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Analysis of Genetic Structure and Population Differentiation in Global Maize Germplasm

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Abstract Maize (*Zea mays* L.) is a vital staple crop worldwide, playing a critical role in global food security and agricultural sustainability. In this study, we analyzed the genetic structure and population differentiation of global maize germplasm by integrating studies on geographic origins, germplasm pool classification, and phenotypic diversity, and by evaluating methodologies such as molecular marker analysis (SSR, SNP, DArTseq), population genetics tools (STRUCTURE, PCA, AMOVA), and multi-omics data integration. We examined patterns of regional clustering, genetic admixture, and core collection identification, explored environmental and human-mediated factors driving differentiation, and discussed their implications for breeding and conservation. A case study comparing African and Latin American maize germplasm highlighted historical adaptation processes, diversity patterns, and cross-regional breeding opportunities. This study underscores the value of high-throughput sequencing, pan-genome approaches, and international collaboration for harnessing global maize diversity, with the expectation that such insights will guide future breeding programs aimed at enhancing resilience, productivity, and genetic conservation.

Keywords Maize germplasm; Genetic structure; Population differentiation; Molecular markers; Breeding strategies

1 Introduction

Corn (*Zea mays* L.) is a very important staple food crop in the world. It has a large planting area and multiple uses. It can be used as food, feed, and industrial raw materials, so it occupies a very important position in global food security (Prasanna, 2012; Adu et al., 2019a). Corn can adapt to many different agricultural ecological zones, and thus has become an indispensable part of many people's lives. Especially in regions such as sub-Saharan Africa, Latin America and Asia, corn is not only a major source of calories but also related to local economic stability (Badu-Apraku et al., 2021).

To do a good job in modern corn breeding, it is necessary to understand the genetic structure and population differences of global corn germplasm resources. The richer the genetic diversity is, the more likely breeders are to develop new varieties with high yield, strong stress resistance and good nutritional quality (Lu et al., 2009; Wu et al., 2015). Mastering information on population structure and differences can help identify heterosis populations, guide parental selection, and rationally utilize unique alleles, thereby accelerating genetic improvement and enhancing adaptability to environmental changes (Wang et al., 2022). Nowadays, with the use of high-throughput genotyping techniques, such as SNP and SSR markers, molecular analysis of corn germplasm can be conducted (Chen et al., 2024a). The research results show that there are many genetic variations and complex population structures in global maize germplasms, which also indicates that it is very important to introduce different germplasms in breeding (Zhang et al., 2016; Shu et al., 2021).

The global corn germplasm resources are widely distributed and diverse in type, and the differences among different regions are also quite obvious. This study does not merely list the results of these genetic structures and population differentiation, but rather aims to compare and examine them within the same framework, especially the overall situation among different geographical regions and germplasm types. When conducting the analysis, some molecular tools will be utilized, and research data from large-scale germplasm populations will also be referred to. Only in this way can we have a more thorough understanding of the distribution of genetic diversity, the process of subpopulation formation, and their possible impact on breeding strategies. Our focus is not limited to superior breeding strains, but also includes local varieties and some wild relatives. Ultimately, what is desired is not a simple conclusion, but an understanding of how these resources can support the continuous improvement of corn and maintain its ability to withstand risks when the agricultural environment is constantly changing.

2 Overview of Global Maize Germplasm

2.1 Geographic origins and historical spread of maize across continents

About 9 000 years ago, corn was domesticated in central and southern Mexico from its wild ancestor, the large ruminant (Matsuoka et al., 2002). From here, corn spread to various parts of the Americas along multiple human migration routes and reached South America approximately 6 500 years ago, where different local varieties were formed (Van Heerwaarden et al., 2010). After Europeans arrived in America, they brought corn to Europe, Africa and Asia. After multiple introductions, local selections and adaptations, corn has gradually been able to grow in various environments (Byerlee, 2020). Studies in genetics, archaeology and linguistics all indicate that the spread history of corn is very complex. Some regions, such as the southwestern part of the Amazon, have become important improvement centers for it, which has also led to the rich diversity of corn worldwide (Kistler et al., 2018).

2.2 Classification of germplasm pools

Corn germplasms around the world can be classified into several types based on their adaptability to different agricultural ecological regions: tropical type, temperate type, subtropical type and highland type. For instance, in Latin America, there are Andean populations, Central American lowland populations and highland populations. The germplasm in Europe includes varieties introduced from the Caribbean region and North America in different periods (Rebourg et al., 2003). In temperate regions such as the United States and China, the horse tooth type germplasm of the maize belt holds a dominant position. Tropical and subtropical germplasms are more common in Africa, Asia and Latin America (Smith et al., 2022). These gene pools not only reflect the propagation process of corn, but also the natural selection pressure it experiences when entering new environments (Mir et al., 2013).

2.3 Diversity in phenotypic traits and adaptation to local agro-ecological conditions

The appearance and characteristics of corn are not determined in one place. It took a long time for it to spread around the world. During this period, it constantly adapted to new environments and gradually changed. The color of the grains varies from light to dark, the height of the plants is different, there are early and late flowering times, and the strength of their stress resistance also varies greatly (Bedoya et al., 2017). In some places, the environment is very unique, which has also led to the formation of distinctive populations and gene pools there. For instance, the Guarani communities in South America, as well as the highlands of Mexico and the Andes Mountains (Bracco et al., 2016). These differences are not just for show; they come in handy in breeding work. These diversities are all very useful resources for increasing yield, enhancing stress resistance, or improving nutritional quality.

3 Methodologies for Assessing Genetic Structure

3.1 Use of molecular markers for genetic profiling

When conducting genetic analysis on corn, many people's first reaction is to use some molecular markers. The names might sound a bit awkward-simple sequence repeats (SSR), single nucleotide polymorphisms (SNP), and DArTseq-but their function is simple: to help us identify the genetic differences among various corns. It is not surprising that SSR and SNP occur more frequently. Firstly, they have high polymorphism. Secondly, the results are stable. Moreover, they can handle many samples at once, making them convenient to use (Bidyananda et al., 2024). Later, with the development of next-generation sequencing (NGS), the discovery and utilization of these markers became even faster (Figure 1). This not only enables a genome-wide assessment but also helps identify significant variations related to breeding or germplasm conservation.

3.2 Population genetics analytical tools

Data alone is not enough; analysis is also necessary. There are many statistical and computational methods used in the research. Some people prefer to use model-based clustering algorithms (such as STRUCTURE), some use principal component analysis (PCA) to identify major differences, and others use molecular variance analysis

(AMOVA) to observe the changes between and within populations (Labate, 2000). As for software, names like Arlequin, GDA, GENEPOP, and POPGENE may not be frequently heard, but their interfaces are quite intuitive and they have many functions, capable of handling various marker types and large amounts of data. With these tools, it is possible to identify which individuals belong to the same subgroup, calculate the genetic distance between them, and also compare the differences between groups.

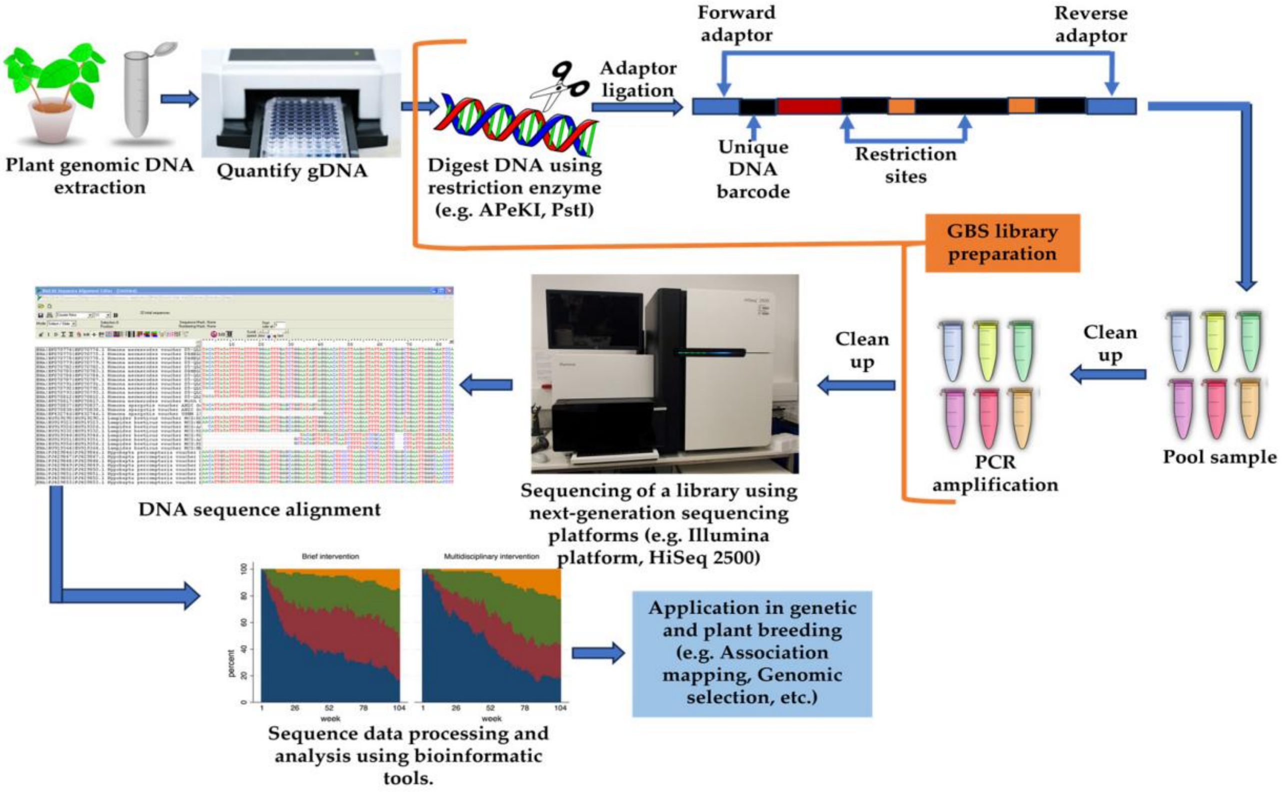

Figure 1 Schematic representation of the steps involved in GBS (genotype-by-sequencing) technology for plant research (Adopted from Bidyananda et al., 2024)

3.3 Integration of genomic, transcriptomic, and phenotypic datasets

In recent years, analyzing genetic data alone is no longer a novelty. Researchers tend to view genomic, transcriptomic and phenotypic data together (Grover and Sharma, 2016). The advantage of doing so is that it enables us to understand the genetic structure and trait differences of corn from multiple perspectives. For instance, by integrating high-density labeling data with transcriptome information and phenotypic data measured in the field, association analysis, genomic prediction, and genes that may affect important agronomic traits can be conducted (Bunjkar et al., 2024). This approach will make the analysis more accurate and be more conducive to breeding new varieties through marker-assisted selection or genomic selection.

4 Patterns of Genetic Structure in Global Maize Populations

4.1 Regional clustering and differentiation

Genetic analysis has found that corn populations often cluster together by region, which reflects their adaptation to the local environment and the different breeding histories of each area. Studies using microsatellites and SNPS have shown that there are several major population types, such as those in the Mexican Highlands, northern United States, tropical lowlands and the Andes. Among them, the genetic diversity of the highland population in Mexico was the highest, while that of the Andes and the northern United States was the lowest (Vigouroux et al., 2008). In China, germplasm used for breeding can be classified into two major categories: tropical and temperate types. Further classification not only reflects local adaptability but also is influenced by foreign germplasm (Shu et al., 2021). Geographical distance isolation and historical migration routes have played a significant role in the formation of these patterns.

4.2 Genetic admixture between landraces, improved varieties, and wild relatives

In the world of corn, the bloodline is rarely "clean". Local varieties can be mixed. In the corn of the southeastern United States, traces of the northern Flint type can be found, as well as genes from tropical lowlands. The situation in the lowlands of South America is different. The varieties there often blend the background of the Andes Mountains and tropical lowlands. Highland corn in Peru is even more interesting-there is little difference among them, indicating that local varieties often hybridize with each other and gene flow is constantly taking place (Arbizu et al., 2025). Modern breeding has pushed this kind of "mixture" to the norm. Breeders will actively combine germplasms from different sources to ensure that superior strains contain more mixed components and bring about richer genetic diversity (Van Inghelandt et al., 2010).

4.3 Identification of core collections for conservation and breeding

Identifying core germplasms with high genetic diversity is of great significance for both resource conservation and breeding efforts. Studies have shown that the germplasm from the Mexican Highlands and the Andes Mountains has not been fully utilized and may be very helpful for breeding projects (Bedoya et al., 2017). Core germplasm is usually determined through cluster analysis and population structure assessment, which ensures that they represent a wide range of genetic and phenotypic diversity in global maize germplasm (Adu et al., 2019b). These resources preserve beneficial genes such as drought tolerance, early maturity and disease resistance, which can provide support for the continuous improvement of corn (Badu-Apraku et al., 2021).

5 Factors Driving Population Differentiation

5.1 Environmental selection pressures and local adaptation mechanisms

Environmental conditions such as temperature, precipitation and altitude can exert significant selective pressure on corn populations. This will cause local adaptations of corn in different places and genetic differentiation to occur. The regions with relatively obvious differentiation in the genome are often related to some adaptive traits, such as flowering time and plant type. These traits are of great significance for the survival of corn in different agricultural ecological zones (Chen et al., 2024b). Research has found that in tropical, subtropical and temperate corn, there are some specific genomic regions related to adaptability, which indicates that environmental selection has a significant impact on population structure (Wu et al., 2015). In addition, some environmental factors, such as the lowest temperature, can also affect the key developmental processes of corn, thereby further promoting differentiation.

5.2 Human-mediated selection through breeding and seed exchange networks

Human activities can also influence population differentiation, including farmers' traditional choices, modern breeding and seed exchange. Farmers will select corn varieties that they like or are suitable for the local area. This choice will cause some quantitative traits to show significant differentiation even when there is a large flow of genes (Pressoir et al., 2004a; Pressoir et al., 2004b). Seed exchange networks are often related to society and culture, and they can affect the genetic structure of local populations. Different directions and frequencies of exchange can enhance or weaken differentiation (Orozco-Ramirez et al., 2016); Del Consuelo Aragon-Martinez et al., 2023. Modern breeding programs also generate different heterosis groups and subpopulations, which further enriches the global diversity of corn (Beckett et al., 2017).

5.3 Genetic drift, gene flow, and historical demographic events shaping diversity

Genetic drift, especially during the bottleneck period of corn domestication and some foundational events, has a significant impact on the diversity of corn. The domestication process will lead to a significant reduction in the effective population size, an increase in the proportion of harmful alleles, and also cause obvious differentiation. For instance, Andean corn has experienced a very strong founder effect (Beissinger et al., 2015). Gene flow, including the infiltration of genes from wild relatives such as ruminant, can bring new alleles and reduce the impact of harmful mutations, especially in highland populations (Wang et al., 2017). Historical population events, such as the expansion or reduction of distribution range, interact with selection and drift to form the complex differentiation pattern seen in global corn today (Van Heerwaarden et al., 2012).

6 Implications for Breeding and Conservation

6.1 Utilizing genetic structure information to broaden the breeding base

When choosing corn germplasm, if one only focuses on the ready-made materials, many potential resources will be overlooked. Genetic structure analysis can help people see further, identify and apply those diverse local and traditional varieties, so that the foundation of breeding will not be too single. The European Maize Evaluation Network once conducted a large-scale classification, dividing 626 local varieties into several different groups, and found that the differences were much greater than expected (Balconi et al., 2024). These differences are not insignificant decorations; on the contrary, they can be used to breed new varieties that are drought-resistant, disease-resistant and suitable for local conditions. Climate change is becoming increasingly evident. If this diversity is not incorporated into breeding programs, it will be even more difficult to ensure the sustainability of agriculture.

6.2 Identifying underrepresented germplasm for targeted introgression

Some gene banks are rarely dealt with passively in breeding, but this does not mean they are of no value. Through genetic and phenotypic assessment, those underrepresented or unique resources can be identified, which may precisely contain the key traits that are missing in the existing breeding lines. For instance, local varieties from Latin America or the highlands often have genes that can adapt to the local environment. Introducing them selectively into breeding not only enhances stress resistance and nutritional quality but also enables corn to adapt to some regions where the original growth conditions were not ideal (Prasanna et al., 2021). This approach is of great help in meeting the needs of small-scale farmers and different agricultural ecological zones.

6.3 Conservation strategies for maintaining genetic diversity in situ and ex situ

The methods for protecting germplasm are not singular. In-situ conservation involves preserving local and traditional varieties in farmlands, often associated with small-scale farming, traditional food production, and farming in remote areas. This enables genetic diversity and local adaptability to persist (Guzzon et al., 2021). Rather than in-situ conservation, such as collecting germplasm into gene banks and establishing core sets, it is more suitable for long-term preservation and future breeding research. In addition, if more market opportunities can be provided for local varieties or farmers can be encouraged to participate in breeding, it will also increase their willingness to continue growing and utilizing these diverse varieties.

7 Case Study

7.1 Historical introduction and adaptation

In the 16th century, corn was introduced to Africa from the Americas and quickly adapted to different agricultural ecological zones in Africa. In sub-Saharan Africa, breeding projects have been developing early-maturing and ultra-early-maturing varieties suitable for local conditions since then, which has accelerated the promotion of corn and enhanced its role in food security (Nelimor et al., 2020). In Latin America, corn is a native crop and has a deep historical connection with the local area. For thousands of years, local farmers have continuously selected and improved local varieties to enable them to grow in various environments such as lowlands and highlands (Guzzon et al., 2021). Latin America remains the core region of global corn diversity to this day, and the local varieties here are of great significance to food security and cultural heritage.

7.2 Comparative analysis of genetic diversity patterns

In Africa, the germplasm resources of corn are very complex, and the varieties vary greatly from place to place. Especially for local varieties and superior strains, their genetic diversity is very high and their population structure is not simple either. These differences are sometimes related to the history of breeding, and sometimes linked to the origin of ancestors and adaptability to the local environment. Studies in West Africa and South Sudan have shown that the differences within populations are quite obvious, and the degree of gene pool differentiation among regions ranges from medium to high. The local varieties of Burkina Faso are a typical example, not only with prominent differentiation but also with very limited gene flow between them and improved strains (Mathiang et al., 2022). The situation in Latin America is a different pattern. Analysis of local populations reveals that there are three main groups that can reflect historical migrations and exchanges: the Mexican/Southern Andes population, the Central American Lowland population, and the Andes population. Although there is a risk of gene loss, in those places where traditional agriculture and food systems are still well preserved, the diversity of local varieties remains high (Figure 2).

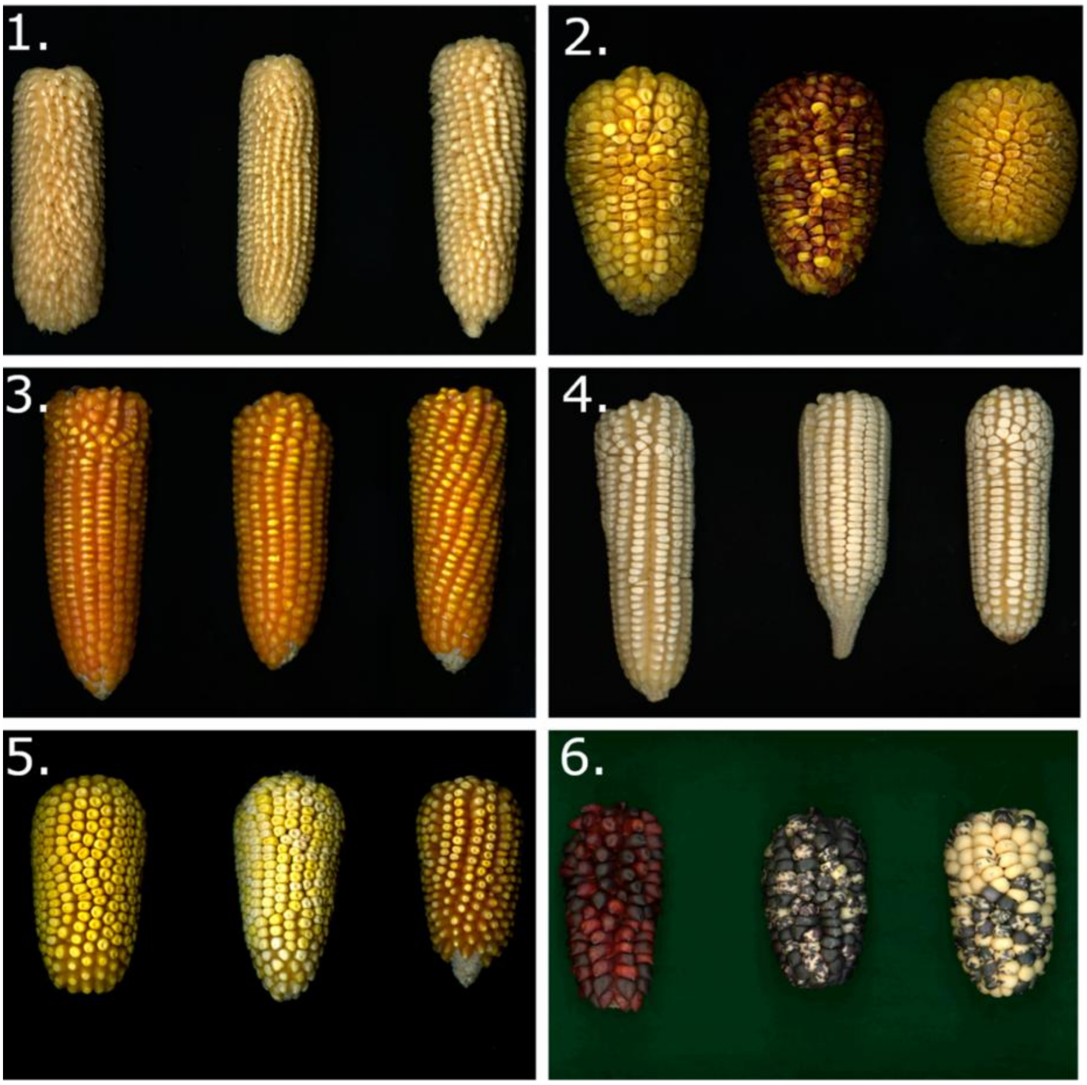

Figure 2 Maize races illustrating grain types: (1). Popcorn of the race ‘Pisingallo’ collected in Argentina (accession number: CIMMYTMA 29717), (2). Sweet corn of the race ′Chullpi′ collected in Peru (CIMMYTMA 18213), (3). Flint corn of the race ′Cuban Flint′ collected in Cuba (CIMMYTMA 2424), (4). Dent corn of the race ′Tuxpeño′ collected in Mexico (CIMMYTMA 679), (5). Dent corn of the race ′Conico′ collected in Mexico (CIMMYTMA 5645), (6). Floury corn of the race ′Cuzco′ collected in Peru (CIMMYTMA 32058). These accessions are conserved in the germplasm bank of the International Maize and Wheat Improvement Center (CIMMYT, Mexico). Photo credits: CIMMYT germplasm bank (Adopted from Guzzon et al., 2021)

7.3 Lessons learned for cross-regional breeding and germplasm exchange

In Africa and Latin America, the situation is not exactly the same, but there is a similarity-the diversity within populations is generally high, while the degree of differentiation is mostly moderate. Such resources are often very useful in breeding. Let's start with Africa. If some special hybrid vigor groups or those gene pools that have not been fully developed can be identified, new alleles may be introduced into hybrid breeding, making crops more resilient and adaptable (Gonhi et al., 2024). The story of Latin America is somewhat different. Local experience emphasizes that to address climate change and ensure food security, it is essential to preserve the diversity of local varieties. Moreover, the participation of farmers and in-situ conservation are not optional here (Del Consuelo Aragon-Martinez et al., 2023). If cross-regional germplasm exchange is based on in-depth analysis of genetic structure, it can not only bring beneficial alleles but also broaden the genetic basis of the two regions, providing more room for the development of breeding programs.

8 Future Perspectives

8.1 Role of high-throughput sequencing and pan-genome analyses

There are many methods for studying the genetic diversity of corn, but it is now difficult to bypass high-throughput sequencing and whole-genome analysis. In the early years, sequencing of important strains such as B73 and Palomero was regarded as a major advancement, but this was only the beginning. The new generation of sequencing platforms that emerged later are not only fast and large-scale, but also capable of conducting large-scale genotyping at one time and performing genome-wide association studies (GWAS) to identify key genes related to agronomic traits. Sometimes, these analyses do not only focus on common variations; rare haplotypes and structural changes can also be captured (Liu et al., 2019). In this way, the detailed picture of the genome becomes more complete. Ultimately, this information will be returned to breeding to assist breeders in more precise seed selection and improvement.

8.2 Integration of climate-resilience traits into breeding programs

Climate change is already an issue at hand. Whether admitted or not, for corn to maintain high yields in the future environment, it will have to rely on global diverse resources. There is no one-size-fits-all solution for this matter. High-throughput genotyping must be used in conjunction with precise phenotypic analysis to identify those alleles that are drought-resistant, heat-resistant and disease-resistant. For instance, the "Discovering Seeds" project of the International Maize and Wheat Improvement Center (CIMMYT) aims to identify genes with stress resistance and high nutritional value in different germplasms (Andorf et al., 2019). Once these genes are identified, they can be included in the breeding program to help develop varieties that are more adaptable to future climates. Ultimately, the speed of improvement largely depends on how closely genomic data and phenotypic data are combined.

8.3 Importance of international collaboration and open-access genetic databases

The challenge of corn is global, so it is difficult for a single institution to solve it alone. Cooperation among different countries and institutions is not only for preserving germplasm resources, but also for sharing data and experience (Shiferaw et al., 2011). If some information is not made open, many resources will be wasted. Therefore, it is urgent to establish an open access gene database and a global phenotypic network (Hou et al., 2024). In this way, researchers and breeders can use these data and germplasm efficiently no matter which country they are in. CIMMYT's SeeD project has demonstrated the benefits of this model-cooperation and openness, enabling the improvement results to be transformed into products useful to the public more quickly.

9 Concluding Remarks

The global corn germplasm resources have a high degree of genetic diversity and a complex population structure. Most genetic differences exist within subpopulations, and there are also moderate differences between subpopulations. Many studies have identified several major heterosis groups and subgroups, which are usually influenced by breeding history, artificial selection and local environmental adaptability. Both phenotypic analysis and molecular analysis have demonstrated that superior inbred lines, local varieties and breeding populations still retain significant genetic differences, which is crucial for the continuous improvement of corn.

Genetic diversity is the foundation for corn to adapt to different agricultural ecological zones and constantly changing environments. Unique hybrid vigor groups and rare alleles help to cultivate hybrid varieties with higher yields, stronger stress resistance and better other agronomic traits. The rational utilization of these diversities can enable breeders to expand the genetic base, leverage hybrid vigor, and adapt to the constantly changing breeding goals, thereby ensuring food security and sustainable production.

Whether corn can maintain high yields consistently and keep up with environmental changes actually depends not only on technology but also on the limited potential of the existing varieties themselves. Germplasm resources must be constantly sought and utilized, and this step cannot be halted. What method can be used? Molecular markers, genome-wide association analysis, and field trials-it is best to combine these to more accurately classify different heterosis groups and make it easier to identify valuable new alleles. But to be honest, this is only one step. The materials themselves should also be more comprehensive, especially those regional resources that have received little research in the past and have weak representativeness. If these resources can be brought in and truly incorporated into breeding projects, then even if major global challenges are encountered in the future, the adaptability of corn and the possibility of stable high yields will be more guaranteed.

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Conflict of Interest Disclosure

The author affirms 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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