research organizations and small-scale farmers. A difficult ethical dilemma that requires serious thought is how to safeguard breeders' and investors' rights while ensuring fair and equal access to genetic resources (Gonal et al., 2023). Additionally, there are ethical questions about consumer acceptability, ecological impact, and safety that are brought up by the creation and marketing of genetically modified organisms (GMOs). GMOs raise concerns about possible unexpected effects, such as the emergence of pests that are resistant or cross-breeding with wild cousins, even if they have the potential to

increase agricultural yields and strengthen resistance to diseases and pests. In order to resolve the bioethical concerns regarding genetically modified organisms (GMOs), transparent risk assessments, strict biosafety measures, and public involvement are essential (Signorelli et al., 2019).

New paths for precise genetic alterations in plants have been made possible by the advent of technologies for gene editing like CRISPR-Cas9. These avenues hold great promise for the development of better crops. But it also brings up moral conundrums concerning how best to use this technology, such as worries about unforeseen side effects, possible ecological disturbance, and how to distinguish between extreme genetic engineering and desirable characteristic enhancement (Wolt et al., 2016). Global food security may be threatened by intensified agricultural methods, such as plant breeding to improve productivity and resistance to disease, which may result in increasing monoculture and decreased genetic variation within plant populations. This would make crops more susceptible to newly developing pests and diseases. Prioritizing ecological resilience, sustainable agriculture methods, and genetic diversity conservation should be the top three ethical goals in plant breeding (Khoury et al., 2014). Furthermore, various agricultural communities may experience varied effects from the use of new crop types and technology, which might result in economic and social disparities. Improved crop varieties could be more advantageous to large-scale commercial farmers, which would disadvantage small-scale and resource-limited farmers. To fulfill the requirements of many agricultural communities and provide fair access to better crop varieties, inclusive and participatory techniques should be the main emphasis of ethical plant breeding (Coomes OT et al., 2021). Another major worry is gene flow, which is the transfer of genes from GM crops to their wild cousins or conventional types via cross-pollination. Strategies to reduce gene flow and avoid transgene contamination while encouraging responsible

stewardship of GM crops are necessary since the inadvertent spread of transgenes may have ecological repercussions, such as the emergence of weeds resistant to herbicides (Hails & Morley, 2005).

CONCLUSION

This review gives an overview of the transformative progress that has taken place in plant breeding from the conventional methods to modern molecular techniques, including Marker-Assisted Selection, QTL mapping, genomic selection, and gene editing technologies—CRISPR/Cas9. All these innovations increase manifold the efficiency and precision for crop trait development of varieties with desirable features in disease tolerance, abiotic stress resistance, and enhanced nutritional value. It has also been advanced in the last few decades due to the integration of omics technologies, and high-throughput phenotyping and precision agriculture improvements. Careful management, of course, needs to be placed regarding ongoing challenges of ethical considerations, intellectual property rights, and possible ecological impacts. Probably, it will be new technologies that drive the future of plant breeding through artificial intelligence, machine learning, and synthetic biology in a manner likely to yield extra acceleration in crop improvement and worldwide food stability, but this is only if ethical and socio-economic considerations remain at the forefront.

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