Molecular Plant Breeding 2025, Vol.16, No.2, 146-155
http://genbreedpublisher.com/index.php/mpb

Case Study **Open Access**

Integrating Haploid Breeding and Germplasm Innovation in Maize Disease Resistance Breeding, Case Study

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Molecular Plant Breeding, 2025, Vol.16, No.2 doi: 10.5376/mpb.2025.16.0015
Received: 19 Mar., 2025
Accepted: 21 Apr., 2025
Published: 30 Apr., 2025

Preferred citation for this article:
Zhao L., Luo L.T., Yue E.K., and Shi J., 2025, Integrating haploid breeding and germplasm innovation in maize disease resistance breeding, case study, Molecular Plant Breeding, 16(2): 146-155 (doi: 10.5376/mpb.2025.16.0015)

Abstract This study analyzed how doubled haploid breeding and germplasm innovation can achieve synergistic effects in disease-resistant maize breeding, with case studies exploring their application in resistance breeding against southern rust, northern leaf blight, and multiple disease resistance. The study highlights the successful applications of these technologies and their future prospects. It was found that doubled haploid breeding significantly accelerates the selection process for disease-resistant traits, particularly enabling rapid screening of resistant genotypes during the induction and doubling stages. Concurrently, germplasm innovation offers a wealth of genetic resources for disease resistance breeding by utilizing local germplasm, wild relatives, and exotic resources to identify and incorporate new resistance genes, thus further improving breeding efficiency. This study demonstrates how these methods can substantially enhance the efficiency and precision of disease-resistant maize breeding, providing an effective technical pathway for future disease control and crop improvement in maize.

Keywords Maize; Doubled haploid breeding; Germplasm innovation; Disease-resistant breeding; Synergy

1 Introduction

Maize (*Zea mays* L.) is one of the most important food crops globally, serving as a staple for millions of people and playing a critical role in food security, animal feed, and biofuel production (Yang et al., 2017; Prasanna et al., 2021; Wang et al., 2022; Hou et al., 2024). Its significance is underscored by its extensive cultivation and the substantial economic value it generates. However, maize production is constantly threatened by various biotic stresses, including diseases caused by pathogens, which can lead to significant yield losses and impact food security (Nelson et al., 2017; Yang et al., 2017; López-Castillo et al., 2018). Effective disease control is therefore essential to ensure stable maize production and to meet the growing global demand for this vital crop.

Maize is susceptible to a wide range of diseases, including those caused by fungi, bacteria, viruses, and nematodes. These diseases can severely impact maize yields and quality, posing a major challenge for breeders (Nelson et al., 2017; Yang et al., 2017; Zhu et al., 2021). Traditional breeding methods have made significant strides in developing disease-resistant varieties, but the complexity of host-pathogen interactions and the need for resistance that is both durable and broad-spectrum remain significant hurdles (Nelson et al., 2017; Zhu et al., 2021). The genetic basis of disease resistance in maize is often complex, involving multiple genes and pathways, which complicates the breeding process (Nelson et al., 2017; Yang et al., 2017).

Doubled haploid (DH) technology has emerged as a powerful tool in modern maize breeding, offering a rapid and efficient method for developing pure lines (Dwivedi et al., 2015; Andorf et al., 2019; Meng et al., 2021). DH breeding involves the induction of haploids, which are then doubled to produce homozygous lines in a single generation, significantly accelerating the breeding process compared to traditional methods. This technology not only speeds up the development of new varieties but also enhances the precision of breeding programs by fixing desirable traits more effectively (Dwivedi et al., 2015; Meng et al., 2021). The integration of DH technology with other advanced breeding techniques, such as genomics-assisted breeding and high-throughput phenotyping, holds great promise for developing disease-resistant maize varieties (Dwivedi et al., 2015; Meng et al., 2021; Prasanna et al., 2021).

This study will utilize case studies to analyze how DH breeding and germplasm innovation achieve synergistic effects in disease-resistant maize breeding, exploring the integration of advanced breeding technologies. It aims to highlight the latest advancements, practical applications, and future prospects of these technologies in maize disease resistance breeding, with the hope of providing insights into the potential advantages and challenges of combining DH technology with germplasm innovation to enhance disease resistance in maize.

2 Application of Doubled Haploid Breeding in Disease-Resistant Maize Breeding

2.1 Principles and development of dh breeding technology

Doubled haploid (DH) breeding technology has revolutionized maize breeding by enabling the rapid production of completely homozygous lines from heterozygous parents. This method involves the in vivo induction of maternal haploids using a male haploid inducer genotype, followed by the identification of haploids at the seed or seedling stage, chromosome doubling of haploid seedlings, and selfing of fertile doubled haploid plants (Prigge et al., 2012; Chaikam et al., 2019). The development of haploid inducers with high haploid induction rates and adaptation to different environments has facilitated the widespread adoption of DH technology, particularly in tropical regions (Prigge et al., 2011;Chaikam et al., 2019). Advances in marker systems, such as the red root marker and high oil marker, have further improved the efficiency of haploid identification (Chaikam et al., 2019).

2.2 DH induction and doubling process

The DH induction process begins with the pollination of a target maize line with a haploid inducer line, which results in the production of seeds containing haploid embryos. These haploids are then identified using specific markers, such as the R1-nj marker, although alternative markers are being developed for germplasm where R1-nj is inhibited (Prigge et al., 2011; Chaikam et al., 2019). The next critical step is chromosome doubling, which can be achieved through chemical treatments or spontaneous doubling. Chemical agents, while effective, pose environmental and health risks, prompting research into spontaneous doubling methods (Boerman et al., 2020; Ren et al., 2020). Once chromosome doubling is successful, the doubled haploid plants are self-pollinated to produce homozygous seeds (Trentin et al., 2020).

2.3 Advantages of DH breeding

DH breeding offers several advantages over conventional breeding methods. It significantly accelerates the breeding process by reducing the number of generations required to achieve homozygosity, thus shortening the breeding cycle and increasing genetic gain (Boerman et al., 2020; Trentin et al., 2020). This rapid production of homozygous lines enhances selection efficiency, allowing breeders to more quickly identify and propagate disease-resistant traits (Prigge et al., 2012; Chaikam et al., 2019). Additionally, DH technology facilitates the integration of genome editing techniques, such as CRISPR/Cas9, enabling the rapid generation of pure elite lines with multiple desired traits (Liu et al., 2019; Wang et al., 2019). The ability to produce homozygous lines in a single generation makes DH breeding particularly valuable for developing disease-resistant maize varieties, as it allows for the swift incorporation and fixation of resistance genes (Chaikam et al., 2019; Trentin et al., 2020).

3 Role of Germplasm Innovation in Disease-Resistant Maize Breeding

3.1 Sources and methods of germplasm innovation

Germplasm innovation in maize breeding involves the strategic use of diverse genetic resources, including local germplasm, wild relatives, and exotic germplasm. Local germplasm, which is well-adapted to specific environmental conditions, provides a valuable source of genetic diversity for breeding programs. For instance, the Germplasm Enhancement of Maize (GEM) program has utilized doubled haploid (DH) breeding methods to expedite the release of lines from 300 exotic maize races, demonstrating the potential of integrating diverse genetic resources into breeding programs (Smith et al., 2008).

Wild relatives of maize, such as Zea diploperennis, have been successfully used to transfer resistance genes for traits like drought tolerance and Striga hermonthica resistance into tropical maize germplasm. This approach has led to the development of new inbred lines with enhanced resistance to these stresses, showcasing the importance of wild relatives in germplasm innovation (Shaibu et al., 2021). Additionally, the incorporation of exotic germplasm, such as temperate and tropical sources, has been shown to improve yield performance and stability in sub-tropical breeding programs, further highlighting the benefits of utilizing diverse genetic resources (Nyoni et al., 2023).

3.2 Germplasm innovation for disease resistance traits

Identifying and incorporating new disease-resistant genes into maize breeding programs is crucial for developing resilient cultivars. The use of doubled haploid technology has significantly accelerated the process of developing pure lines with desired traits, including disease resistance. This technology allows for the rapid fixation of traits and the unlocking of genetic variation, making it a valuable tool in modern maize breeding (Dwivedi et al., 2015; Meng et al., 2021).

For example, the REGNUR project has focused on identifying and increasing access to disease-resistant germplasm in eastern and southern Africa. Through diallel analysis, the project has evaluated the combining ability of elite inbred lines for grain yield and resistance to multiple diseases, enabling the pyramiding of resistance genes in new cultivars (Vivek et al., 2010). This approach has led to the development of hybrids with enhanced resistance to several diseases, demonstrating the effectiveness of germplasm innovation in improving disease resistance traits.

3.3 Successful cases of germplasm innovation in maize disease-resistant breeding

Several successful cases of germplasm innovation have significantly enhanced disease resistance in maize breeding. The CIMMYT, in collaboration with public and private sector institutions, has developed and deployed elite tropical maize germplasm with tolerance to key abiotic and biotic stresses, including diseases (Figure 1). This has resulted in the release of stress-tolerant maize cultivars across sub-Saharan Africa, Asia, and Latin America, showcasing the impact of multi-institutional efforts in germplasm innovation (Prasanna et al., 2021).

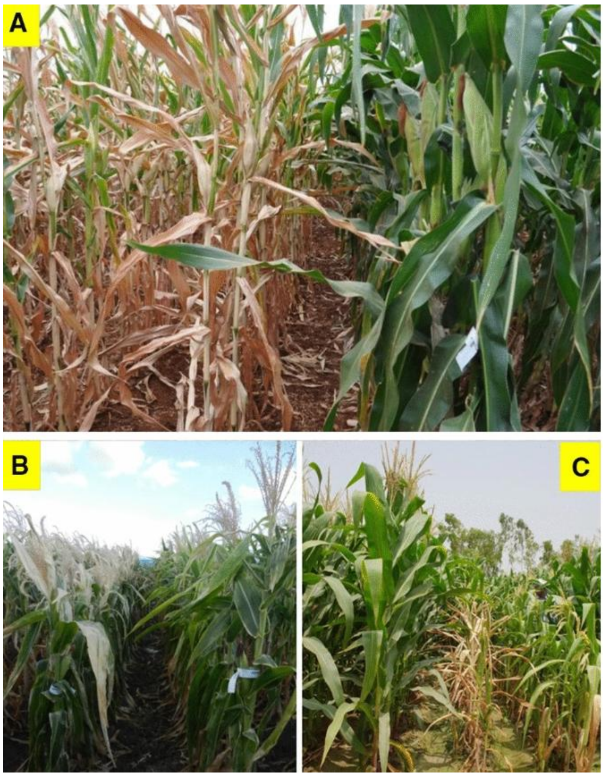

Figure 1 Phenotypic comparison of maize hybrids developed by CIMMYT-Mexico under different stress conditions (Adopted from Prasanna et al., 2021)

Image caption: A: Phenotypic comparison under controlled drought stress, showing leaf yellowing and plant wilting; B: Phenotypic comparison under controlled heat stress, illustrating the growth response of different maize hybrids to heat stress; C: Phenotypic comparison under controlled waterlogging stress, with some plants exhibiting stunted growth or leaf yellowing due to excess water (Adopted from Prasanna et al., 2021)

Another notable example is the use of wild maize relative *Zea diploperennis* to develop inbred lines with improved resistance to *Striga hermonthica* and drought. Hybrids derived from these inbred lines have shown superior performance and stability across different environments, highlighting the practical benefits of incorporating wild relatives into breeding programs (Shaibu et al., 2021). Additionally, the integration of exotic germplasm into sub-tropical breeding programs has led to the development of high-yielding and stable hybrids, further demonstrating the success of germplasm innovation in enhancing disease resistance (Nyoni et al., 2023).

4 Breeding Strategies Integrating DH Breeding and Germplasm Innovation in Maize

4.1 Strategies for integrating germplasm innovation with DH breeding

Integrating germplasm innovation with doubled haploid (DH) breeding involves combining the genetic diversity and desirable traits from various germplasm sources with the efficiency of DH technology to produce homozygous lines rapidly. One effective strategy is the introgression of resistance loci from diverse landraces into elite maize lines. For instance, European flint landraces have been successfully used to improve resistance to Gibberella ear rot (GER) in elite maize lines through DH breeding (Akohoue et al., 2023). Additionally, the development of haploid-inducer lines carrying CRISPR/Cas9 cassettes allows for targeted genome editing, further enhancing the integration of desirable traits into elite lines (Meng et al., 2022). This approach can significantly shorten the breeding cycle by bypassing the need for repeated backcrossing.

4.2 Process for rapid selection of disease-resistant genotypes

The DH breeding process accelerates the selection of superior genotypes by producing homozygous lines in a single generation. After germplasm innovation, such as the introduction of disease resistance genes, DH technology can be employed to rapidly fix these traits. For example, DH lines derived from biparental populations have been evaluated for resistance to multiple diseases, including maize lethal necrosis (MLN), under various environmental conditions. The use of genome-wide association studies (GWAS) and genomic predictions further aids in the rapid identification and selection of disease-resistant genotypes (Sadessa et al., 2022). This process ensures that only the most resistant lines are advanced in the breeding program.

4.3 Doubling and propagation of disease-resistant germplasm

Ensuring stable inheritance and large-scale propagation of disease-resistant traits involves the efficient doubling of haploid chromosomes and the subsequent propagation of DH lines. Traditional methods of chromosome doubling often involve the use of toxic chemicals, but recent advances have explored the natural fertility of haploids to reduce reliance on artificial treatments (Kleiber et al., 2012). Additionally, the overexpression of modified CENH3 in haploid inducer lines has been shown to improve maternal haploid induction rates, facilitating the production of DH lines with higher efficiency (Meng et al., 2022). These advancements ensure that disease-resistant traits are stably inherited and can be propagated on a large scale.

4.4 Successful cases of integrating disease-resistant germplasm with DH breeding in maize

Several successful cases highlight the integration of disease-resistant germplasm with DH breeding in maize. For instance, the introgression of resistance loci from European flint landraces into elite maize lines resulted in DH populations with significantly lower GER severity compared to the original elite lines (Akohoue et al., 2023). Another example is the use of DH technology to develop lines resistant to multiple diseases, such as gray leaf spot and turcicum leaf blight, through the identification of associated SNPs and the application of marker-assisted selection (Sadessa et al., 2022). These cases demonstrate the effectiveness of combining germplasm innovation with DH breeding to enhance disease resistance in maize.

5 Case Study: Application of Integrated DH Breeding and Germplasm Innovation in Specific Maize Diseases

5.1 Case study on resistance breeding for southern rust

Southern corn rust (SCR), caused by *Puccinia polysora*, is a major threat to maize production, leading to significant yield losses. The integration of doubled haploid (DH) breeding and germplasm innovation has shown promising results in developing resistant lines. For example, a study utilizing four DH populations and their testcross hybrids identified five loci associated with SCR resistance, with an important locus on chromosome 10 closely linked to the known resistance genes RPPC and RPPK. Resistance evaluation revealed diversity in disease resistance across different DH and hybrid populations (Figure 2) (Li et al., 2023).. Another research identified seven SNPs associated with partial resistance to SCR, highlighting the importance of resistant germplasms such as 'DH02' and 'Zheng39' (Zhou et al., 2018). Additionally, the discovery of the major QTL qSCR6.01 on chromosome 6, which accounted for up to 24.15% of phenotypic variation, further underscores the potential of DH breeding in SCR resistance (Lu et al., 2020). The identification and cloning of the RppM gene, encoding a CC-NBS-LRR protein, also demonstrate the effectiveness of integrating molecular markers in breeding programs (Wang et al., 2022).

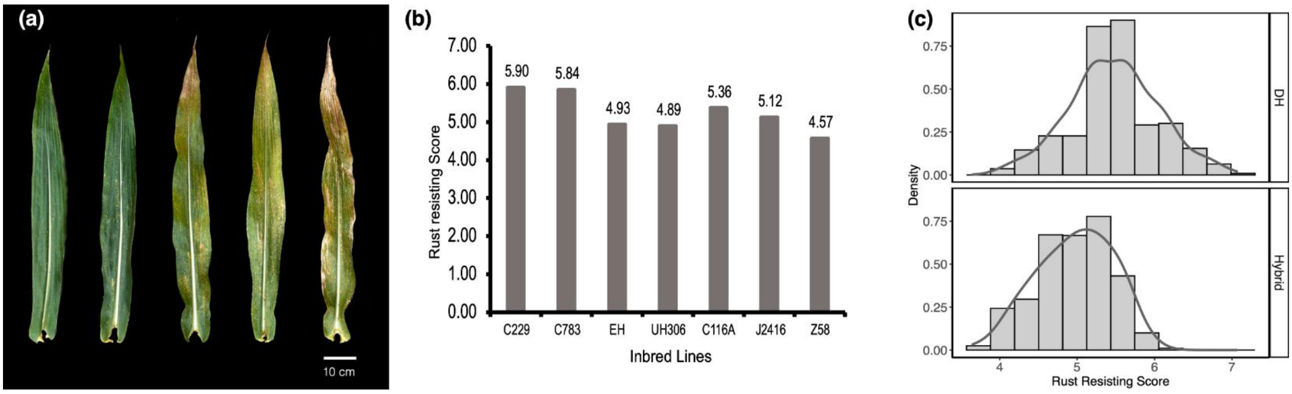

Figure 2 Southern Corn Rust Resistance Score (SCRRS) and its distribution (Adopted from Li et al., 2023)

Image caption: (A): The manifestation of susceptible leaves, the SCRRS of leaves were 9, 7, 5, 3, 1 from left to right; (B): the SCRRSs in DH founders and testers; (C): The distribution of SCRRS in DH (top) and hybrid (bottom) populations (Adopted from Li et al., 2023)

5.2 Case study on resistance breeding for northern leaf blight

Northern leaf blight (NLB), caused by *Exserohilum turcicum*, is another major disease affecting maize. The use of integrated technologies, including DH breeding and genomic tools, has facilitated the identification and promotion of resistant genotypes. For example, a study on multiple DH populations identified several SNPs associated with resistance to NLB, providing valuable markers for breeding programs (Sadessa et al., 2022). The use of genome-wide association studies (GWAS) and linkage mapping has also been instrumental in dissecting the genetic architecture of resistance to common rust, a related foliar disease, revealing significant SNPs and QTLs that can be targeted for NLB resistance breeding (Ren et al., 2020). These integrated approaches enable the accumulation of resistance alleles and the development of robust, resistant maize varieties.

5.3 Case study on breeding for multi-disease resistance

Breeding for multi-disease resistance in maize involves the accumulation of multiple resistance genes to provide broad-spectrum protection. The use of DH breeding has been particularly effective in this regard. For instance, the introgression of resistance loci from European flint landraces into elite maize lines has significantly improved resistance to Gibberella ear rot (GER) while maintaining desirable agronomic traits (Akohoue et al., 2023). Similarly, the evaluation of DH lines under various conditions, including artificial inoculation of maize lethal necrosis (MLN), has identified SNPs associated with resistance to multiple diseases, such as gray leaf spot and turcicum leaf blight (Sadessa et al., 2022). These findings highlight the potential of DH breeding to combine multiple resistance genes, thereby enhancing the overall disease resistance of maize cultivars. The integration of genomic prediction models further aids in the selection of superior lines with enhanced resistance profiles (Ren et al., 2020; Sadessa et al., 2022; Li et al., 2023).

6 Advantages and Limitations of the Integrated Strategy

6.1 Advantages of the integrated breeding strategy

The integration of haploid breeding and germplasm innovation in maize disease resistance breeding offers several significant advantages. Firstly, it improves the efficiency and precision of breeding programs. Doubled haploid (DH) technology accelerates the development of pure lines, which is crucial for heterosis utilization in maize hybrids, thereby significantly speeding up the breeding process compared to conventional methods (Dwivedi et al., 2015; Chaikam et al., 2019; Meng et al., 2021). This rapid generation of homozygous lines allows for quicker selection and deployment of disease-resistant varieties, which is essential in combating the various biotic stresses that maize faces, such as Fusarium and Gibberella ear rots (Miedaner et al., 2020; Akohoue and Miedaner, 2022).

Moreover, the integration of genomics-assisted breeding with DH technology enhances the precision of selecting high-quality resistant varieties. Genomics-assisted breeding allows for the identification of stable quantitative trait loci (QTL) associated with disease resistance, which can be effectively incorporated into breeding programs to improve selection efficiency (Miedaner et al., 2020; Akohoue and Miedaner, 2022). This combined approach ensures that the improved maize varieties are not only resistant to diseases but also possess other desirable agronomic traits, thus providing a comprehensive solution to the challenges faced by maize breeders (Wang et al., 2019; Prasanna et al., 2021).

6.2 Limitations in technology and resources

Despite the numerous advantages, the integrated strategy also faces several limitations, particularly in terms of technology and resources. One of the primary challenges is the high cost associated with DH breeding. The process of inducing haploids and subsequently doubling their chromosomes often involves expensive and toxic chemicals, which can be a significant barrier for small-scale breeding programs, especially in developing countries (Kleiber et al., 2012; Chaikam et al., 2019). Additionally, the need for specialized equipment and expertise further adds to the cost and complexity of DH technology (Dwivedi et al., 2015).

Access to diverse germplasm resources is another critical limitation. The success of germplasm innovation relies heavily on the availability of a wide range of genetic material. However, obtaining and maintaining such a diverse germplasm pool can be challenging due to regulatory, logistical, and financial constraints (Kleiber et al., 2012). Furthermore, the integration of new germplasm into existing breeding programs requires extensive testing and adaptation, which can be time-consuming and resource-intensive (Miedaner et al., 2020; Prasanna et al., 2021).

6.3 Solutions and technology optimization

To overcome these limitations, several solutions and technological optimizations can be implemented. One promising approach is the development of haploid inducers with higher induction rates and better adaptation to different environments. This can reduce the reliance on artificial chromosome doubling and lower the overall cost of DH line production (Kleiber et al., 2012; Chaikam et al., 2019). Additionally, advancements in marker systems for haploid identification, such as the red root marker and high oil marker, can improve the efficiency and accuracy of haploid selection, making the technology more accessible and cost-effective (Chaikam et al., 2019).

Another solution is the integration of genomics-assisted breeding with DH technology. By leveraging high-throughput phenotyping and precise genotyping, breeders can more effectively identify and select for disease-resistant traits, thus reducing the time and resources required for developing new varieties (Figure 3) (Miedaner et al., 2020; Akohoue and Miedaner, 2022). Public-private partnerships and multi-institutional collaborations can also play a crucial role in addressing resource constraints. These collaborations can facilitate the sharing of germplasm resources, expertise, and funding, thereby enhancing the overall efficiency and effectiveness of breeding programs (Wang et al., 2019; Prasanna et al., 2021).

7 Future Research Directions and Application Prospects

7.1 Development of efficient haploid induction technology

The development of efficient haploid induction technology holds significant promise for enhancing disease-resistant breeding in maize. Doubled haploid (DH) technology has already revolutionized maize breeding by enabling the rapid production of pure lines, which are crucial for heterosis utilization and hybrid development (Chaikam et al., 2019; Meng et al., 2021). Recent advancements in haploid induction, such as the development of haploid inducers with high haploid induction rates (HIR) and the integration of new marker systems for haploid identification, have further improved the efficiency and accessibility of DH technology (Chaikam et al., 2018; Chaikam et al., 2019). These advancements can significantly accelerate the breeding process, allowing for quicker incorporation of disease resistance traits into elite maize lines. Additionally, the combination of conventional breeding methods with genetic manipulation techniques, such as the overexpression of modified CENH3, has shown potential to further enhance HIR, providing a robust tool for disease-resistant breeding (Meng et al., 2022).

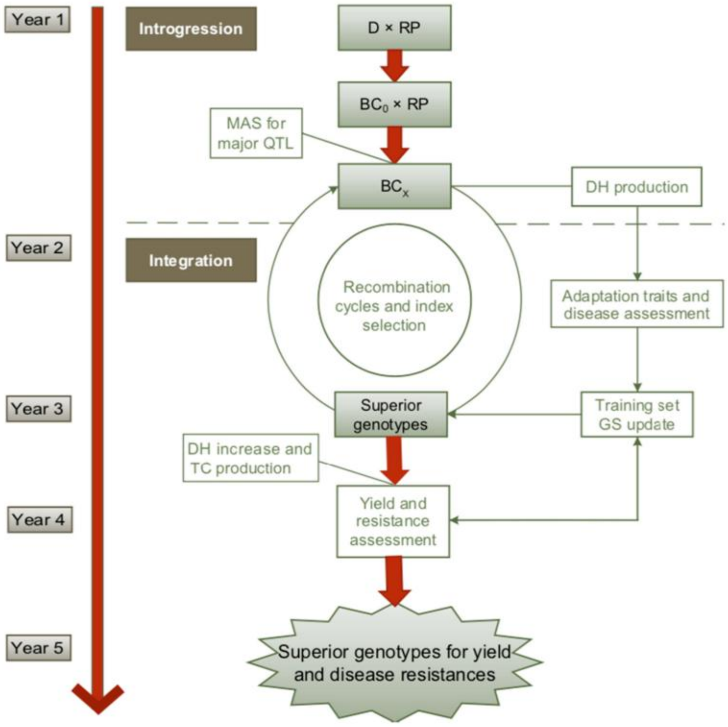

Figure 3 Schematic illustration of a rapid genomics-assisted breeding approach for using genetic resources in maize (Adopted from Miedaner et al., 2020)

Image caption: D=donor of resistance, RP=recurrent parent, BC=backcross, MAS=marker assisted selection, DH=doubled haploid lines, GS=genomic selection, TC=testcross (Adopted from Miedaner et al., 2020)

7.2 Application of gene editing in disease-resistant breeding

Gene editing technologies, particularly CRISPR/Cas9, offer unprecedented opportunities to enhance breeding efficiency for disease resistance traits in maize. The integration of CRISPR with DH technology, as demonstrated by the Haploid-Inducer Mediated Genome Editing (IMGE) approach, allows for the rapid generation of genome-edited haploids in elite maize backgrounds. This method can produce homozygous pure DH lines with desired trait improvements within two generations, bypassing the lengthy procedures of conventional breeding (Wang et al., 2019). Furthermore, the use of gene editing in conjunction with haploid induction systems has been shown to be effective across different genetic backgrounds, making it a versatile tool for disease-resistant breeding (Liu et al., 2019). The potential to precisely target and modify genes associated with disease resistance can lead to the development of maize varieties with enhanced resilience to various pathogens, thereby improving crop yields and food security.

7.3 Global collaboration and germplasm resource sharing

Global collaboration and germplasm resource sharing are critical for advancing disease-resistant breeding in maize. The success of breeding programs often relies on the availability of diverse genetic resources and the exchange of knowledge and technologies across borders (Li and Huang 2024). Initiatives like the International Maize and Wheat Improvement Center (CIMMYT) have demonstrated the importance of multi-institutional efforts in developing and deploying stress-tolerant maize cultivars (Prasanna et al., 2021). Public-private partnerships and international collaborations can facilitate the sharing of germplasm, breeding techniques, and technological advancements, thereby accelerating the development of disease-resistant maize varieties (Andorf et al., 2019; Prasanna et al., 2021). Additionally, the Germplasm Enhancement of Maize (GEM) program's utilization of DH technology to expedite the development and release of lines derived from exotic maize races highlights the potential benefits of leveraging global genetic diversity for breeding purposes (Smelser et al., 2016). By fostering a collaborative environment, researchers and breeders can collectively address the challenges posed by diseases and enhance the resilience of maize crops worldwide.

8 Concluding Remarks

The integration of doubled haploid (DH) breeding and germplasm innovation plays a pivotal role in advancing disease-resistant maize breeding. DH technology, which allows for the rapid development of homozygous inbred lines, has become a cornerstone in modern maize breeding programs due to its efficiency and effectiveness in fixing desirable traits. The use of DH lines offers significant economic, logistic, and genetic benefits over conventional inbred lines, facilitating the accelerated development of disease-resistant cultivars. Moreover, the development of haploid inducers with high haploid induction rates and the integration of new marker systems have further enhanced the accessibility and efficiency of DH technology in diverse germplasm, including tropical and landrace materials.

Germplasm innovation, particularly through the utilization of diverse genetic resources and advanced genomic tools, has been instrumental in enhancing the genetic gains in maize breeding programs. The integration of genomics-assisted breeding, high-throughput phenotyping, and precise breeding data management has enabled the development of elite maize cultivars with improved resistance to various biotic and abiotic stresses. These advancements have been crucial in addressing the challenges posed by climate-induced stresses and ensuring the sustainability of maize production in stress-prone environments.

To further enhance maize yield and disease resistance, it is imperative to adopt a multi-technology integration approach in disease-resistant breeding. Combining DH technology with genome editing tools such as CRISPR/Cas9, as demonstrated by the Haploid-Inducer Mediated Genome Editing (IMGE) approach, can significantly accelerate the development of pure elite lines with integrated favorable traits. Additionally, leveraging the natural fertility of haploids and optimizing chromosome doubling protocols can reduce production costs and make DH technology more accessible to small and medium-scale breeding programs, particularly in developing countries.

The potential of integrating DH breeding and germplasm innovation extends beyond improving maize disease resistance. This approach holds promise for enhancing global food security by increasing maize yields and ensuring the availability of resilient cultivars capable of withstanding diverse environmental stresses. By promoting sustainable agriculture practices and fostering public-private partnerships, the widespread adoption of these advanced breeding technologies can contribute to the development of robust agricultural systems that support the livelihoods of millions of farmers worldwide.

Acknowledgments

Thank you to the anonymous peer review for providing targeted revision suggestions for the manuscript.

Funding

This research was supported by Hangzhou Academy of Agricultural Sciences Science and Technology Innovation and Demonstration Promotion Fund Project (2022HNCT-08).

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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