

Marker-Assisted Selection (MAS) in Soybean Breeding

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Molecular Plant Breeding, 2025, Vol.16, No.1 doi: [10.5376/mpb.2025.16.0004](https://doi.org/10.5376/mpb.2025.16.0004)

Received: 20 Dec., 2024

Accepted: 23 Jan., 2025

Published: 31 Jan., 2025

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Preferred citation for this article:

Gao H.T., and Li H.Y., 2025, Marker-assisted selection (MAS) in soybean breeding, Molecular Plant Breeding, 16(1): 35-43 (doi: [10.5376/mpb.2025.16.0004](https://doi.org/10.5376/mpb.2025.16.0004))

Abstract Marker-assisted selection (MAS) has become an indispensable tool in modern soybean breeding, enabling precise and efficient improvement of key agronomic traits. This study explores the principles and applications of MAS in enhancing both biotic and abiotic stress resistance, as well as quality and yield traits in soybean. The study begins by outlining the various genetic markers utilized in MAS, such as simple sequence repeats (SSRs), single nucleotide polymorphisms (SNPs), and quantitative trait loci (QTLs), along with the key techniques and tools employed, including high-throughput genotyping platforms, marker-assisted backcrossing (MABC), and genomic selection (GS). Following this, the study delves into the successful application of MAS in soybean trait improvement, providing an in-depth case study on soybean cyst nematode resistance, which exemplifies the effectiveness of MAS in addressing significant agricultural challenges. Recent technological advancements, such as the integration of MAS with genomic selection and the potential of CRISPR/Cas9 to complement MAS strategies, are discussed. The study also addresses current limitations, including cost, resource requirements, and genetic background effects, while providing insights into future directions that emphasize the integration of MAS with other emerging breeding technologies. Ultimately, this paper highlights the pivotal role of MAS in accelerating soybean breeding and its potential to contribute to the development of climate-resilient and high-yielding soybean varieties.

Keywords Marker-assisted selection; Soybean breeding; Genetic markers; Biotic and abiotic stress resistance; Trait improvement

1 Introduction

Soybean (*Glycine max* (L.) Merr.) is a globally significant crop, primarily valued for its high protein and oil content. Historically, soybeans have been cultivated for thousands of years, originating in China and Eastern Asia, and have since become the most cultivated oilseed crop worldwide, with the majority of production now occurring in the Western Hemisphere. The crop's versatility extends beyond human consumption to include livestock feed, aquaculture, and industrial applications, making it a critical component of global agriculture (Choi et al., 2022). The continuous improvement of soybean varieties through breeding has been essential to meet the increasing demand for high-quality protein and oil, as well as to enhance resistance to various biotic and abiotic stresses (Anderson et al., 2019; Miller et al., 2023).

Marker-assisted selection (MAS) is a modern breeding technique that utilizes molecular markers to select desirable traits in plants, thereby accelerating the breeding process and improving accuracy. This method has been particularly beneficial in soybean breeding, where it aids in the identification and selection of quantitative trait loci (QTL) associated with important agronomic traits such as yield, protein, and oil content (Miller et al., 2023; Rani et al., 2023). MAS leverages genetic markers linked to specific traits, allowing breeders to screen large populations efficiently and select individuals with the desired genetic makeup without the need for extensive phenotypic evaluations (Fields et al., 2023; Yao et al., 2023). This approach not only enhances the efficiency of breeding programs but also facilitates the development of soybean varieties with improved nutritional profiles and stress resistance.

The study is to provide a comprehensive overview of the application and impact of Marker-Assisted Selection (MAS) in soybean breeding. This includes an examination of the historical context and significance of soybean breeding, a detailed discussion on the principles and methodologies of MAS, and an evaluation of its effectiveness

in improving key traits in soybean. The study will also explore recent advancements in MAS technology and its integration with other breeding techniques such as genomic selection and CRISPR/Cas9-based gene editing.

2 Principles and Techniques of Marker-Assisted Selection (MAS)

2.1 Genetic markers used in soybean breeding

Simple sequence repeats (SSRs), also known as microsatellites, are short, repetitive DNA sequences that are highly polymorphic. SSRs have been widely used in soybean breeding due to their high level of polymorphism, co-dominant inheritance, and ease of detection. They are particularly useful for constructing genetic linkage maps and identifying quantitative trait loci (QTLs) associated with important agronomic traits (Campos-Rivero et al., 2017). SSR markers have been successfully applied in the early selection of individual plants with desirable traits, such as disease resistance and yield components.

Single nucleotide polymorphisms (SNPs) are the most abundant type of genetic variation in genomes and have become the marker of choice for many plant breeding programs. SNPs offer several advantages, including high density across the genome, ease of automation, and the ability to provide high-resolution mapping. In soybean breeding, SNPs have been used extensively for genome-wide association studies (GWAS) and genomic selection (GS) to identify markers linked to traits such as yield, maturity, and seed composition (He et al., 2014; Ravelombola et al., 2021; Qin et al., 2022). The development of high-throughput genotyping platforms has further facilitated the use of SNPs in MAS.

Quantitative trait loci (QTLs) are genomic regions that contain genes influencing quantitative traits, which are typically controlled by multiple genes. QTL mapping involves identifying the location and effect of these loci on traits of interest. In soybean, QTL mapping has been used to identify regions associated with traits such as plant height, seed weight, and protein content (Zhang et al., 2004; Takagi et al., 2013; Qin et al., 2022). The integration of QTL mapping with MAS allows breeders to select for multiple traits simultaneously, improving the efficiency of breeding programs (Collard et al., 2005; Francia et al., 2005).

2.2 Techniques and tools for MAS implementation

High-throughput genotyping platforms, such as genotyping-by-sequencing (GBS), have revolutionized the field of plant breeding by enabling the rapid and cost-effective genotyping of large populations. GBS combines molecular marker discovery and genotyping in a single step, making it an ideal tool for MAS. This technique involves the digestion of genomic DNA with restriction enzymes, followed by the ligation of barcode adapters, PCR amplification, and sequencing. The resulting data can be used for GWAS, genetic diversity studies, and genomic selection (He et al., 2014; Ravelombola et al., 2021).

Marker-assisted backcrossing (MABC) is a technique used to introgress specific genes or QTLs from a donor parent into the genetic background of an elite cultivar. This method involves selecting individuals that carry the desired marker alleles at each backcross generation, thereby accelerating the recovery of the recurrent parent genome. MABC has been successfully used in soybean breeding to incorporate traits such as disease resistance and improved yield (Francia et al., 2005).

Genomic selection (GS) is a breeding approach that uses genome-wide marker data to predict the breeding values of individuals. Unlike traditional MAS, which focuses on a few markers linked to specific traits, GS considers the effects of all markers across the genome. This allows for the selection of individuals with superior genetic potential for complex traits. In soybean, GS has been shown to improve the accuracy of selection for traits such as yield and protein content, making it a valuable tool for modern breeding programs (Ravelombola et al., 2021; Qin et al., 2022). By integrating these principles and techniques, soybean breeders can enhance the efficiency and effectiveness of their breeding programs, ultimately leading to the development of superior cultivars with desirable agronomic traits.

3 Application of MAS in Soybean Trait Improvement

3.1 Enhancing biotic stress resistance

Marker-assisted selection (MAS) has been effectively utilized to enhance disease resistance in various crops, including soybeans. One notable application is the development of resistance to soybean cyst nematode (SCN), a significant pest affecting soybean yields. MAS enables the identification and incorporation of resistance genes into elite cultivars, thereby accelerating the breeding process and improving resistance durability. The use of molecular markers linked to SCN resistance genes allows for precise selection and pyramiding of multiple resistance genes, which can provide broad-spectrum and long-lasting resistance (Miklas et al., 2006; Devi et al., 2017; Dormatey et al., 2020).

Insect resistance in soybeans has also benefited from MAS. By identifying and utilizing markers linked to insect resistance genes, breeders can develop soybean varieties that are less susceptible to pests such as the soybean aphid and the bean pod weevil. This approach not only enhances the plant's inherent resistance but also reduces the reliance on chemical pesticides, promoting a more sustainable agricultural practice. The integration of insect resistance genes through MAS has shown promising results in other crops, suggesting similar potential for soybeans (Miklas et al., 2006; Dormatey et al., 2020).

3.2 Enhancing abiotic stress tolerance

Drought tolerance is a critical trait for maintaining soybean productivity under water-limited conditions. MAS has been employed to identify and incorporate quantitative trait loci (QTL) associated with drought tolerance into soybean breeding programs. For instance, the use of marker-assisted backcrossing (MABC) has been successful in improving drought tolerance in maize, which can serve as a model for similar efforts in soybeans. By selecting for favorable alleles at key loci, breeders can develop soybean varieties that maintain higher yields under drought stress (Ribaut and Ragot, 2006; Das et al., 2017).

Flooding and salinity are other abiotic stresses that significantly impact soybean production. MAS facilitates the identification of QTLs and genes associated with tolerance to these stresses, enabling the development of resilient soybean varieties. For example, the successful pyramiding of genes for submergence and salinity tolerance in rice through MAS demonstrates the potential for similar strategies in soybeans. This approach can lead to the development of soybean cultivars that can thrive in adverse environmental conditions, thereby ensuring stable yields (Ludwików et al., 2015; Das et al., 2017; Eltaher et al., 2023).

3.3 Quality and yield traits

Improving the oil and protein content of soybeans is a major breeding objective, given their economic importance. MAS has been instrumental in identifying markers linked to high oil and protein content, allowing for the selection of superior genotypes. The integration of these markers into breeding programs accelerates the development of high-quality soybean varieties. Advances in genotyping technologies have further enhanced the precision and efficiency of MAS in improving these complex traits (Francia et al., 2005).

Seed size and pod number are key yield components in soybeans. MAS enables the identification of QTLs associated with these traits, facilitating their incorporation into elite breeding lines. By selecting for favorable alleles, breeders can develop soybean varieties with improved yield potential. The success of MAS in enhancing yield traits in other crops, such as maize and rice, underscores its potential for similar applications in soybeans. This approach not only improves yield but also contributes to the overall efficiency and sustainability of soybean production (Francia et al., 2005; Ribaut and Ragot, 2006; Ludwików et al., 2015).

4 Advances in MAS Technology in Soybean Breeding

4.1 Integration of MAS with genomic selection

The integration of marker-assisted selection (MAS) with genomic selection (GS) has significantly enhanced the efficiency of soybean breeding programs. Genomic selection leverages high-throughput genotyping and advanced statistical models to predict the genetic value of breeding candidates, thereby accelerating the selection process. The combination of MAS and GS allows for the simultaneous selection of multiple traits, improving the overall

genetic gain. This approach has been successfully applied in various crops, including tomatoes, where it has expedited the breeding process by identifying genes and SNP markers associated with phenotypic variation (Varshney et al., 2013; Tiwari et al., 2022).

4.2 Use of high-density genetic maps

High-density genetic maps are crucial for the effective implementation of MAS in soybean breeding. These maps provide detailed information on the location of genes and quantitative trait loci (QTLs) associated with important agronomic traits. Advances in next-generation sequencing (NGS) technologies have facilitated the development of dense genetic maps, enabling precise marker-trait associations. For instance, genotyping-by-sequencing (GBS) has been employed to create high-density maps that combine molecular marker discovery and genotyping, thus enhancing the resolution of genetic studies (He et al., 2014; Hasan et al., 2021).

4.3 Role of bioinformatics and computational tools

Bioinformatics and computational tools play a pivotal role in analyzing and interpreting the vast amounts of data generated by NGS and other high-throughput genotyping methods. These tools are essential for managing large datasets, conducting genome-wide association studies (GWAS), and performing QTL mapping. The integration of bioinformatics in MAS has streamlined the identification of marker-trait associations and facilitated the development of robust breeding strategies. For example, bioinformatic pipelines are used to process GBS datasets, enabling the efficient discovery and genotyping of SNPs in crop genomes (He et al., 2014; Tiwari et al., 2022).

4.4 Recent advances in molecular markers

Recent advancements in molecular markers have revolutionized MAS in soybean breeding. The development of various types of markers, such as single nucleotide polymorphisms (SNPs), simple sequence repeats (SSRs), and amplified fragment length polymorphisms (AFLPs), has provided breeders with powerful tools for genetic analysis. SNP markers, in particular, have gained prominence due to their abundance and high-throughput genotyping capabilities. These markers have been effectively used in the identification and mapping of genes associated with disease resistance, yield, and other important traits (Figure 1) (Francia et al., 2005; Hasan et al., 2021; Jing et al., 2024).

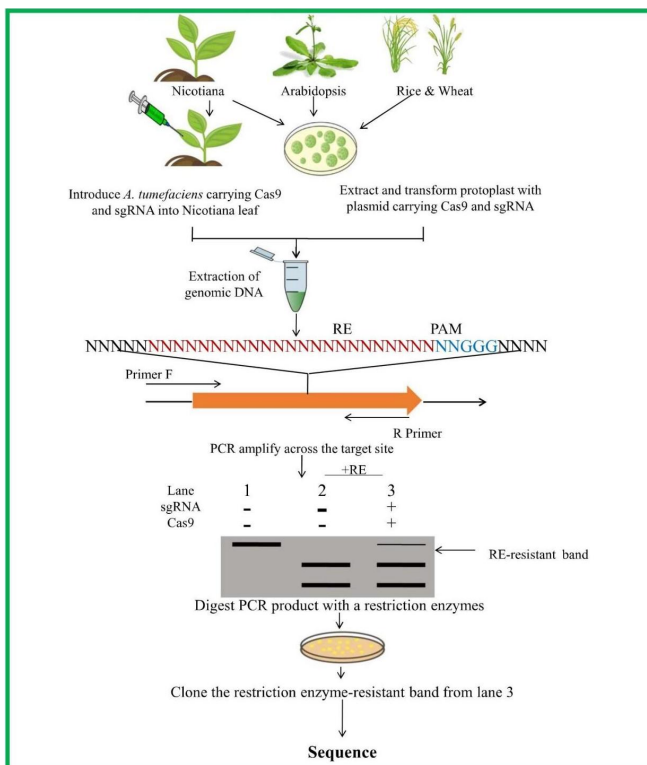


Figure 1 A schematic drawing illustrating an example of genome editing for crop improvement through the CRISPR/Cas9 strategy (Adopted from Hasan et al., 2021)

4.5 CRISPR/Cas9 and its potential synergy with MAS

The CRISPR/Cas9 genome editing technology holds great promise for enhancing MAS in soybean breeding. This technology allows for precise modifications of specific genes, enabling the introduction of desirable traits or the elimination of deleterious ones. The potential synergy between CRISPR/Cas9 and MAS lies in the ability to combine targeted gene editing with marker-assisted selection to achieve rapid and accurate trait improvement. While the application of CRISPR/Cas9 in soybean breeding is still in its early stages, its integration with MAS could lead to significant advancements in crop improvement (Francia et al., 2005; Jena and Mackill, 2008).

5 Challenges and Limitations of MAS in Soybean Breeding

5.1 Cost and resource requirements

Marker-assisted selection (MAS) in soybean breeding, while promising, is often hindered by significant cost and resource requirements. The process involves extensive genotyping and phenotyping, which can be expensive and labor-intensive. For instance, the need for high-throughput genotyping platforms and advanced bioinformatics tools to analyze large datasets adds to the overall cost (He et al., 2014; Chen et al., 2016). Additionally, the development and validation of molecular markers require substantial investment in both time and resources, making it challenging for smaller breeding programs to adopt MAS (Babu et al., 2004; Kumawat et al., 2020).

5.2 Marker density and genomic coverage

Another critical challenge in MAS is achieving adequate marker density and genomic coverage. High-density markers are essential for accurately mapping and selecting for traits, especially in complex genomes like that of soybean. However, the use of low or medium-density markers can lead to incomplete genomic coverage, reducing the efficiency of MAS (Babu et al., 2004; Sandhu et al., 2022). This limitation is particularly pronounced in polygenic traits, where multiple genes across the genome influence the trait, necessitating a comprehensive marker system to capture all relevant genetic variations (Miedaner and Korzun, 2012).

5.3 Genetic background effects

The genetic background of the breeding material can significantly impact the effectiveness of MAS. The presence of background genetic noise can obscure the association between markers and target traits, leading to inaccurate selection (Francia et al., 2005; Miedaner and Korzun, 2012). This issue is exacerbated in quantitative traits, where the effects of individual quantitative trait loci (QTL) are often small and influenced by the genetic context in which they are expressed. Consequently, the introgression of desirable traits can be less predictable and more challenging to achieve (Ribaut and Ragot, 2006; Wang et al., 2024).

5.4 Challenges in trait introgression and stability

Introgressing traits into elite soybean lines using MAS can be complicated by several factors. One major issue is the stability of the introgressed traits across different environments and genetic backgrounds. Traits that perform well in one genetic context may not exhibit the same level of expression or stability in another, leading to inconsistent breeding outcomes (Miedaner and Korzun, 2012; Kumawat et al., 2020). Additionally, the process of backcrossing to recover the recurrent parent genome while retaining the target trait can be time-consuming and may not always result in complete trait stability (Francia et al., 2005; Ribaut and Ragot, 2006). This challenge underscores the need for careful planning and extensive field testing to ensure the successful integration and stability of desired traits in soybean breeding programs.

6 Case Study: Successful Implementation of MAS for Soybean Cyst Nematode Resistance

6.1 Background and problem statement

Soybean cyst nematode (SCN, *Heterodera glycines* Ichinohe) is a significant pest affecting soybean production worldwide, causing substantial yield losses. Traditional breeding methods for SCN resistance are time-consuming and labor-intensive, necessitating the development of more efficient approaches. Marker-assisted selection (MAS) offers a promising solution by enabling the identification and selection of resistant genotypes based on genetic markers linked to SCN resistance traits (Li et al., 2009; Kadam et al., 2016; Santana et al., 2014).

6.2 Genetic basis of soybean cyst nematode resistance

The genetic basis of SCN resistance in soybeans primarily involves two major loci: Rhg1 and Rhg4. The Rhg1 locus is associated with copy number variations, where high copy numbers confer resistance (PI 88788-type), and low copy numbers are linked to susceptibility (Williams 82-type) (Kadam et al., 2016; Shaibu et al., 2020). The Rhg4 locus, on the other hand, involves a resistant allele that disrupts folate homeostasis at SCN feeding sites. Additionally, other quantitative trait loci (QTL) such as GmSNAP11 have been identified, contributing to the complex genetic architecture of SCN resistance (Yang et al., 2020).

6.3 Marker development and validation

Several studies have focused on developing and validating genetic markers for SCN resistance. For instance, SNP markers for Rhg1 and Rhg4 have been developed and validated using diverse soybean germplasm lines and recombinant inbred line (RIL) populations (Li et al., 2009; Kadam et al., 2016). These markers have shown high efficiency in differentiating resistant and susceptible genotypes, with selection efficiencies exceeding 90% in some cases (Santana et al., 2014). Additionally, novel markers such as KASPar assays and InDel markers have been introduced to enhance the precision of MAS (Yang et al., 2020).

6.4 Breeding program design and field implementation

Breeding programs utilizing MAS for SCN resistance typically involve several stages, including marker development, validation, and field implementation. For example, microsatellite markers near QTL for SCN resistance have been used to select resistant genotypes in populations derived from crosses between resistant and susceptible cultivars (Santana et al., 2014; Espindola et al., 2016). Field trials are then conducted to evaluate the performance of selected lines under SCN-infested conditions. The integration of MAS into breeding programs has significantly reduced the reliance on phenotypic evaluations, thereby accelerating the development of SCN-resistant cultivars.

6.5 Outcomes and impact on soybean production

The implementation of MAS for SCN resistance has led to the successful development of several resistant soybean cultivars. These cultivars have shown improved resistance to multiple SCN races, resulting in enhanced yield stability and reduced economic losses for soybean producers (Santana et al., 2014; Kadam et al., 2016). The use of MAS has also facilitated the pyramiding of multiple resistance genes, further strengthening the durability and effectiveness of SCN resistance in soybean breeding programs (Maroof et al., 2008; Yang et al., 2020). Overall, the adoption of MAS has had a positive impact on soybean production, contributing to sustainable agricultural practices and food security.

7 Future Directions and Perspectives

7.1 Enhancing MAS efficiency through genomic innovations

The efficiency of Marker-Assisted Selection (MAS) in soybean breeding can be significantly enhanced through the integration of advanced genomic technologies. Genotyping-by-sequencing (GBS) has emerged as a powerful tool, providing high-throughput sequencing capabilities that facilitate the discovery and genotyping of single nucleotide polymorphisms (SNPs) across large crop genomes. This approach not only accelerates the breeding process but also reduces costs, making it an ultimate MAS tool for large-scale plant breeding programs. Additionally, the development of next-generation marker genotyping platforms, such as AmpSeq, offers high accuracy, flexibility, and speed, further bridging the gap between marker development and MAS implementation. These innovations are crucial for improving the precision and efficiency of MAS, enabling the selection of superior genotypes with desirable traits.

7.2 Combining MAS with emerging breeding technologies

Combining MAS with emerging breeding technologies holds great promise for advancing soybean breeding programs. Integrated Genomic Selection (IGS), which combines MAS with genomic selection (GS), leverages molecular genetic markers to enhance the selection of complex traits such as yield and stress tolerance. This approach reduces the breeding cycle time and resources required, while increasing genetic gain. Moreover, the integration of MAS with technologies like speed breeding, machine learning, and environmental data can further

optimize breeding strategies, making them more robust and efficient. The use of marker-assisted backcrossing, forward breeding, and doubled haploid technology in conjunction with MAS has already shown success in improving various traits in crops like wheat, and similar strategies can be adapted for soybean breeding.

7.3 Potential of MAS in climate-resilient soybean varieties

The potential of MAS in developing climate-resilient soybean varieties is immense. As climate change poses significant challenges to crop production, the ability to breed varieties that can withstand abiotic stresses such as drought, salinity, and extreme temperatures is critical. MAS can be effectively used to monitor and select for genes associated with stress resistance, thereby accelerating the development of climate-resilient cultivars. The context-specific MAS (CSM) approach, which models target genotypes within specific environmental contexts, has shown promising results in improving grain yield in elite soybean populations and can be adapted to enhance climate resilience.

Acknowledgments

We are grateful to Dr. Xuanjun Fang, Director and Professor of the Hainan Institute of Tropical Agricultural Resources, and Director of the Hainan Provincial Key Laboratory of Crop Molecular Breeding for critically reading the manuscript and providing valuable feedback that improved the clarity of the text. We express our heartfelt gratitude to the two anonymous reviewers for their valuable comments on the manuscript.

Funding

This work was supported by the National Natural Science Foundation of China (32171937) and Hainan Province Science and Technology Special Funds (ZDYF2023GXJS153, ZDYF2023XDNY180).

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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