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# The Contribution of Exotic Varieties to Maize Genetic Improvement

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**Abstract** Maize (*Zea mays* L.) is one of the most important staple crops globally, providing essential food and energy resources for millions of people. The genetic improvement of maize has been a focal point of agricultural research, aiming to enhance yield, resilience, and adaptability to various environmental conditions. The introduction of exotic maize lines into adapted germplasm has shown significant potential in increasing genetic variability and improving agronomic traits. For instance, testcrosses of backcross-derived lines exhibited substantial yield improvements, with some lines producing up to 1 056 kg/ha more grain than the control. RNA-sequencing of diverse maize lines revealed extensive genetic and transcriptomic diversity, identifying novel transcripts that contribute to heterosis. Screening of elite exotic inbreds demonstrated that certain tropical lines performed well in temperate environments, suggesting their utility in broadening the genetic base of U.S. maize. Additionally, molecular marker studies confirmed high levels of polymorphism and genetic diversity in tropical maize germplasm. Adaptation efforts have successfully integrated tropical germplasm into temperate breeding programs, enhancing genetic gains. The findings underscore the value of exotic germplasm in maize breeding programs. The integration of exotic alleles has not only expanded the genetic base but also led to the development of high-yielding hybrids with improved agronomic traits. These results highlight the importance of utilizing diverse genetic resources to achieve sustainable genetic improvement in maize.

**Keywords** Maize (*Zea mays* L.); Genetic diversity; Exotic germplasm; Yield improvement; Tropical maize; Temperate breeding

## 1 Introduction

Genetic diversity is crucial for the sustainability and improvement of crop species. In maize, genetic diversity allows for the development of varieties that can withstand biotic and abiotic stresses, thereby ensuring food security and agricultural productivity. The iterative selection process during domestication has often restricted the genetic diversity available in modern maize varieties, making it imperative to explore alternative sources of genetic variation (Hake and Richardson, 2019). Wild relatives of maize, such as teosinte (*Zea mays* ssp. *parviglumis*), offer a rich reservoir of genetic traits that have been lost during domestication but can be reintroduced to enhance modern maize varieties (Hake and Richardson, 2019; Kong et al., 2020).

Exotic varieties refer to maize strains that originate from different geographical regions or wild relatives that have not been subjected to the same selection pressures as domesticated varieties. These exotic varieties possess unique genetic traits that can be harnessed to improve modern maize. For instance, the genetic diversity found in teosinte has been shown to contain sequences that can directly increase maize yields under field conditions (Hake and Richardson, 2019). By incorporating these exotic genetic traits, breeders can develop maize varieties with improved yield, disease resistance, and adaptability to high-density planting (Kong et al., 2020; Cai et al., 2024).

This study aims to evaluate the contribution of exotic maize varieties to the genetic improvement of maize. This involves identifying and integrating beneficial genetic traits from exotic varieties into modern maize breeding programs. The study also aims to assess the genetic diversity present in exotic maize varieties and their wild relatives, identify specific genetic sequences from exotic varieties that can enhance yield and other agronomic traits in maize, and develop breeding strategies that effectively incorporate these exotic traits into modern maize varieties to improve overall performance and sustainability. By achieving these objectives, the research hopes to provide a comprehensive understanding of how exotic varieties can be utilized to enhance the genetic base of maize, ultimately contributing to increased agricultural productivity and food security.

## 2 Historical Context

### 2.1 Early use of exotic varieties in maize breeding

The utilization of exotic germplasm in maize breeding has a long history, primarily aimed at broadening the genetic base of local populations. Early efforts focused on integrating genes from temperate, tropical, and sub-tropical regions to enhance the genetic diversity and adaptability of maize. For instance, the Germplasm Enhancement of Maize (GEM) project, initiated in 1993, was a significant early effort to incorporate exotic germplasm into U.S. maize breeding programs. This project involved crosses between elite temperate lines and exotic parents, leading to the release of numerous useful breeding lines (Rogers et al., 2022). Similarly, the International Maize and Wheat Improvement Center (CIMMYT) has been actively involved in breeding elite tropical maize germplasm with tolerance to various abiotic and biotic stresses, leveraging exotic varieties to improve resilience in stress-prone environments (Prasanna et al., 2021).

### 2.2 Historical milestones and key contributions

Several key milestones have marked the historical journey of exotic germplasm utilization in maize breeding. The GEM project stands out as a pivotal initiative, demonstrating the potential of exotic germplasm to enhance genetic diversity and yield potential in U.S. maize crops (Rogers et al., 2022). Another significant contribution comes from the CIMMYT's efforts over the past four decades, which have led to the development and deployment of stress-tolerant maize cultivars across sub-Saharan Africa, Asia, and Latin America (Figure 1) (Prasanna et al., 2021). Additionally, the integration of temperate germplasm into sub-tropical breeding programs in Africa has shown promising results, with hybrids demonstrating high yield potential and stability across diverse agro-ecologies (Nyoni et al., 2023).

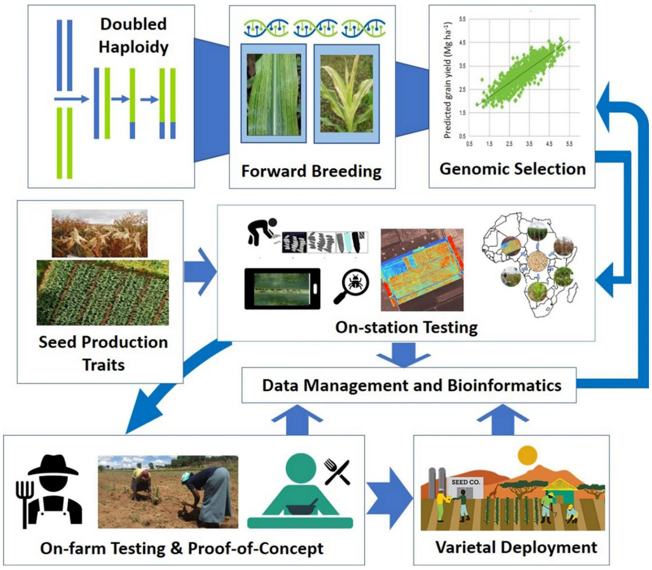

Figure 1 Schematic depiction of the maize breeding pipeline of CIMMYT for developing and deploying elite multiple stress-tolerant tropical maize germplasm for sub-Saharan Africa, Asia, and Latin America (Adopted from Prasanna et al., 2021)

### 2.3 Shifts in breeding strategies over time

Over time, maize breeding strategies have evolved significantly, incorporating advanced technologies and methodologies to enhance genetic gains. The transition from conventional breeding to more sophisticated approaches such as genomic selection, doubled haploidy, and genome optimization marks a significant shift in breeding strategies. For example, the proposed "genomic design breeding" pipeline integrates these advanced techniques to optimize maize genomes for desired traits, representing a move towards more precise and efficient breeding practices (Jiang et al., 2019). Furthermore, the resurgence of introgression breeding, facilitated by genomic tools, has renewed interest in utilizing exotic genes to drive genetic advances in maize (Hao et al., 2020).

These shifts reflect a broader trend towards leveraging multi-disciplinary technologies to achieve sustainable genetic improvement in maize breeding programs.

## 3 Genetic Basis of Exotic Varieties

### 3.1 Sources of exotic germplasm

Exotic germplasm, which includes genetic material from outside the breeder's target area, has been a valuable resource for broadening the genetic base of local maize populations. Sources of exotic germplasm include temperate, tropical, and sub-tropical regions. For instance, the Germplasm Enhancement of Maize (GEM) project has been instrumental in incorporating exotic germplasm into U.S. maize breeding programs by selecting progeny lines from crosses between elite temperate lines and exotic parents (Rogers et al., 2022). Additionally, landraces from regions such as Sahel and Coastal West Africa have shown significant genetic diversity, offering novel alleles for enriching elite maize germplasm (Nelimor et al., 2020).

### 3.2 Genetic characteristics and traits

Exotic germplasm is characterized by a wide range of genetic traits that can be beneficial for maize improvement. For example, teosinte alleles have been found to increase oil and carotenoid traits in maize kernels, highlighting their potential for nutritional enhancement (Figure 2) (Fang et al., 2019). Furthermore, hybrids derived from temperate and tropical germplasm have shown high grain yield potential and stability across diverse agro-ecologies, as well as early maturity (Nyoni et al., 2021). The genetic diversity in exotic germplasm also includes traits such as resistance to lodging and higher number of leaves above the cob, which are crucial for improving yield under high plant density conditions (Ndou et al., 2021).

### 3.3 Methods of identifying useful exotic traits

Identifying useful traits in exotic germplasm involves several methods, including phenotypic characterization, quantitative trait loci (QTL) mapping, and genomic prediction. Phenotypic characterization helps in elucidating variation in agronomic traits, as demonstrated by the assessment of 196 maize landraces for 26 agronomic traits, which revealed significant genetic variability (Nelimor et al., 2020). QTL mapping has been used to identify loci associated with nutritional traits, such as oil and carotenoid content, providing insights into the genetic basis of these traits (Fang et al., 2019). Genomic prediction models, like those developed for the GEM project, have shown promise in predicting genetic gain and enhancing the efficiency of breeding programs by leveraging genotype data (Rogers et al., 2022; Tibbs-Cortes et al., 2022). Additionally, haplotype-trait association mapping has been employed to discover beneficial haplotypes for complex traits, making native diversity accessible for elite germplasm improvement (Mayer et al., 2020).

By integrating these methods, breeders can effectively harness the genetic potential of exotic germplasm to improve maize varieties, ensuring better yield, nutritional quality, and resilience to environmental stresses.

## 4 Techniques for Incorporating Exotic Varieties

Incorporating exotic varieties into maize breeding programs is essential for enhancing genetic diversity and improving various agronomic traits. Several techniques have been developed to effectively integrate these exotic germplasms into elite maize lines. This section discusses four primary techniques: introgression and backcrossing, marker-assisted selection (MAS), genomic selection (GS), and hybrid breeding strategies.

### 4.1 Introgression and backcrossing

Introgression and backcrossing are traditional methods used to introduce desirable traits from exotic germplasm into elite lines. This process involves crossing an elite line with an exotic donor and then backcrossing the progeny with the elite parent to recover the elite genetic background while retaining the desired exotic traits. For instance, the introgression of temperate maize germplasm into tropical elite lines has shown significant improvements in grain yield and ear prolificacy, demonstrating the effectiveness of this technique in enhancing adaptability to different environments (Musundire et al., 2021).

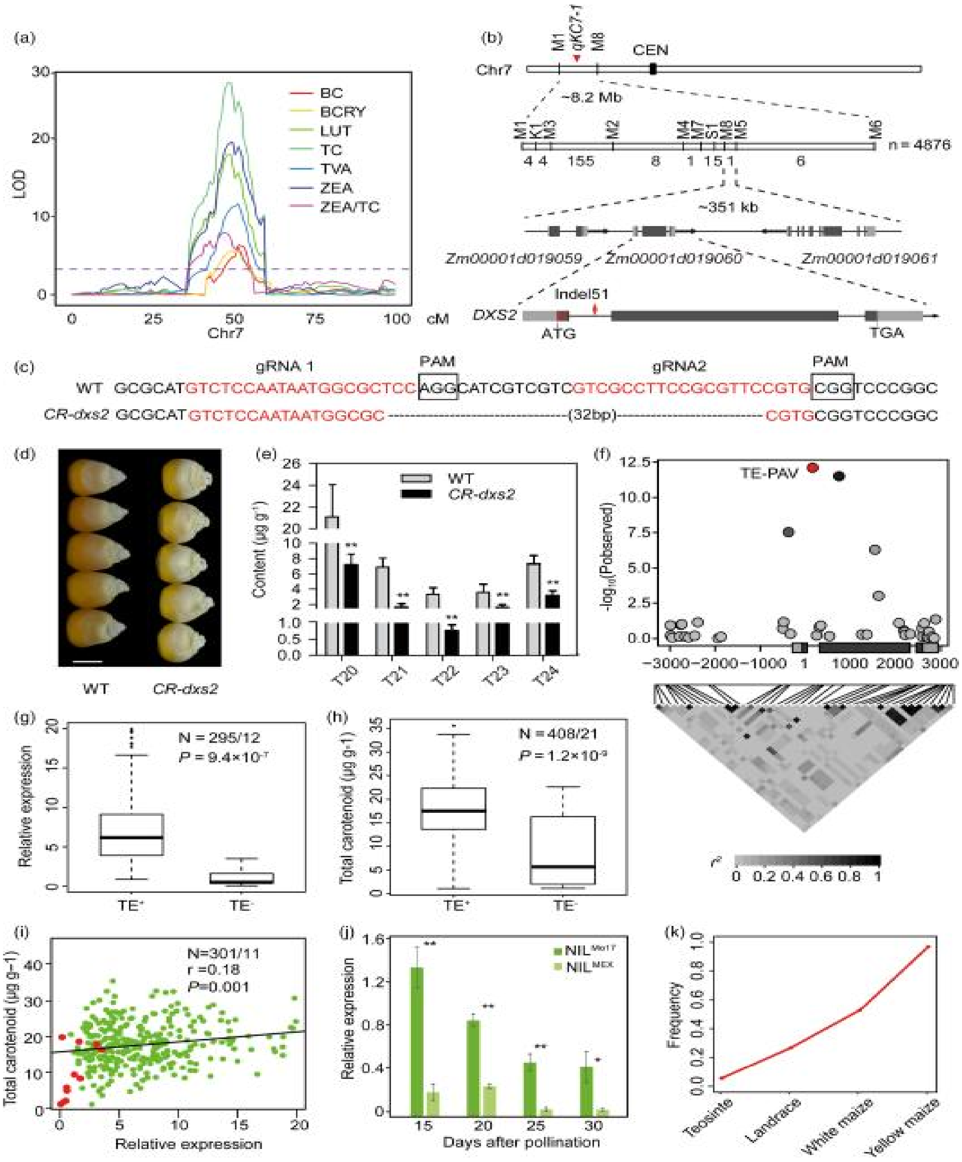

Figure 2 *DXS2* alters carotenoid biosynthesis in maize kernels, and changes in allele frequency of the favorable *DXS2* allele during maize domestication and improvement (Adopted from Fang et al., 2019)

Image caption: (a) LOD profiles of the QTL cluster *qKC7-1* for carotenoid-related traits. (b) Fine mapping of *qKC7-1* and gene structure of *DXS2*. Numbers near markers denote the number of recombinants. Dark-gray and light-gray shading represents exons and UTRs, respectively. The red diamond indicates the 51-bp InDel in exon 1 of *DXS2*. The red bars in exon 1 indicate the targeting sites for sgRNA. (c) Sequences of *DXS2* in a *CR-dxs2* plant and its wide type (WT). Nucleotides in red denote the sgRNA targets, and boxed nucleotides indicate the protospacer-adjacent motif (PAM, i.e. NGG). (d) Kernel performance for *CR-dxs2* and WT. Scale bar, 0.5 cm. (e) Comparison of kernel carotenoids between *CR-dxs2* and WT. Error bars indicate SE based on five biological replicates. $*P < 0.05$, $**P < 0.01$, Student's *t*-test. (f) DXS2-based candidate-gene association analysis for kernel color and the linkage disequilibrium (LD) patterns for all identified variants (MAF≥0.05) at the *DXS2* locus. The most significant TE-PAV is shown in red. The intensity of gray shading indicates the extent of LD ($r^2$) between TE-PAV and the other variants identified in this region. The gene structure is shown on the x-axis. Dark-gray and light-gray shading represents exons and UTRs, respectively. (g) Comparison of DXS2 expression in $TE^+$ and $TE^-$ genotypes. (h) The effect of TE-PAV in an association mapping panel. (i) Correlation of kernel total carotenoid content with the relative expression of *DXS2* in kernels at 15 DAP. Dot color: red, $TE^-$; green, $TE^+$. (j) Expression pattern of *DXS2* in endosperms at different developmental stages. NIL, near-isogenic line. (k) Changes in the frequency of the TE during maize domestication and improvement (Adopted from Fang et al., 2019)

### 4.2 Marker-assisted selection (MAS)

Marker-assisted selection (MAS) leverages molecular markers linked to desirable traits to accelerate the breeding process. This technique allows for the precise selection of individuals carrying the target traits, thereby reducing the number of breeding cycles required. An example of MAS in action is the introgression of the opaque2 (o2) allele into elite maize hybrids to enhance protein quality. By using gene-based simple sequence repeat (SSR) markers, researchers successfully developed quality protein maize (QPM) inbreds with improved lysine and tryptophan content, while maintaining high phenotypic resemblance to the original hybrids (Hossain et al., 2018).

### 4.3 Genomic selection (GS)

Genomic selection (GS) is a powerful tool that uses genome-wide marker data to predict the breeding values of individuals. This method has been shown to increase genetic gains with fewer breeding cycles compared to traditional selection methods. For example, GS was used to improve the kernel dehydration rate (KDR) in an exotic×adapted maize population, resulting in significant genetic gains for KDR and other important traits (Yong et al., 2021). Additionally, GS has been applied to improve shelling percentage and other traits in maize, demonstrating its potential to enhance selection efficiency and accelerate breeding progress (Sun et al., 2018).

### 4.4 Hybrid breeding strategies

Hybrid breeding strategies involve the development of hybrids by crossing two or more inbred lines. This approach can combine the desirable traits of different parental lines, resulting in superior hybrid performance. For instance, the introgression of temperate donor inbred lines into tropical elite maize lines led to the development of experimental single-cross hybrids with high grain yield potential and good ear prolificacy. These hybrids outperformed commercial check hybrids, highlighting the effectiveness of hybrid breeding strategies in improving maize performance (Musundire et al., 2021; Chen et al., 2024).

In conclusion, the incorporation of exotic varieties into maize breeding programs through techniques such as introgression and backcrossing, MAS, GS, and hybrid breeding strategies has proven to be highly effective in enhancing genetic diversity and improving various agronomic traits. These methods offer significant potential for the continued improvement of maize cultivars to meet the demands of different environments and market needs.

## 5 Contributions to Agronomic Traits

### 5.1 Yield improvement

Exotic maize varieties have significantly contributed to yield improvement through various genetic and agronomic advancements. For instance, the identification of quantitative trait loci (QTL) for grain yield under different nitrogen environments has enabled the development of low-nitrogen tolerant genotypes, which are crucial for improving food security in developing countries (Ribeiro et al., 2021). Additionally, the integration of doubled haploidy, high-throughput phenotyping, and genomics-assisted breeding has led to the development of elite stress-tolerant maize cultivars, further enhancing yield potential (Prasanna et al., 2021). Moreover, the discovery of gene leads that improve yield in field-grown elite maize breeding germplasm has provided valuable insights for future crop improvement (Simmons et al., 2021).

### 5.2 Abiotic stress tolerance (drought, heat, soil salinity)

Exotic maize varieties have also played a pivotal role in enhancing tolerance to abiotic stresses such as drought, heat, and soil salinity. Intensive breeding efforts have led to the development of climate-resilient maize cultivars that can withstand various climate-induced stresses, including drought and heat (Prasanna et al., 2021). The genetic dissection of drought and heat-responsive agronomic traits has identified loci associated with stress tolerance, providing valuable targets for breeding programs (Li et al., 2019). Furthermore, metabolomics-driven gene mining has identified candidate genes that improve tolerance to salt-induced osmotic stress, demonstrating the potential for genetic improvement of maize under saline conditions (Figure 3) (Liang et al., 2021).

### 5.3 Biotic stress resistance (disease, pests)

The development of exotic maize varieties has also contributed to biotic stress resistance, including resistance to diseases and pests. The breeding of elite tropical maize germplasm with tolerance to key biotic stresses has been a focus of multi-institutional efforts, resulting in the deployment of stress-tolerant maize cultivars across various regions (Prasanna et al., 2021). These efforts have been crucial in ensuring the resilience of maize crops against biotic stressors, thereby safeguarding yield and productivity.

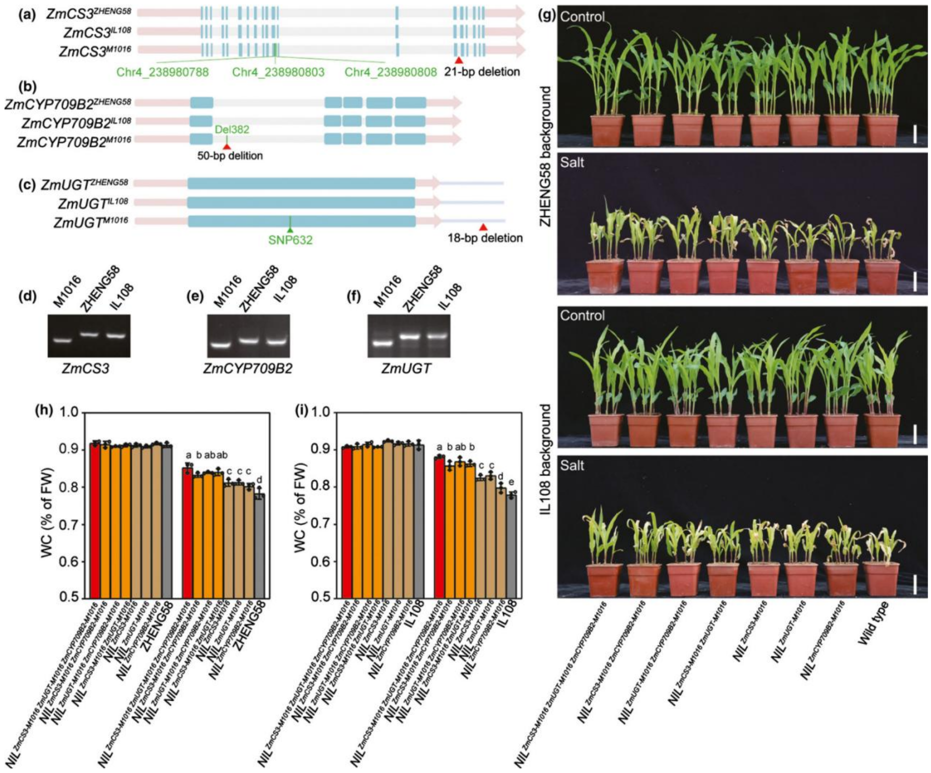

Figure 3 Characterization and application of the salinity-induced osmotic stress (SIOS)-tolerant sulfotransferase *ZmSOT* alleles in maize (*Zea mays* ssp. *mays*) (Adopted from Liang et al., 2021)

Image caption: (a–f) The molecular marker for the SIOS-tolerant *ZmSOT* alleles. The green lines indicate the variants likely associated with the functional variations of *ZmCS3* (a), *ZmCYP709B2* (b) and *ZmUGT* (c). The red arrows in (a)–(c) indicate the location of the InDels that have been used to develop the PCR-based marker for the favorable alleles of *ZmCS3* (d), *ZmCYP709B2* (e) and *ZmUGT* (f). (g–i), The appearances (g) and leaf water contents (WCs) (h–i) of the control and salt-treated maize plants (genotypes as indicated). Data in (h) and (i) are means ± SD of three independent experiments. Statistical significance was determined by one-way ANOVA test. Bars, 5 cm (g) (Adopted from Liang et al., 2021)

### 5.4 Nutritional quality enhancement

Enhancing the nutritional quality of maize has been another significant contribution of exotic varieties. The integration of advanced breeding techniques and genetic tools has facilitated the improvement of nutritional traits in maize. For example, the development of maize cultivars with enhanced nitrogen-use efficiency not only improves yield but also contributes to better nutritional quality by optimizing nutrient uptake and utilization (Liu et al., 2019). Additionally, the focus on breeding for nutritional limitations, such as improving nitrogen-use efficiency, has been a key objective in modern crop breeding programs (Benavente et al., 2021).

In summary, the contributions of exotic maize varieties to agronomic traits are multifaceted, encompassing yield improvement, abiotic and biotic stress tolerance, and nutritional quality enhancement. These advancements have been driven by a combination of genetic discoveries, advanced breeding techniques, and collaborative efforts across various institutions and regions.

## 6 Case Studies

### 6.1 Successful incorporation of exotic traits in commercial hybrids

The integration of exotic germplasm into commercial maize hybrids has shown significant promise in enhancing yield potential and stability. For instance, the study by Nyoni et al. (2023) demonstrated that incorporating exotic genes, particularly from temperate regions, into sub-tropical maize germplasm resulted in hybrids with higher grain yield and stability across diverse agro-ecologies. One notable hybrid, G44, exhibited a grain yield of 10.52 t/ha and matured earlier than the best commercial check hybrid, highlighting the potential benefits of exotic germplasm in improving local maize varieties.

### 6.2 Regional impacts and specific examples

The regional impacts of incorporating exotic traits into maize hybrids are evident in various studies. In Uganda, the genetic gains in maize yield and key agronomic traits from 2008 to 2020 were significant, with CIMMYT entries showing a gain of 1.98% per year or 106 kg/ha/year (Asea et al., 2023). This underscores the importance of public-private partnerships in the development and delivery of new genetics to farmers. Similarly, in China, the genetic improvement in maize yield from the 1980s to the 2010s was substantial, with a global gain in yield potential of 559.3 kg/ha/year or 3.4% per year of release (Liu et al., 2021). These examples illustrate the positive regional impacts of integrating exotic germplasm into local breeding programs.

### 6.3 Lessons learned from failed attempts

Despite the successes, there have been challenges and lessons learned from failed attempts to incorporate exotic traits into commercial hybrids. One key lesson is the importance of understanding the genetic mechanisms and environmental interactions that influence hybrid performance. For example, the study by Yu et al. (2020) highlighted that heterosis is a trait-dependent and environment-specific phenotype, and the response of parental lines and their hybrids to environments resulted in various levels of heterosis. This indicates that careful selection and testing of hybrids in target environments are crucial for successful integration of exotic traits. Additionally, the study by Kamara et al. (2020) found no significant correlation between genetic distance and hybrid performance, suggesting that genetic diversity alone is not a reliable predictor of hybrid success. These insights emphasize the need for comprehensive evaluation and targeted breeding strategies to overcome the challenges associated with incorporating exotic germplasm into commercial maize hybrids.

## 7 Challenges and Limitations

### 7.1 Genetic incompatibility and linkage drag

One of the primary challenges in utilizing exotic varieties for maize genetic improvement is genetic incompatibility and linkage drag. The introduction of exotic germplasm often results in the transfer of undesirable traits along with the desired ones due to the close genetic linkage of these traits. This phenomenon, known as linkage drag, can significantly hinder the breeding process by introducing deleterious alleles that negatively impact yield and other agronomic traits (Hao et al., 2020). For instance, while exotic germplasm can introduce beneficial traits such as drought tolerance, it may also bring along traits that reduce overall plant vigor or increase susceptibility to diseases (Goldstein et al., 2019; Liu and Qin, 2021).

### 7.2 Complexity of trait expression

The expression of complex traits, such as yield and stress tolerance, is governed by multiple genes and their interactions with the environment. This complexity makes it challenging to predict and select for these traits accurately. Advances in genomic tools and molecular breeding techniques, such as CRISPR/Cas9 and genome-wide marker-assisted selection, have provided more precise methods for trait improvement. However, the polygenic nature of these traits still poses significant challenges in achieving consistent and predictable outcomes (Jiang et al., 2019; Lorenzo et al., 2022). The integration of multi-omics approaches and advanced phenotyping is essential to better understand and manipulate these complex traits (Gedil et al., 2019; Liu and Qin, 2021).

### 7.3 Economic and logistical barriers

The economic and logistical barriers associated with the use of exotic germplasm are substantial. The process of identifying, acquiring, and integrating exotic germplasm into breeding programs is resource-intensive and time-consuming. Additionally, the need for extensive field trials across multiple environments to evaluate the performance of new hybrids adds to the cost and complexity (Rogers et al., 2022; Nyoni et al., 2023). Public-private partnerships and international collaborations are crucial to sharing resources and expertise, thereby mitigating some of these economic and logistical challenges (Ying et al., 2019; Prasanna et al., 2021).

### 7.4 Regulatory and intellectual property issues

Regulatory and intellectual property (IP) issues also pose significant challenges in the use of exotic germplasm. The introduction of new genetic material often requires compliance with various national and international regulations, which can be cumbersome and time-consuming. Moreover, the IP rights associated with new varieties and breeding technologies can complicate the sharing and utilization of genetic resources (Goldstein et al., 2019; Hao et al., 2020). Ensuring that breeding programs adhere to these regulations while also protecting the rights of breeders and farmers is essential for the sustainable use of exotic germplasm in maize improvement (Jiang et al., 2019; Prasanna et al., 2021).

In conclusion, while the incorporation of exotic varieties holds great promise for enhancing maize genetic improvement, it is fraught with challenges related to genetic incompatibility, trait complexity, economic and logistical constraints, and regulatory and IP issues. Addressing these challenges requires a concerted effort involving advanced breeding technologies, robust partnerships, and supportive regulatory frameworks.

## 8 Future Directions

### 8.1 Advances in genomic tools and technologies

The integration of advanced genomic tools and technologies holds significant promise for the future of maize genetic improvement. Genomic selection (GS) models, for instance, have shown potential in enhancing the rate of genetic gain. The Germplasm Enhancement of Maize (GEM) project has demonstrated that GS can predict genetic gains more effectively than traditional phenotypic selection, with prediction abilities ranging from 0.36 to 0.75 for grain yield and from 0.78 to 0.96 for grain moisture (Rogers et al., 2022). Additionally, the use of genomic best linear unbiased prediction (gBLUP) has achieved high prediction accuracies for traits such as tocochromanols, which are essential for biofortification efforts. These advancements suggest that leveraging genomic tools can significantly enhance the efficiency and effectiveness of breeding programs.

### 8.2 Potential new sources of exotic germplasm

Exploring new sources of exotic germplasm is crucial for broadening the genetic base of maize. Studies have shown that landraces from regions such as Sahel and Coastal West Africa exhibit marked genetic diversity and hold great potential for genetic improvement. These landraces can provide novel alleles that are not present in the current elite germplasm pools, offering opportunities for pre-breeding and the development of new, resilient maize varieties. Furthermore, the incorporation of exotic genes from temperate regions has been shown to improve yield potential and stability in sub-tropical maize populations (Nyoni et al., 2022).

### 8.3 Strategies for overcoming current limitations

To overcome current limitations in maize breeding, several strategies can be employed. One approach is the use of managed-stress screening and selection for key secondary traits, which has been successfully implemented by CIMMYT to develop stress-tolerant maize varieties. Additionally, the adoption of modern breeding tools such as doubled haploid (DH) technology, molecular marker-assisted breeding, and transgenics can enhance breeding efficiency and genetic gains. It is also essential to address the challenges posed by genotype x environment interactions (GEI) by conducting multi-environment trials to identify stable and high-yielding genotypes (Nyoni et al., 2022).

### 8.4 Collaboration and data sharing among global breeding programs

Collaboration and data sharing among global breeding programs are vital for the successful integration of exotic germplasm and the development of improved maize varieties. The GEM project exemplifies the benefits of cooperative efforts between public and private sector breeders in enhancing the genetic diversity of maize. Multi-institutional efforts, particularly public-private alliances, are crucial for ensuring that improved varieties reach vulnerable farming communities and for developing technologies to protect maize crops from emerging biotic threats. By fostering collaboration and sharing data, breeding programs can leverage collective knowledge and resources to achieve greater genetic gains and address global challenges in maize production.

In conclusion, the future of maize genetic improvement lies in the continued advancement of genomic tools, exploration of new exotic germplasm sources, implementation of innovative breeding strategies, and fostering of global collaboration. These efforts will collectively contribute to the development of resilient, high-yielding maize varieties that can meet the growing demands of food security and climate resilience.

## 9 Concluding Remarks

The integration of exotic maize varieties into breeding programs has shown significant potential for enhancing genetic diversity and improving yield performance. Studies have demonstrated that exotic germplasm can broaden the genetic base of local populations, leading to increased yield stability and adaptability across diverse agro-ecologies. For instance, the incorporation of temperate exotic genes into sub-tropical maize germplasm pools in Zimbabwe resulted in hybrids with higher grain yield potential and earlier maturity compared to local commercial checks. Similarly, the genetic improvement of maize cultivars in China from the 1980s to the 2010s has led to substantial gains in yield potential, with a notable contribution from optimized plant traits such as leaf angle and photosynthetic capacity.

Moreover, the genetic dissection of drought tolerance in maize has highlighted the importance of advanced molecular breeding techniques, including genome editing and marker-assisted selection, in enhancing stress resilience. The potential of newer maize varieties to mitigate nitrogen emissions while increasing grain yield further underscores the environmental benefits of modern breeding practices. Additionally, the identification of gene resources for nutrient improvement in maize kernels offers promising avenues for enhancing the nutritional quality of maize.

The future of maize breeding lies in the strategic utilization of exotic germplasm to address the challenges posed by climate change, resource limitations, and the need for sustainable agricultural practices. The genetic diversity present in early and extra-early maturing maize germplasm adapted to sub-Saharan Africa provides a valuable resource for developing resilient maize varieties capable of thriving in diverse agro-ecological zones. Phenotypic characterization of maize landraces from West Africa has revealed significant genetic variability, which can be harnessed to improve agronomic traits and stress tolerance.

Furthermore, the genomic analysis of maize landraces has confirmed their potential as a rich source of novel genetic variation, essential for future breeding programs aimed at enhancing yield and adaptability. The integration of these diverse genetic resources into breeding pipelines will be crucial for achieving sustainable maize production and food security in the face of global environmental changes.

In conclusion, the continued exploration and incorporation of exotic maize varieties into breeding programs hold immense promise for the genetic improvement of maize. By leveraging the genetic diversity and unique traits of these exotic germplasm, breeders can develop high-yielding, resilient, and nutritionally enhanced maize varieties that meet the demands of a growing population and a changing climate.

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### Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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