

Research Insight

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Improving Soybean Breeding Efficiency Using Marker-Assisted Selection

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Abstract This study provides an in-depth analysis of recent advances in MAS technology in soybeans, focusing on the identification of quantitative trait loci (QTLs) associated with key agronomic traits such as insect resistance, disease resistance, yield enhancement, and improved nutritional quality. The results showed that the integration of MAS into soybean breeding programs significantly shortened the breeding cycle and improved the accuracy of trait selection. This study also delves into case studies of the successful application of MAS in commercial soybean breeding programs. The aim of this study was to explore ways to improve the efficiency of soybean (*Glycine max*) breeding using marker-assisted selection (MAS), highlighting the potential of MAS to revolutionize soybean breeding and provide opportunities for the development of high-yield, disease-resistant and nutrient-enhanced soybean varieties.

Keywords Soybean (*Glycine max*); Marker-assisted selection; Quantitative trait loci (QTLs); Breeding efficiency; Disease resistance

1 Introduction

Soybean (*Glycine max* (L.) Merr.) is a cornerstone of global agriculture, serving as a vital source of protein and oil. It has been cultivated for thousands of years, initially in China and Eastern Asia, and has since become the most cultivated and utilized oilseed crop worldwide (Zhang, 2024). Today, approximately 80%~85% of the world's soybeans are grown in the Western Hemisphere, covering around 88 million hectares. Soybeans are integral to various industries, providing high-quality protein for livestock and aquaculture, oil for industrial uses, and essential components for human diets (Anderson et al., 2019). The crop's economic significance is underscored by its role in meeting the increasing global demand for protein and oil, making it a critical agricultural commodity.

Traditional soybean breeding methods, while successful in many respects, face several challenges. Classical breeding techniques, which rely on phenotypic selection, are often time-consuming and labor-intensive. Additionally, the complex genetic architecture of traits such as yield, protein, and oil content complicates the breeding process. Environmental factors further influence these traits, making it difficult to achieve consistent improvements across different growing conditions. The negative correlation between seed protein and oil concentration adds another layer of complexity, as improving one trait can adversely affect the other (Fields et al., 2023). These challenges necessitate the development of more efficient and precise breeding methods.

Marker-assisted selection (MAS) has emerged as a powerful tool to enhance the efficiency and precision of soybean breeding. MAS leverages molecular markers linked to desirable traits, allowing breeders to select plants with the desired genetic makeup early in the breeding process. This method significantly reduces the time and resources required for developing new cultivars. Studies have demonstrated the effectiveness of MAS in identifying quantitative trait loci (QTLs) associated with key traits such as seed protein and oil content, thereby facilitating the development of soybean varieties with improved nutritional profiles (Van and McHale, 2017; Fields et al., 2023). The integration of MAS with other advanced breeding technologies, such as genomic selection and CRISPR/Cas9 gene editing, holds promise for further accelerating soybean improvement (Miller et al., 2023; Yao et al., 2023).



This study aims to evaluate the impact of marker-assisted selection on soybean breeding efficiency; assess the current state of soybean breeding and the limitations of traditional methods; review the advancements in MAS and its application in soybean breeding; analyze the integration of MAS with other modern breeding technologies and provide recommendations for optimizing MAS to achieve higher breeding efficiency and better trait improvement.

2 Basics of Marker-Assisted Selection (MAS)

2.1 Definition and principles of marker-assisted selection

Marker-assisted selection (MAS) is a modern plant breeding technique that utilizes molecular markers to select plants with desirable traits. Unlike conventional breeding, which relies heavily on phenotypic selection, MAS leverages genetic information to make more precise and efficient selections. The principle behind MAS is to identify and use markers- specific DNA sequences linked to traits of interest- to track the presence of these traits in breeding populations. This method allows for the early and accurate selection of plants with desired characteristics, thereby accelerating the breeding process and improving the efficiency of developing new cultivars (Babu et al., 2004; Torres et al., 2010; Boopathi, 2020).

2.2 Types of molecular markers used in MAS

Several types of molecular markers are employed in MAS, each with its own advantages and applications. Simple sequence repeats (SSRs) also known as microsatellites, SSRs are short, repetitive DNA sequences that are highly polymorphic. They are widely used due to their high level of variability, co-dominant inheritance, and ease of detection (Santana et al., 2014). Single nucleotide polymorphisms (SNPs) are single base-pair variations in the DNA sequence. They are the most abundant type of genetic variation and can be efficiently detected using high-throughput genotyping technologies. SNPs are particularly useful for fine mapping and association studies (Babu et al., 2004; He et al., 2014). Genotyping-by-sequencing (GBS) is a next-generation sequencing approach that combines marker discovery and genotyping. It involves sequencing a reduced representation of the genome, which allows for the identification and genotyping of thousands of SNPs simultaneously. This method is cost-effective and suitable for large-scale breeding programs (He et al., 2014).

2.3 Advantages of MAS over conventional breeding techniques

MAS offers several advantages over traditional breeding methods. MAS allows for the selection of desirable traits at the seedling stage, reducing the time and resources needed for phenotypic evaluations over multiple generations (Torres et al., 2010; Boopathi, 2020). By using molecular markers linked to specific traits, MAS enables more accurate selection, reducing the likelihood of retaining undesirable traits and increasing the probability of achieving breeding goals (Babu et al., 2004; Sebastian et al., 2010). Although the initial setup for MAS can be expensive, the overall cost of breeding programs can be reduced due to fewer field trials and faster development of new cultivars (He et al., 2014). MAS is particularly useful for traits that are difficult to select phenotypically, such as disease resistance, drought tolerance, and other polygenic traits. It allows breeders to combine multiple desirable traits more effectively (Torres et al., 2010; Santana et al., 2014).

3 Key Traits Targeted in Soybean Breeding Using MAS

3.1 Yield improvement

Yield improvement is a primary focus in soybean breeding programs utilizing marker-assisted selection (MAS). The identification and utilization of quantitative trait loci (QTL) associated with grain yield have shown promising results. For instance, a study on elite soybean cultivars demonstrated that context-specific MAS (CSM) could effectively detect yield QTL within specific genetic and environmental contexts. This approach led to statistically significant yield gains of up to 5.8% in selected sublines, with some improved sublines being released as new cultivars (Sebastian et al., 2010). Despite the complexity of yield as a trait, advancements in genotyping technologies and the integration of MAS have facilitated the selection of genotypes with superior agronomic performance (Francia et al., 2005).

3.2 Resistance to biotic stresses (pests and diseases)

Breeding for resistance to biotic stresses, such as pests and diseases, is another critical area where MAS has been effectively applied. The use of molecular markers linked to resistance genes has enabled the rapid deployment of



these genes in breeding programs. For example, MAS has been successfully used to pyramid resistance genes for various diseases in crops like rice, providing broad-spectrum resistance (Jena and Mackill, 2008; Haque et al., 2021). In common beans, MAS has facilitated the detection and selection of resistance genes for multiple pathogens, simplifying the breeding process and enhancing resistance to diseases such as angular leaf spot, anthracnose, and various viruses (Miklas et al., 2006). These advancements highlight the potential of MAS in developing soybean varieties with enhanced resistance to biotic stresses.

3.3 Resistance to abiotic stresses

Abiotic stresses, including drought and salinity, pose significant challenges to soybean production. MAS has been instrumental in breeding for resistance to these stresses by identifying and incorporating QTL associated with stress tolerance. For instance, in rice, MAS has been used to pyramid genes conferring tolerance to submergence and salinity, resulting in varieties with improved stress resistance (Ludwików et al., 2015; Haque et al., 2021). Similarly, breeding programs for other crops have utilized MAS to combine traits such as root growth and phosphorus uptake mechanisms, addressing the complexity of abiotic stress resistance (Miklas et al., 2006; Araus et al., 2008). These strategies can be adapted to soybean breeding to enhance tolerance to abiotic stresses.

3.4 Enhancing nutritional quality and oil content

Improving the nutritional quality and oil content of soybeans is another important objective in breeding programs. MAS has the potential to accelerate the selection of genotypes with desirable traits related to nutritional quality. For example, the integration of MAS in conventional breeding has been shown to improve grain quality traits in rice by monitoring the presence of specific genes linked to these traits (Jena and Mackill, 2008). Although the application of MAS for enhancing nutritional quality and oil content in soybeans is still evolving, the success in other crops suggests that similar approaches can be employed to achieve these goals in soybean breeding programs.

4 Molecular Markers and Their Development in Soybean

4.1 Overview of marker discovery and mapping technologies

The discovery and development of molecular markers have significantly advanced plant breeding, particularly in crops like soybean. DNA markers, such as single nucleotide polymorphisms (SNPs) and quantitative trait loci (QTLs), have become essential tools in marker-assisted selection (MAS). These markers facilitate the identification of genetic variations linked to desirable traits, thereby enhancing the efficiency and precision of breeding programs. The process of marker discovery involves several steps, including polymorphism detection, linkage analysis, and map construction. These steps are crucial for understanding the genetic architecture of traits and for developing reliable markers for MAS (Collard et al., 2005; Hasan et al., 2021).

4.2 Identification of quantitative trait loci (QTLs) linked to key agronomic traits

Quantitative trait loci (QTLs) are genomic regions that contribute to the variation in quantitative traits, which are typically controlled by multiple genes. The identification of QTLs linked to key agronomic traits in soybean, such as protein content, disease resistance, and yield, is vital for improving these traits through MAS. Techniques like genome-wide association studies (GWAS) and linkage mapping have been employed to identify QTLs (Fu, 2024). For instance, a study identified 22 SNPs associated with protein content and five QTLs using various mapping approaches. Major QTLs were found on chromosomes 6 and 20, with significant implications for soybean breeding programs (Takagi et al., 2013; Qin et al., 2022).

4.3 Role of single nucleotide polymorphisms (SNPs) in MAS

Single nucleotide polymorphisms (SNPs) are the most abundant type of genetic variation in genomes and play a crucial role in MAS. SNPs are highly informative markers due to their abundance and stability, making them ideal for high-resolution mapping and selection. In soybean breeding, SNPs have been used to identify and select for traits such as protein content, disease resistance, and yield. The integration of SNP markers into MAS pipelines has improved the accuracy and efficiency of selection processes. For example, SNP markers identified through GWAS and other mapping techniques have been used to enhance the genomic selection (GS) of protein content in soybean, demonstrating the practical applications of SNPs in MAS (Hasan et al., 2021; Qin et al., 2022).



5 Integration of MAS in Soybean Breeding Programs

5.1 Workflow of MAS in soybean breeding

Marker-Assisted Selection (MAS) integrates molecular genetics with traditional breeding methods to enhance the efficiency and precision of selecting desirable traits in soybean breeding programs. The workflow of MAS typically involves several key steps. The first step is to identify molecular markers linked to traits of interest, such as yield, disease resistance, and stress tolerance. This involves genetic mapping and the use of technologies like Random Amplified Polymorphic DNA (RAPD) markers. Once markers are identified, genotyping is performed on breeding populations to detect the presence of these markers. This step is crucial for selecting individuals that carry the desired traits (Francia et al., 2005; Singh and Singh, 2015). Based on the genotyping results, individuals with favorable marker profiles are selected. This selection can be done at early stages, such as the seedling stage, which saves time and resources (Miedaner and Korzun, 2012; Devi et al., 2017). Selected individuals are then used in hybridization and backcrossing programs to combine desirable traits and develop new cultivars. Marker-assisted backcrossing (MABC) is a common approach used to introgress specific traits into elite lines (Ribaut and Ragot, 2006). The selected lines are validated through field trials across multiple environments to ensure that the desired traits are expressed consistently. This step helps in confirming the effectiveness of MAS in improving traits like yield and stress resistance (Sebastian et al., 2010).

5.2 Examples of MAS breeding programs for yield and stress resistance improvement

Several successful MAS breeding programs have been implemented to improve yield and stress resistance in soybeans. A context-specific MAS (CSM) approach was used to detect yield QTL within elite soybean populations. This approach led to statistically significant yield gains of up to 5.8% in selected sublines, with two improved sublines being released as new cultivars (Sebastian et al., 2010). In common bean, MAS was used to identify RAPD markers associated with drought resistance. The selected genotypes showed improved performance under stress conditions, demonstrating the effectiveness of MAS in enhancing drought tolerance. MAS has been successfully applied to select for disease resistance in various crops. For instance, in wheat and barley, MAS has been used to transfer resistance genes for rust, eyespot, and Fusarium head blight into elite breeding material (Miedaner and Korzun, 2012).

5.3 Integration of MAS with traditional breeding methods

Integrating MAS with traditional breeding methods offers several advantages. MAS allows for the selection of desirable traits at early stages, reducing the time and resources required for breeding. This is particularly beneficial for traits with low heritability, such as abiotic stress resistance (Singh and Singh, 2015; Devi et al., 2017). MAS provides a more precise selection process by targeting specific genetic markers linked to traits of interest. This reduces the risk of linkage drag and ensures that only the desired traits are selected (Francia et al., 2005). MAS can be combined with traditional phenotypic selection to enhance the overall efficiency of breeding programs. For example, Marker-Assisted Recurrent Selection (MARS) is designed to accumulate favorable QTLs in cross- and self-pollinated crops, complementing traditional selection methods (Singh and Singh, 2015). While the initial costs of genotyping and marker development can be high, the long-term benefits of MAS, such as reduced breeding cycles and improved trait selection, make it a cost-effective approach.

6 Challenges in Implementing MAS in Soybean Breeding

6.1 High costs of marker development and genotyping

The implementation of marker-assisted selection (MAS) in soybean breeding is often hindered by the high costs associated with marker development and genotyping. The initial phase of MAS requires scoring genotypes at numerous molecular marker loci, which can be financially demanding. Although advancements in next-generation sequencing (NGS) technologies, such as genotyping-by-sequencing (GBS), have made genotyping more cost-effective, the overall expenses remain significant, especially in the early stages of marker development (He et al., 2014). Additionally, the economic efficiency of MAS compared to traditional phenotypic selection is often questioned due to the high costs of genotyping, which can limit its application to traits with low heritability unless substantial investments are made (Moreau et al., 2000; Kuchel et al., 2005).



6.2 Limitations in identifying reliable markers for complex traits

Identifying reliable markers for complex traits, such as yield and abiotic stress tolerance, poses a significant challenge in MAS. Complex traits are often controlled by multiple genes and are influenced by genotype-environment interactions, making it difficult to pinpoint specific markers that consistently correlate with the desired traits (Babu et al., 2004; Francia et al., 2005). The efficiency of MAS is further complicated by the variability in genetic gains across different generations, as markers that are effective in early generations may lead to the fixation of unfavorable alleles in later generations. This complexity necessitates a robust understanding of the genetic architecture of the traits and the development of sophisticated statistical models to accurately associate markers with phenotypic traits (Sebastian et al., 2010).

6.3 Difficulties in applying MAS in developing countries due to resource limitations

The application of MAS in developing countries is often constrained by limited resources, including financial, technical, and infrastructural support. The high costs of marker development and genotyping, coupled with the need for advanced laboratory facilities and skilled personnel, make it challenging for developing countries to adopt MAS on a large scale (Collard and Mackill, 2008; Torres et al., 2010). Additionally, the lack of access to cutting-edge technologies and bioinformatics tools further hampers the effective implementation of MAS in these regions. As a result, the potential benefits of MAS in improving crop yields and resilience to environmental stresses remain largely untapped in developing countries, highlighting the need for international collaboration and investment to bridge this gap (Babu et al., 2004; He et al., 2014).

7 Case Study: Successful Application of MAS in Soybean Breeding

7.1 Description of a soybean breeding program using MAS

One notable soybean breeding program utilizing marker-assisted selection (MAS) focused on developing pest-resistant and pod shattering-resistant varieties. Pod shattering is a significant issue in soybean cultivation, leading to substantial yield losses during harvest. The breeding program aimed to incorporate resistance to pod shattering by leveraging specific DNA markers associated with this trait. The KSS-SNP5 SNP marker on chromosome 16 was identified as a key marker for pod shattering resistance and was integrated into the MAS system for soybean breeding (Kim et al., 2020).

7.2 Breeding strategy, markers used, and outcomes

The breeding strategy involved the use of the TaqMan SNP assay to detect the A/G allele of the KSS-SNP5 marker in various breeding materials, including $F_{2:3}$ populations and yield trial stage breeding lines. The MAS prediction accuracy was evaluated by comparing genotyping data from the TaqMan assay with phenotype data obtained through the dry-oven method. The results demonstrated high prediction accuracy, with 92.5% and 96.2% accuracy in two $F_{2:3}$ populations and breeding lines, respectively. Under severe conditions, the accuracy was 85% and 96% (Kim et al., 2020).

Additionally, another study focused on improving grain yield in elite soybean populations using context-specific MAS (CSM). This approach involved detecting yield QTL within specific genetic and environmental contexts, modeling a target genotype, and selecting subline haplotypes that matched the target genotype. The selected subline haplotypes were then compared to their mother lines in yield trials across multiple environments and years. Statistically significant yield gains of up to 5.8% were confirmed in some of the selected sublines, and two improved sublines were released as new cultivars (Sebastian et al., 2010).

7.3 Lessons learned and key takeaways for future breeding efforts

The successful application of MAS in soybean breeding programs has provided several key lessons and takeaways for future efforts. The use of specific markers, such as KSS-SNP5 for pod shattering resistance, can achieve high prediction accuracy, making MAS a reliable tool for selecting desirable traits (Kim et al., 2020). MAS allows for the efficient utilization of resources by enabling the selection of traits at early stages, thus expediting the breeding process. This efficiency is particularly beneficial for traits that are labor-intensive and time-consuming to evaluate phenotypically (Singh and Singh, 2015; Kim et al., 2020). The context-specific MAS approach demonstrated that considering the genetic and environmental contexts can lead to significant yield improvements. This approach can



be adapted to other traits and crops to enhance breeding outcomes (Sebastian et al., 2010). Combining MAS with conventional breeding methods, such as phenotypic selection and backcrossing, can enhance the overall effectiveness of breeding programs. This integrated approach can help accumulate favorable QTLs and improve complex traits (Miedaner and Korzun, 2012; Singh and Singh, 2015). The scalability of MAS depends on the availability of resources and the specific traits being targeted. While MAS has shown great promise in soybean breeding, its broader adoption will require continued advancements in genotyping technologies and the development of more robust markers for various traits (Francia et al., 2005; Collard and Mackill, 2008).

8 Technological Advancements to Support MAS

8.1 Advances in genome sequencing and genotyping platforms

The advent of next-generation sequencing (NGS) technologies has significantly advanced the field of genome sequencing and genotyping, providing ultra-throughput sequences that have revolutionized plant genotyping and breeding. Genotyping-by-sequencing (GBS) is a notable application of NGS protocols, which combines molecular marker discovery and genotyping in a cost-effective manner. GBS involves the digestion of genomic DNA with restriction enzymes, followed by the ligation of barcode adapters, PCR amplification, and sequencing of the amplified DNA pool on a single lane of flow cells. This method has been successfully used in genome-wide association studies (GWAS), genomic diversity studies, genetic linkage analysis, and genomic selection in large-scale plant breeding programs (He et al., 2014). Additionally, high-throughput genotyping (HTG) platforms provide higher genome-wide marker density, which is crucial for the success of quantitative trait loci (QTL) and candidate gene identification in soybean improvement (Figure 1) (Bhat and Yu, 2021).



Figure 1 Diagram showing the critical role of high-throughput phenotyping (HTP) and high-throughput genotyping (HTG) in the precise and accurate identification of quantitative trait loci (QTLs)/quantitative trait nucleotides (QTNs)/genes as well as genomic selection (GS)-based estimation of genomics-estimated breeding values (GEBVs) (Adopted from Bhat and Yu, 2021)

8.2 Application of genomic selection alongside MAS

Genomic selection (GS) is a promising approach that complements marker-assisted selection (MAS) by using genome-wide markers to predict the breeding value of individuals. This method addresses the limitations of conventional phenotypic-based selection, which is often time-consuming and influenced by environmental factors. By integrating GS with MAS, breeders can achieve higher genetic gains per unit time and improve the efficiency of breeding programs. For instance, the use of high-throughput digital phenotyping (HTP) platforms alongside



HTG can significantly enhance the precision and accuracy of phenotyping, thereby increasing the practical utility of genomics-assisted breeding (GAB) in soybean improvement (Bhat and Yu, 2021). Moreover, context-specific MAS (CSM) approaches have been developed to model target genotypes within specific genetic and environmental contexts, leading to significant yield gains in selected sublines (Sebastian et al., 2010).

8.3 Use of bioinformatics and computational tools to accelerate marker identification

The integration of bioinformatics and computational tools is essential for analyzing and interpreting the vast datasets generated by advanced genotyping platforms. Bioinformatic pipelines are required to process GBS datasets, enabling the identification and genotyping of single nucleotide polymorphisms (SNPs) in crop genomes and populations (He et al., 2014). Additionally, the development of semi-automated pipelines that incorporate trait-associated SNP marker discovery, low-cost genotyping through amplicon sequencing (AmpSeq), and decision-making processes has been demonstrated in grapevine breeding. This approach offers several advantages, including accuracy, flexibility, speed, high-throughput, low-cost, and easily automated analysis, making it broadly applicable to diverse crop species (Yang et al., 2016). Furthermore, comparative and functional genomic approaches, along with extensive mapping of resistance gene analogs (RGAs), can reveal new candidate genes and selectable markers for use in MAS, thereby facilitating the genetic improvement of crops (Francia et al., 2005; Torres et al., 2010).

9 Future Prospects for MAS in Soybean Breeding

9.1 Emerging trends in MAS

The integration of marker-assisted selection (MAS) with advanced gene editing technologies such as CRISPR is a promising trend in soybean breeding. This combination can significantly enhance the precision and efficiency of breeding programs. CRISPR technology allows for targeted modifications at specific genomic loci, which, when combined with MAS, can accelerate the development of soybean varieties with desirable traits. For instance, the use of CRISPR in conjunction with MAS can facilitate the precise introduction of beneficial alleles identified through marker-assisted selection, thereby improving traits such as disease resistance and yield potential (Figure 2) (Ribaut and Ragot, 2006; Rosero et al., 2020). This integrated approach is expected to overcome some of the limitations of traditional breeding methods and enable the rapid development of superior soybean cultivars.



Figure 2 Dual strategy of breeding for drought tolerance and the introduction of underutilized crops to make more resilient cropping systems to water deficiency conditions (Adopted from Rosero et al., 2020)

9.2 Potential for MAS to enhance climate-resilient soybean varieties

The potential of MAS to enhance climate-resilient soybean varieties is substantial. Climate change poses significant challenges to agriculture, including increased frequency of droughts, floods, and extreme temperatures. MAS can be employed to identify and select for traits that confer resilience to these stresses. For example, MAS has been successfully used to improve drought tolerance in crops like maize, which can be translated to soybean breeding programs (Ribaut and Ragot, 2006). Additionally, integrating MAS with genomic selection (GS) and other advanced breeding techniques can further enhance the development of climate-smart soybean varieties that can withstand abiotic stresses while maintaining high yield and quality (Araus et al., 2008; Rosero et al., 2020; Sinha et al., 2023).



9.3 Expanding MAS to improve complex traits and biofortified crops

Expanding the application of MAS to improve complex traits and biofortified crops is another promising prospect. Complex traits, such as yield, stress tolerance, and nutritional quality, are often controlled by multiple genes and are influenced by environmental factors. MAS, combined with high-throughput genotyping and phenotyping, can facilitate the selection of these complex traits by identifying and utilizing quantitative trait loci (QTLs) associated with them (Babu et al., 2004; Francia et al., 2005; Gupta et al., 2010). Moreover, MAS can be used to develop biofortified soybean varieties with enhanced nutritional profiles, such as increased protein content or improved fatty acid composition. This approach has already shown success in other crops, such as rice and wheat, where MAS has been used to incorporate traits like disease resistance and improved grain quality (Jena and Mackill, 2008). By leveraging the power of MAS, soybean breeding programs can achieve significant advancements in developing varieties that meet the nutritional needs of a growing population while also addressing environmental challenges.

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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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