Utilizing Genetic Diversity for Maize Improvement: Strategies and Success Stories

Bin Chen [1], Junfeng Hou [1], Yunfei Cai [2], Guiyue Wang [1], Renxiang Cai [3], Fucheng Zhao [1] ✉

1 Institute of Maize and Featured Upland Crops, Zhejiang Academy of Agricultural Sciences, Dongyang, 322100, Zhengjiang, China

2 Seed Management Station of Zhejiang Province, Hangzhou, 310009, Zhengjiang, China

3 Institute of Life Science, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhengjiang, China

✉ Corresponding author: ymszfc@163.com

Abstract Utilizing genetic diversity for maize improvement is crucial for enhancing agricultural productivity and addressing climate change. As a major global crop, maize's genetic diversity is key to improving disease resistance, stress tolerance, and yield. This study reviews the sources of maize genetic diversity, including wild relatives, landraces, germplasm banks, and synthetic populations, and explores the main strategies for using these resources for maize improvement. These strategies include introgression breeding, heterosis breeding, marker-assisted breeding, genome-wide association studies (GWAS), genomic selection (GS), and CRISPR/Cas9 gene editing technology. Through case studies, the study demonstrates the successful application of these strategies in enhancing disease resistance, stress tolerance, nutritional quality, and yield in maize. The aim is to integrate traditional and modern breeding methods to propose future research directions for maize genetic improvement, providing new ideas and methods for maize variety improvement to meet global food demand and agricultural sustainability challenges. The significance of the research lies in providing a scientific basis for increasing maize productivity, economic benefits, and biodiversity conservation, promoting sustainable agricultural development.

Keywords Maize; Genetic diversity; Breeding strategies; Genomic selection; CRISPR/Cas9

1 Introduction

Genetic diversity is fundamental to crop improvement, providing invaluable resources for breeding programs to enhance yield, disease resistance, and environmental adaptability. In the evolution of maize (*Zea mays* L.), genetic diversity has played a pivotal role in its transformation from a wild grass into one of the world's most important staple crops. Effectively harnessing this diversity is crucial for sustaining agricultural productivity and food security, especially in the face of climate change and evolving pest and disease pressures (Hufford et al., 2012; Alves et al., 2017; Mayer et al., 2020).

The domestication and subsequent improvement of maize have a history of approximately 10 000 years, involving a series of evolutionary experiments that have significantly altered its genetic composition (Hufford et al., 2012). Traditional breeding methods, such as mass selection and hybridization, have long been used to enhance desirable traits. For instance, participatory breeding programs have successfully improved agronomic performance through stratified mass selection while maintaining genetic diversity (Alves et al., 2017). Additionally, the introduction of early and extra-early maturing cultivars has expanded maize cultivation into diverse agro-ecologies, particularly in sub-Saharan Africa, thereby contributing significantly to food and nutritional security (Badu-Apraku et al., 2021).

This study aims to explore the strategies and success stories in utilizing genetic diversity for maize improvement. By examining comprehensive genomic studies, participatory breeding programs, and innovative approaches to harnessing genetic resources, this study seeks to provide a detailed understanding of how genetic diversity can be effectively leveraged to enhance maize breeding programs. The ultimate goal is to highlight the immense potential of genetic diversity in driving sustainable maize production and addressing future agricultural challenges.

2 Sources of Genetic Diversity

2.1 Wild relatives and landraces

Wild relatives and landraces of maize are crucial sources of genetic diversity, playing a significant role in crop improvement. The wild ancestor of maize, Teosinte, exhibits considerable phenotypic and genetic variation, including higher protein content and unique zein profiles compared to modern inbred lines and landraces (Flint-Garcia et al., 2009). Landraces, which are traditional maize varieties developed by farmers over many generations, harbor rich genetic diversity. For example, landraces from Morelos, Mexico, display significant genetic diversity and selection signatures across different municipalities. These landraces show notable phenotypic diversity and potential for genetic improvement in agronomic traits By comparing the genetic diversity of samples preserved in situ and ex situ, McLean-Rodríguez et al. revealed the geographical patterns of genetic variation and selection pressure, providing a scientific basis for the conservation and improvement of maize (Figure 1) (McLean-Rodríguez et al., 2021).
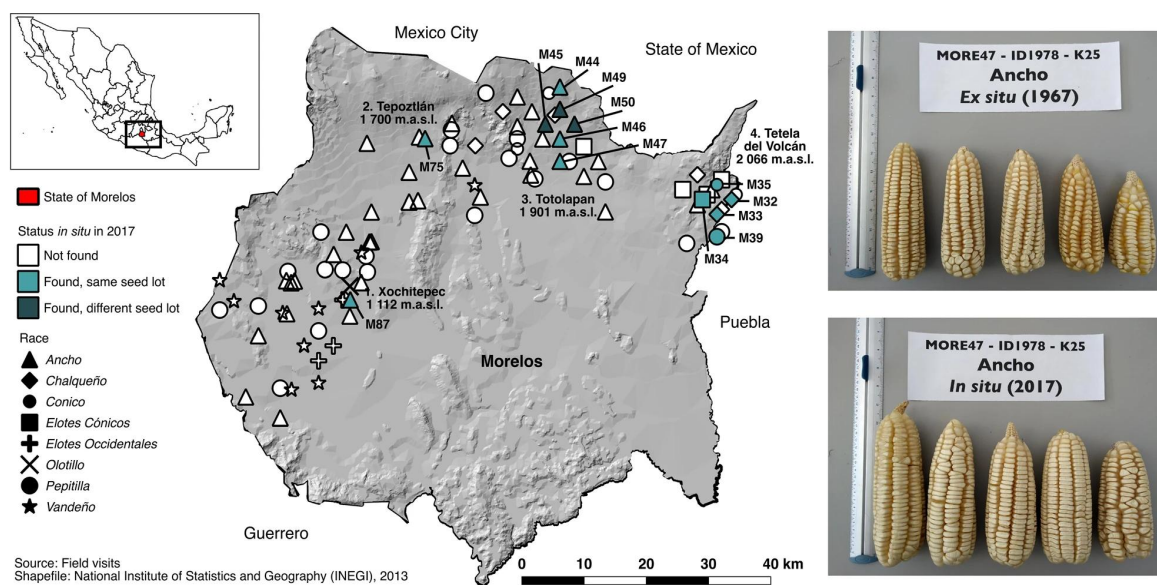

Figure 1 Geographical distribution of the 93 ex situ samples collected in 1967 in Morelos state, Mexico (Kato 1967), with the 13 samples collected in situ for the genetic comparison with their ex situ counterparts in 2017 (Adopted from McLean-Rodríguez et al., 2021)

Image caption: Figure 1 shows the geographic distribution of 93 ex situ samples collected in 1967 and 13 in situ samples resampled in 2017 from Morelos, Mexico. These samples represent maize landraces from different municipalities, providing detailed geographic references and information on the sample races. Different colors and shapes in the figure indicate the status of the samples in 2017 and their respective races, such as Ancho, Chalqueño, Cónico, Pepitilla, and Elotes Cónicos. Through these geographic distributions and sample descriptions, the study reveals genetic diversity and selection pressures in different regions. This figure demonstrates that landraces exhibit significant genetic variation across different geographic areas, highlighting the importance of in situ and ex situ conservation strategies in maintaining and utilizing maize genetic diversity. This information provides valuable scientific insights into the sources of genetic diversity in maize (Adopted from McLean-Rodríguez et al., 2021)

2.2 Germplasm banks and genetic resources

Germplasm banks play a critical role in preserving and providing genetic resources for maize improvement. The International Maize and Wheat Improvement Center (CIMMYT) maintains a diverse collection of maize germplasm, including landraces, open-pollinated varieties (OPVs), and inbred lines adapted to non-temperate growing regions. These germplasm resources contain numerous unique alleles and represent a vast genetic reservoir for unexplored maize improvement (Warburton et al., 2008). Moreover, by collaborating with farmers, researchers can resample in situ conserved maize germplasm. These resources exhibit genome-wide diversity similar to ex situ preserved samples, demonstrating the importance and effectiveness of in situ conservation (McLean-Rodríguez et al., 2021).

2.3 Synthetic populations and hybrids

Creating new genetic combinations by crossing diverse germplasm to develop synthetic populations and hybrids is a strategy used in maize improvement. For instance, synthetic populations derived from crosses of DH lines from landraces, while not showing yield improvement, maintained phenotypic diversity, indicating their potential for association mapping and breeding (Strigens et al., 2013). Large-scale analyses of the combining ability and heterosis of diverse maize germplasm resources have shown that hybrids from temperate and tropical maize inbred lines exhibit higher heterosis and hybrid performance in yield-related traits. This suggests that germplasm from different ecological environments can be used to enhance the yield potential of maize varieties (Yu et al., 2020). Furthermore, genetic variation in maize breeding populations, including F2 populations and synthetic populations, has been shown to affect the effectiveness of yield improvement selection. Broad-based synthetic populations exhibit greater potential for genetic gains (Fountain and Hallauer, 1996).

3 Strategies for Utilizing Genetic Diversity

3.1 Introgression breeding

Introgression breeding involves the incorporation of beneficial alleles from donor lines into elite breeding lines. This strategy is particularly useful for introducing traits such as disease resistance, drought tolerance, and other abiotic stress tolerances. For example, the development of maize introgression populations can be optimized using high-throughput marker assays and specific crossing schemes to ensure the effective incorporation of desired traits while maintaining genetic diversity (Herzog et al., 2014). The use of donor chromosome segments and double haploid (DH) crossing schemes has been shown to be effective in creating introgression populations with clearly separated and evenly distributed target segments.

3.2 Heterosis and hybrid breeding

Heterosis, or hybrid vigor, is a phenomenon where hybrid offspring exhibit superior traits compared to their parents. This strategy is widely used in maize breeding to enhance yield and stress tolerance. Studies have shown that combining ability and heterosis can be effectively utilized by developing hybrids from diverse germplasm resources, including temperate and tropical maize lines (Yu et al., 2020). The identification of specific combining ability (SCA) and general combining ability (GCA) among parental lines can help predict hybrid performance and optimize breeding strategies (Betrán et al., 2003; Yu et al., 2020).

3.3 Marker-assisted breeding (MAB)

Marker-assisted breeding (MAB) leverages molecular markers to select for desirable traits, thereby accelerating the breeding process. For instance, marker-assisted backcrossing (MABC) has been successfully used to improve drought adaptation in maize by introgressing favorable alleles at target regions involved in yield components and flowering traits. This approach has resulted in hybrids with significantly higher grain yield under severe water stress conditions compared to control hybrids (Ribaut and Ragot, 2006). The use of MAB can thus enhance the efficiency of breeding programs by enabling precise selection for complex traits.

3.4 Genome-wide association studies (GWAS)

Genome-wide association studies (GWAS) identify genetic variants associated with specific traits across the genome. This approach has been instrumental in understanding the genetic architecture of traits and informing breeding strategies. For example, GWAS has been used in conjunction with genomic selection (GS) to improve the accuracy of predicting breeding values in rice, which can be translated to maize breeding (Spindel et al., 2015). By identifying quantitative trait loci (QTL) associated with important traits, GWAS can guide the selection of superior genotypes and enhance the efficiency of breeding programs (Spindel et al., 2015; Bernardeli et al., 2023).

3.5 Genomic selection (GS)

Genomic selection (GS) uses genome-wide marker data to predict the breeding value of individuals, thereby increasing genetic gains with fewer breeding cycles. GS has been shown to be a powerful tool in maize breeding, enabling the development of superior inbreds and hybrids (Rice and Lipka, 2021). Rapid cycling genomic selection (RCGS) has demonstrated significant genetic gains in tropical maize populations, achieving high genetic gains while conserving genetic diversity (Zhang et al., 2017). The integration of high-throughput phenotypic and

genotypic data into GS models can further enhance the accuracy of predictions and accelerate the breeding process (Zhang et al., 2017; Rice and Lipka, 2021).

3.6 CRISPR/Cas9 and gene editing

CRISPR/Cas9 and other gene-editing technologies offer precise tools for modifying specific genes associated with desirable traits. These technologies can be used to introduce or knock out genes to enhance traits such as yield, stress tolerance, and disease resistance. While the provided data does not include specific examples of CRISPR/Cas9 applications in maize, the potential for these technologies to revolutionize maize breeding is immense. By enabling targeted modifications, gene editing can complement traditional breeding strategies and accelerate the development of improved maize varieties.

The utilization of genetic diversity in maize improvement involves a combination of traditional and modern breeding strategies. Introgression breeding, heterosis and hybrid breeding, marker-assisted breeding, GWAS, genomic selection, and gene editing each play a crucial role in enhancing the genetic potential of maize and addressing the challenges posed by changing environmental conditions and increasing food demand.

4 Case Studies of Successful Maize Improvement

4.1 Disease resistance

4.1.1 Northern corn leaf blight

Northern Corn Leaf Blight (NCLB), caused by the fungal pathogen Setosphaeria turcica, is a major threat to global maize production. Resistance to NCLB has been a key focus in maize breeding programs. Genome-wide association studies (GWAS) have identified multiple significant SNPs and haplotypes associated with NCLB resistance, which can be targeted in breeding programs (Rashid et al., 2020). The research highlights the polygenic nature of NCLB resistance, and in tropical environments, quantitative resistance is preferred due to its robustness against evolving pathogens (Figure 2). This study provides valuable insights into utilizing genetic markers to enhance crop disease resistance, laying the groundwork for future breeding efforts. By integrating quantitative resistance strategies controlled by multiple minor-effect genes, it is possible to achieve durable NCLB resistance across diverse environments (Galiano-Carneiro and Miedaner, 2017). Additionally, large-scale genomic prediction models can improve the accuracy of disease resistance breeding by using genotyped and phenotyped training sets (Technow et al., 2013).

4.1.2 Maize lethal necrosis

Maize Lethal Necrosis (MLN) is a devastating disease caused by the synergistic interaction of Maize chlorotic mottle virus (MCMV) and any of the cereal-infecting potyviruses. Breeding for MLN resistance involves evaluating maize lines under artificial inoculation and identifying genomic regions associated with resistance traits. Recent studies have identified several SNPs linked to MLN resistance, providing valuable markers for marker-assisted selection and genomic prediction (Technow et al., 2013). These findings are crucial for developing MLN-resistant maize varieties, particularly in sub-Saharan Africa where the disease is prevalent.

4.2 Abiotic stress tolerance

4.2.1 Drought tolerance

Drought stress is a major constraint to maize production, and improving drought tolerance has been a key objective in maize breeding. Advances in genetic dissection through linkage mapping and association mapping have identified key genetic components underlying drought tolerance(Liu and Qin, 2021). The use of transgenic approaches and genome editing technologies has further enhanced the efficiency of breeding for drought tolerance (Liu and Qin, 2021). Additionally, the identification of genetic variants in genes such as *ZmVPP1*, which contribute to drought tolerance, has provided direct targets for genetic engineering and selection (Wang et al., 2016).

4.2.2 Heat tolerance

Heat stress, often occurring in conjunction with drought, poses a significant challenge to maize production. Studies have shown that certain maize landraces exhibit combined tolerance to drought and heat stresses, making them valuable genetic resources for breeding climate-resilient maize varieties (Nelimor et al., 2019). The

identification of landraces with high yield potential and desirable secondary traits under heat stress conditions is crucial for developing heat-tolerant maize varieties (Nelimor et al., 2019).
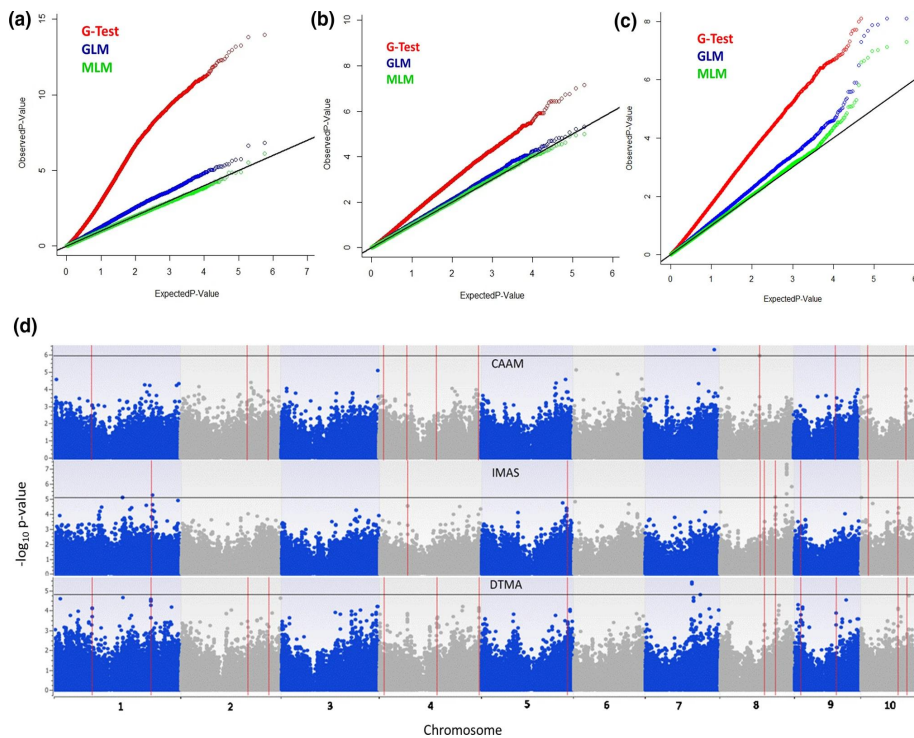

Figure 2 Inflation depicted by Q-Q plots of observed versus expected -log10 (P values) plots for NCLB using the naïve association model (G-test), GLM (G + Q) and MLM (G + Q + K); G = genotype (fixed), Q = ten principal components (fixed), K = kinship matrix (random) for (a) CAAM panel (b) DTMA panel and (c) IMAS panel; Highly significant SNPs identified from MLM model using Manhattan plot (d), plotted with the individual SNPs on the X-axis and − log10 P value of each SNP on the Y-axis for the three panels, CAAM, IMAS and DTMA. The horizontal line shows the cut off P value and the vertical lines represent the common haplotypes identified in haplotype regression analysis across different panels for NCLB resistance (Adopted from Rashid et al., 2020)

Image caption: Figure 2 shows the Quantile-Quantile (QQ) plots and Manhattan plots for NCLB resistance association analysis using different models (G-test, GLM, and MLM). The QQ plots illustrate the effects of different models on correcting for genome structure and kinship, with the MLM model displaying the smallest genomic inflation, indicating its high efficiency in NCLB resistance association analysis. The Manhattan plots demonstrate the significant SNP loci identified in the MLM model, highlighting their distribution across the genome and their association with NCLB resistance. These loci provide crucial genetic targets for further molecular breeding and marker-assisted selection, offering valuable insights into the study of maize genetic diversity and its application in disease resistance improvement (Adopted from Rashid et al., 2020)

4.3 Nutritional and quality improvement

4.3.1 Provitamin A biofortification

Biofortification of maize with provitamin A is an important strategy to address vitamin A deficiency in populations that rely heavily on maize as a staple food. Genetic approaches to enhance provitamin A content in maize involve the identification and incorporation of favorable alleles associated with increased carotenoid levels. This strategy has shown success in developing maize varieties with significantly higher provitamin A content, contributing to improved nutritional quality (Wen et al., 2011).

4.3.2 Quality protein maize

Quality Protein Maize (QPM) is enriched with essential amino acids, particularly lysine and tryptophan, which are deficient in conventional maize. Breeding for QPM involves the incorporation of the *Opaque-2* (*O2*) gene and associated modifiers that improve kernel texture and nutritional quality. The development of QPM varieties has been a significant achievement in enhancing the protein quality of maize, benefiting populations with maize-based diets (Wen et al., 2011).

4.4 Yield enhancement

4.4.1 High-yield hybrids

The development of high-yielding maize hybrids has been a cornerstone of maize improvement programs. Conventional breeding strategies, combined with modern genomic tools, have led to the identification of key genetic loci associated with yield traits. The use of multi-environment trials and managed stress environments has facilitated the selection of hybrids with superior yield potential under diverse conditions (Campos et al., 2004). These high-yield hybrids contribute significantly to meeting the growing demand for maize.

4.4.2 Efficient nitrogen use

Improving nitrogen use efficiency (NUE) in maize is critical for sustainable agriculture. Genetic studies have identified several loci associated with NUE, providing targets for breeding programs aimed at developing maize varieties that require less nitrogen input while maintaining highyields (Wen et al., 2011). The integration of genomic selection and marker-assisted breeding has accelerated the development of maize varieties with enhanced NUE, contributing to reduced environmental impact and increased agricultural sustainability.

5 Impact of Utilizing Genetic Diversity

5.1 Agricultural productivity

Utilizing genetic diversity in maize has significantly enhanced agricultural productivity. The development of diverse inbred lines and their subsequent crossing has led to the phenomenon of heterosis, resulting in superior offspring with improved traits such as yield and resilience (McMullen et al., 2009). The comprehensive genomic mapping of maize has facilitated the identification of numerous quantitative trait loci (QTLs) that contribute to phenotypic variation, thereby enabling more targeted breeding strategies (McMullen et al., 2009). Additionally, the integration of molecular and conventional breeding techniques has accelerated genetic gains, leading to increased yields in various agroecological zones (Gedil and Menkir, 2019). For instance, the introduction of high-yielding cultivars and improved production technologies has substantially boosted maize productivity in India (Yadav et al., 2015).

5.2 Economic benefits for farmers

The economic benefits of utilizing genetic diversity in maize are profound, particularly for smallholder farmers. The development and dissemination of improved maize varieties have led to increased yields and, consequently, higher incomes for farmers. In West and Central Africa, for example, the adoption of genetically improved maize has resulted in significant yield increases, thereby enhancing the livelihoods of smallholder farmers (Gedil and Menkir, 2019). Similarly, in India, the widespread adoption of high-yielding maize cultivars has contributed to a substantial increase in maize production and productivity, translating into economic gains for farmers (Yadav et al., 2015). Moreover, the ability to grow locally adapted or 'creolized' versions of improved maize varieties has allowed farmers to maintain crop diversity while benefiting from the superior traits of improved varieties (Moreno et al., 2006).

5.3 Biodiversity conservation

The conservation of biodiversity is another critical impact of utilizing genetic diversity in maize. Traditional maize storage methods, as practiced by Mayan farmers in Yucatan, Mexico, play a crucial role in maintaining genetic diversity. These methods involve selecting and storing seeds based on specific traits, which helps preserve a wide range of maize varieties (Moreno et al., 2006). Additionally, the recovery of genetic diversity through introgression from wild relatives has been observed in modern maize, indicating that breeding programs can enhance biodiversity while improving crop traits (Hufford et al., 2012). The use of diverse germplasm in breeding programs ensures the conservation of genetic resources, which is vital for the long-term sustainability of maize cultivation (Yadav et al., 2015).

5.4 Climate resilience

Genetic diversity in maize is pivotal for enhancing climate resilience. Breeding programs that focus on developing stress-tolerant maize cultivars have been successful in mitigating the adverse effects of climate-induced stresses such as drought, heat, and diseases (Prasanna et al., 2021). For instance, the International Maize and Wheat

Improvement Center (CIMMYT) has developed elite tropical maize germplasm with tolerance to key abiotic and biotic stresses, which has been deployed across sub-Saharan Africa, Asia, and Latin America (Prasanna et al., 2021). Crop rotation diversification has also been shown to increase maize yields and resilience to adverse growing conditions, further highlighting the importance of genetic diversity in building climate-resilient agricultural systems (Bowles et al., 2020). The integration of advanced genomic tools and breeding strategies continues to enhance the climate resilience of maize, ensuring stable production in the face of changing environmental conditions (Gedil and Menkir, 2019; Bailey-Serres et al., 2019).

6 Challenges and Future Directions

6.1 Barriers to germplasm utilization
One of the primary challenges in utilizing genetic diversity for maize improvement is the limited genetic diversity within elite germplasm pools. This limitation restricts the potential for breeding new varieties that can address emerging agricultural challenges such as climate change and evolving pest pressures (Gorjanc et al., 2016; Allier et al., 2019). Additionally, the integration of diverse germplasm into breeding programs is often hampered by logistical constraints, including the management of large-scale pre-breeding programs and the accurate phenotyping of diverse genetic materials (Gorjanc et al., 2016). The complexity of polygenic traits further complicates the effective utilization of landrace diversity, necessitating advanced strategies for targeted trait improvement (Rogers et al., 2022).

6.2 Advances in genomic tools and techniques
Recent advancements in genomic tools and techniques have significantly enhanced the potential for maize improvement. Genomic selection (GS) and genome-wide association studies (GWAS) have been pivotal in identifying beneficial alleles and haplotypes for complex traits (Rogers et al., 2022). The integration of doubled haploid production, genomic selection, and genome optimization represents a new model for maize breeding, facilitating the rapid incorporation of superior alleles into breeding programs (Hufford et al., 2012). These tools enable the precise mapping of trait-associated loci and the development of predictive models that can accelerate genetic gain (Hufford et al., 2012; Rogers et al., 2022).

6.3 Integrating traditional and modern breeding
The integration of traditional breeding methods with modern genomic tools is essential for maximizing genetic gain in maize improvement programs. Traditional methods, such as phenotypic selection and the use of heterotic groups, remain valuable for their proven effectiveness in hybrid performance (Yu et al., 2020). However, combining these methods with genomic tools, such as marker-assisted selection and genomic prediction, can enhance the efficiency and accuracy of breeding programs (Hufford et al., 2012; Gedil and Menkir, 2019). This integrated approach allows for the systematic incorporation of diverse genetic resources, including landraces and wild relatives, into elite breeding pools (Warburton et al., 2008; Allier et al., 2019).

6.4 Policy and regulatory frameworks
Effective policy and regulatory frameworks are crucial for facilitating the utilization of genetic diversity in maize breeding. Policies that support the conservation and sharing of genetic resources, such as the establishment of collaborative diversity panels, are essential for broadening the genetic base of elite germplasm (Allier et al., 2019). Additionally, regulatory frameworks that promote the adoption of advanced genomic tools and techniques can accelerate the development and dissemination of improved maize varieties (Gedil and Menkir, 2019). Ensuring that these policies are aligned with international standards and agreements will enhance global collaboration and resource sharing (Warburton et al., 2008).

6.5 International collaboration and funding
International collaboration and funding are vital for the success of maize improvement programs. Collaborative projects that bring together public and private sector breeders, such as the Germplasm Enhancement of Maize (GEM) project, have demonstrated the potential for significant genetic gain through the sharing of resources and expertise (Rogers et al., 2022). Funding from international organizations and governments can support the development of innovative breeding strategies and the implementation of advanced genomic tools (Gedil and

Menkir, 2019). Strengthening partnerships between research institutions, breeding programs, and funding agencies will be key to addressing the challenges of maize improvement and ensuring food security in the face of global challenges (Gedil and Menkir, 2019; Yu et al., 2020).

By addressing these challenges and leveraging the advancements in genomic tools and international collaboration, the potential for utilizing genetic diversity in maize improvement can be fully realized, leading to the development of resilient and high-yielding maize varieties.

7 Concluding Remarks

The utilization of genetic diversity in maize improvement has been approached through various innovative strategies, each contributing to significant advancements in yield, stress tolerance, and overall agronomic performance. One notable strategy is the long-term participatory breeding and on-farm conservation program in Portugal, which employed stratified mass selection to enhance agronomic traits while maintaining genetic diversity. This method proved effective in improving yield without compromising the genetic heterogeneity essential for adaptability.

Modern breeding techniques have also introduced dynamic genetic changes, significantly impacting the maize genome. These changes, driven by artificial selection, have led to a reduction in nucleotide diversity but an increase in rare alleles, providing new targets for future crop improvement. Additionally, the integration of genomic tools and model plants has been indispensable in optimizing maize yield under stress conditions, particularly drought.

The exploration of wild relatives, such as teosinte, has revealed valuable genetic sequences that can enhance maize yields, demonstrating the potential of redomestication to uncover beneficial traits lost during domestication. Furthermore, the genetic dissection of drought tolerance through linkage and association mapping has identified key quantitative trait loci (QTL) and facilitated the development of more resilient maize varieties.

In sub-Saharan Africa, the assessment and utilization of genetic diversity in early and extra-early maturing maize germplasm have been crucial for rapid adaptation to diverse agro-ecologies, contributing to food and nutritional security. The physiological basis of successful breeding strategies has also been examined, highlighting the importance of balancing source and sink components to achieve yield improvements.

Looking ahead, the future of maize genetic improvement will likely be shaped by the continued integration of advanced genomic approaches and the strategic use of genetic diversity. The application of multi-omics studies, including genomics, transcriptomics, and phenomics, will provide a more comprehensive understanding of the genetic basis of complex traits, enabling more precise and efficient breeding strategies.

The development of large-scale managed stress environments (MSE) will be essential for validating candidate genes and regions, ensuring that new varieties can withstand the challenges posed by climate change. Additionally, the incorporation of beneficial haplotypes from landraces into elite germplasm will harness untapped genetic variation, offering new opportunities for trait improvement.

In India, the focus on developing high-yielding cultivars with tolerance to abiotic stresses and resistance to diseases will remain a priority. The combination of conventional and molecular breeding approaches will continue to drive progress, supported by agronomic research targeting optimal management practices.

Overall, the future of maize genetic improvement will depend on a holistic approach that leverages genetic diversity, advanced genomic tools, and innovative breeding strategies to meet the growing demands for food security and climate resilience.

Conflict of Interest Disclosure

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