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Marker-Assisted Selection in Cassava: From Theory to Practice

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Abstract Cassava (*Manihot esculenta* Crantz) is an important food crop in tropical and subtropical regions of the world, with high starch content and significant industrial application value. Marker-assisted selection (MAS) is an important technology in plant breeding, especially in cassava improvement, showing great potential for application. Mas provides an efficient genetic improvement method for cassava breeding, which can accelerate the improvement process of traits, especially in key agronomic traits such as starch content and disease resistance. This study systematically reviews the relevant theories of MAS, discusses the discovery of cassava genetic markers, and highlights the role of MAS in improving the efficiency and accuracy of selection, especially in accelerating the development of new cassava varieties through case studies. Despite the technical and resource challenges, the application prospect of MAS technology in cassava breeding remains optimistic. This review aims to provide in-depth scientific reference and practical guidance for cassava breeders and researchers worldwide, and to provide directions for future research.

Keywords Cassava; Marker-assisted selection; Starch synthesis; Quantitative trait loci; Gene editing

Cassava (*Manihot esculenta* Crantz) is a staple food crop that plays a key role in global food security, especially in tropical and subtropical regions, where it is the main energy source for millions of people and has important industrial applications. Despite its importance, cassava has historically received less research investment attention than other crops. Traditional breeding has made progress in enhancing cassava's tolerance to biological and abiotic stresses, increasing productivity in terms of fresh root and dry matter content, and improving quality traits such as starch quality and carotenoid content (Ceballos et al., 2012).

Marker assisted selection (MAS) is a modern breeding technique that uses molecular markers to select desirable traits in plants, thereby speeding up the breeding process. MAS has been successfully applied to many crops to improve yield, disease resistance and quality traits. In cassava, the application of MAS is still in its infancy, but holds great promise for genetic improvement of crops. The development of double haploid production protocols in cassava is an example of increasing the efficiency of genetic improvement through MAS (Ceballos et al., 2012).

The theory behind MAS is based on identifying genetic markers associated with specific traits. These markers can be used to screen breeding populations and select individuals with desired traits even before they manifest. This approach is particularly beneficial in cassava, where high heterogogginess, irregular flowering and poor seed setting present challenges to conventional breeding, and biotechnology tools, including genetic engineering and MAS, have the potential to overcome these challenges and drive cassava improvement (Petersen et al., 2005).

However, the practical application of MAS in cassava faces several bottlenecks, including the need for efficient and reliable phenotypic analysis, the availability of genotyping methods, and the integration of MAS with traditional breeding programs. The completion of cassava genome sequence provides a valuable resource for identifying markers associated with key traits and is expected to enhance the impact of MAS on cassava breeding (Ceballos et al., 2012).

This review will discuss the current status of MAS in cassava breeding, identify bottlenecks and challenges, and discuss the practical application and role of MAS in cassava improvement. The biosafety aspects of molecular tools used in cassava biotechnology will also be considered, as the use of selectable and gradeable markers must be evaluated for safety in terms of toxicity, allergenicity, pleiotropy, horizontal gene transfer and their overall impact on food, feed and environmental safety (Petersen et al., 2005). This review aims to provide a comprehensive overview of how MAS can be effectively implemented in cassava breeding programmes to achieve improvements in crop varieties that contribute to food security and economic development in regions where cassava is a major crop.

1 Theoretical Basis of Marker-assisted Selection

1.1 Definitions and types of genetic markers

Genetic markers are tools used in the field of molecular biology and genetics to identify a specific DNA sequence of an organism that can be located at a specific location on a chromosome, usually associated with certain genetic traits or able to reveal patterns of transmission of genetic information. Genetic markers have important biological significance due to their wide application in disease research, genetic diversity research, genetic relationship analysis, and plant and animal breeding.

There are many types of genetic markers, common ones include restricted fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), simple sequence repeats (SSR, also known as microsatellites), single nucleotide polymorphism (SNP), cleaved amplified polymorphic sequence (CAPS), and randomly amplified polymorphic DNA (RAPD). Each markup type has its own unique characteristics and scope of application.

RFLP is an early commonly used genetic marker, which depends on the difference in the cutting pattern of DNA fragments under the action of a specific restriction enzyme, and it has a high resolution, but the operation process is cumbersome and expensive. AFLP technology combines the advantages of PCR and restriction enzyme cleavage to generate a large number of markers without specific sequence information and is suitable for species with wide genetic diversity. SSR markers are composed of short nucleotide sequences, such as (CA)_n repeats. This marker with high polymorphism and genetic stability is very suitable for the analysis of population genetic structure and genetic linkage map. SNP is the most popular genetic marker at present, which can provide extremely high resolution and is suitable for fine genetic analysis and precise breeding. SNP detection technology is becoming more and more efficient and economical. CAPS labeling is a simple and effective method to identify single nucleotide variation by revealing the restriction enzyme cleavage polymorphism of PCR amplified fragments. RAPD received initial attention due to its simple operation, but its application has been limited due to its low repeatability and specificity.

1.2 Basic principles and workflow of marker-assisted selection

Mark-assisted selection (MAS) is a key technique in modern crop improvement, which uses molecular markers to directly select individuals with desired genetic characteristics, thereby improving breeding efficiency and accuracy. The basic principle of MAS is based on genetic markers that are closely related to the target trait, which are usually DNA sequences such as single nucleotide polymorphisms (SNPS) or simple sequence repeats (SSR) (Hasan et al., 2021). By identifying markers that carry beneficial alleles, breeders can select those individuals who perform best in advance, without the need for phenotypic assessment.

The MAS workflow includes several key steps: The first is the development and validation of genetic markers, a step that requires the identification of markers associated with target traits through molecular biology techniques. The second is the construction of populations and the screening of molecular markers, which involves genotyping in large populations using selected markers to determine which individuals carry beneficial genetic information. Statistical and genetic analysis tools are then used to establish the strength of the association between markers and trait expression, which often requires quantifying trait locus (QTL) mapping (Figure 1) (Hasan et al., 2021).

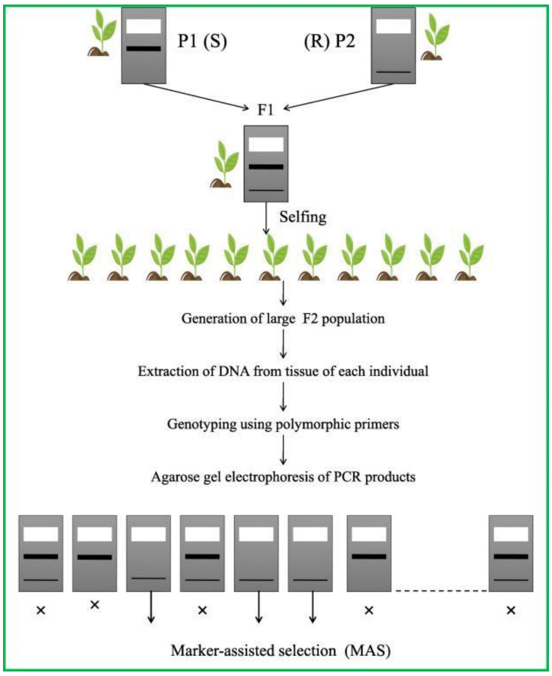

Figure 1 The basic procedure of marker-assisted selection (Hasan et al., 2021)

Once the correlation between markers and traits has been established, marker-assisted selection can be implemented. In practical breeding, by rapidly screening populations through genotyping and selecting individuals with the desired genetic markers for next generation crossing or breeding, breeders can effectively accumulate favorable genes and accelerate the development of new varieties, especially for traits where phenotypic evaluation is time-consuming or costly.

1.3 Principles of quantitative trait locus (QTL) mapping and its application in MAS

Quantitative trait loci (QTL) mapping is a technique used to identify gene regions that control complex genetic traits such as yield, disease resistance or quality for quantitative traits. The rationale relies on statistical analysis methods that can correlate the distribution of genetic markers with variation in phenotypic traits (Diaz et al., 2011). By constructing a genetic linkage map, which includes genetic marker data from individuals in a population, the researchers are able to identify which markers are significantly correlated with the expression of a target trait, indicating that the target trait is likely to be controlled by a specific chromosomal region, which in turn revealed the genes influencing the trait.

The application of QTL mapping is very important in marker-assisted selection (MAS). By precisely locating QTLS that control key agricultural traits, breeders can use this information to select individuals with superior genetic backgrounds (Diaz et al., 2011). For example, if a QTL is strongly associated with high yield, then plants containing this QTL can be selected as fathers for future crossbreeding programs to improve the overall yield performance of the offspring population. This method of selection based on genetic information is more efficient than traditional phenotypic selection because it allows breeders to assess the genetic potential of plants at the seedling stage.

The application of QTL mapping in MAS is not limited to improving the economic traits of crops, but also extends to a wider range of applications such as disease resistance and adaptability. In rice, for example, multiple gene regions associated with drought resistance were identified through QTL mapping, and this information was then used to develop new varieties with better drought adaptability. In addition, QTL mapping improves the understanding of crop genetic diversity and deepens our understanding of genetic mechanisms, leading to more precise breeding strategies.

2 Genetic Background and Genetic Resources of Cassava

2.1 Genetic diversity and genomic characteristics of cassava

As an important tropical crop, cassava (*Manihot esculenta* Crantz) is a staple food source for millions of people in many developing countries around the world, as well as an important industrial raw material, and the genetic diversity and genomic characteristics of cassava are critical to improving its agricultural and economic value. The genetic diversity of cassava is manifested in its wide range of morphological characteristics and physiological responses (Gomes et al., 2016), which enable it to adapt to a variety of environmental conditions such as drought and poor soils.

The cassava genome is relatively large in size and contains a large number of repeat sequences and transposition elements, which make its genome assembly and analysis challenging. Even so, recent advances in high-throughput sequencing technology have allowed scientists to explore the genomic structure of cassava more deeply, and studies of the cassava genome have revealed a large number of genes related to its stress resistance, growth cycle, and starch accumulation (Gomes et al., 2016), offering the possibility of improving these traits.

2.2 Genetic control of important traits

Cassava is an important food and industrial crop in many tropical and subtropical regions of the world. Important traits include yield, starch content, disease resistance and drought tolerance. The genetic control of these traits is complex and is usually influenced by multiple genes, and the expression of these genes is significantly influenced by environmental factors. Understanding the genetic control of cassava traits is crucial to guide breeding and improve crop performance.

Yield is one of the most important traits of cassava, which is directly related to the size and weight of the roots. Yield was controlled by multiple quantitative trait loci (QTLs) involved in the regulation of root formation and growth. Starch content is another key, which determines the value of cassava in food and industrial applications (Bechoff et al., 2018). Key enzymes in the starch synthesis pathway, such as ADPG pyrophosphorylase (AGPase) and starch synthetase (SS), have been identified in cassava. Its activity and expression level directly affect the yield and quality of starch.

Disease resistance is another important goal in cassava breeding, especially resistance to cassava mosaic virus and cassava bacterial wilt. The genetic basis of these traits involves several genes related to plant immunity, including resistance genes and signaling molecules associated with pathogen interactions, and through traditional genetic analysis and modern molecular marker techniques, researchers have been able to locate some QTLS that control resistance to these diseases (Bechoff et al., 2018). Drought tolerance is a key characteristic of cassava as an important food source in arid areas. Drought tolerance is controlled by multiple genes, involving multiple physiological pathways such as water retention, root development, and plant hormone regulation, and through QTL and genome-wide association studies (GWAS), scientists have identified several candidate genes associated with drought tolerance.

2.3 Existing cassava genetic resources and their utilization strategies

Cassava is considered an important pillar of food security and energy production in developing countries because of its good performance in arid and poor soil conditions, and its genetic resources are very rich, including a variety of wild and cultivated species. Wild species tend to possess key traits that cultivated species lack, such as excellent resistance to pests and diseases and adaptability to extreme environments, while cultivated species are superior in terms of yield and food quality. These valuable genetic resources are preserved in multiple gene banks around the globe, such as the International Center for Tropical Agriculture and the Brazilian Agricultural Research Corporation (Embrapa) (Ferguson et al., 2019).

In order to make efficient use of these genetic resources, researchers have adopted a variety of strategies, first combining traditional breeding with modern biotechnology (such as marker-assisted selection MAS and CRISPR-Cas9 gene editing technology) to improve cassava agronomic traits, such as increasing yield, enhancing disease resistance, improving nutritional value and processing quality (Ferguson et al., 2019). Further, the genetic diversity of cassava is protected by establishing and maintaining a seed bank, and detailed phenotypic and genotypic descriptions of wild and traditional varieties are carried out to improve the understanding and utilization of these resources.

Strengthening interdisciplinary cooperation is also an important strategy to promote cassava improvement. Collaboration between plant breeders, geneticists, agronomists and molecular biologists can integrate knowledge and technology from different fields to promote the efficient use of cassava genetic resources. International cooperation is also essential, especially in the context of cassava cultivation in many developing countries around the world, through international projects and research networks that can promote conservation, research and utilization of cassava genetic resources.

3 Case Studies of Marker-assisted Selection

3.1 Successful marker-assisted cassava breeding projects

Marker-assisted selection (MAS) has been successfully applied to cassava breeding to increase genetic gain and improve traits such as disease resistance and root quality. A notable example is the introduction of the *CMD2* gene from Latin American germplasm into African cassava varieties, where it confers resistance to Mosaic disease. This work, using MAS to pre-select genotypes for the *CMD2* gene, resulted in high resistance under field conditions in Africa and has developed 14 genotypes that combine resistance to CMD with high yield and is now in the advanced stages of breeding programmes in Africa (Okogbenin et al., 2007).

3.2 Application of marker-assisted selection in improving cassava yield and quality

The application of MAS in cassava is also aimed at improving yield and quality traits. For example, SNP markers associated with increased carotenoid content (Figure 2) and dry matter content (Figure 3) were validated, confirming their effectiveness in multiple genetic contexts. This reinforces their value in cassava biofortification and productivity, contributing to nutritional security and variety performance (Ige et al., 2022).

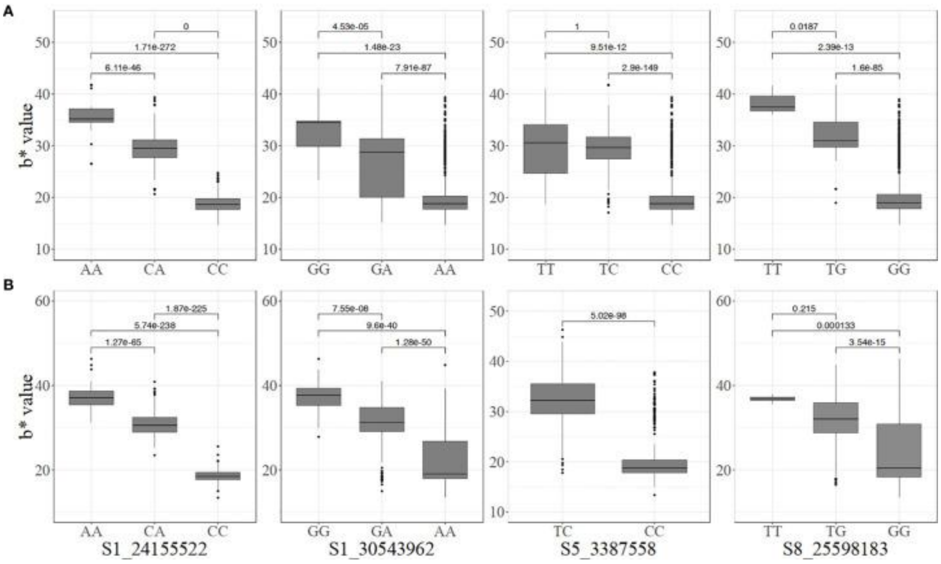

Figure 2 Allelic substitution effects of the markers associated with increased carotenoid content in the (A) breeding, and (B) pre-breeding populations (For marker S5_3387558, the mean and standard deviation cannot be estimated because one genotype had TT) (Ige et al., 2022)

In addition, Ceballos' group and others at the International Center for Tropical Agriculture have proposed integrating genomic selection (Figure 4) and using inbreeding ancestors (Figure 5) to accelerate genetic gains in cassava, particularly in complex traits such as fresh root yield and starch content (Ceballos et al., 2015). In conclusion, the practical application of MAS in cassava breeding shows that it has the potential to make a significant contribution to the development of improved varieties with increased resistance to disease, higher yields and better quality, thereby supporting food security and agricultural development.

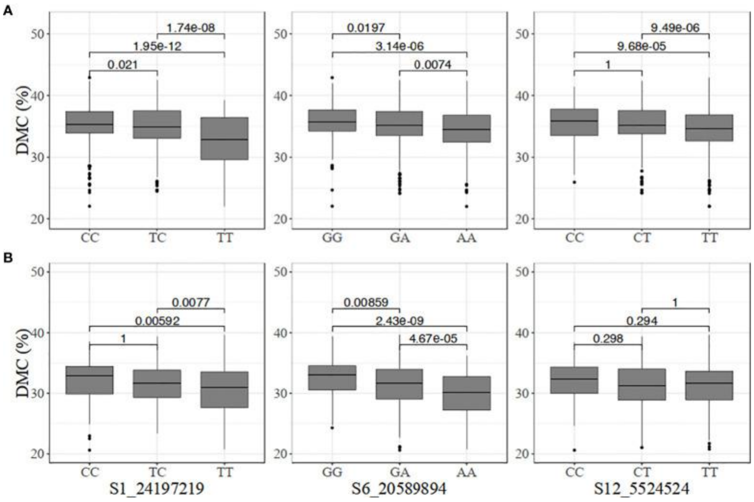

Figure 3 Allelic substitution effects of the markers associated with increased dry matter content (DMC) in the (A) breeding, and (B) pre-breeding populations (Ige et al., 2022)

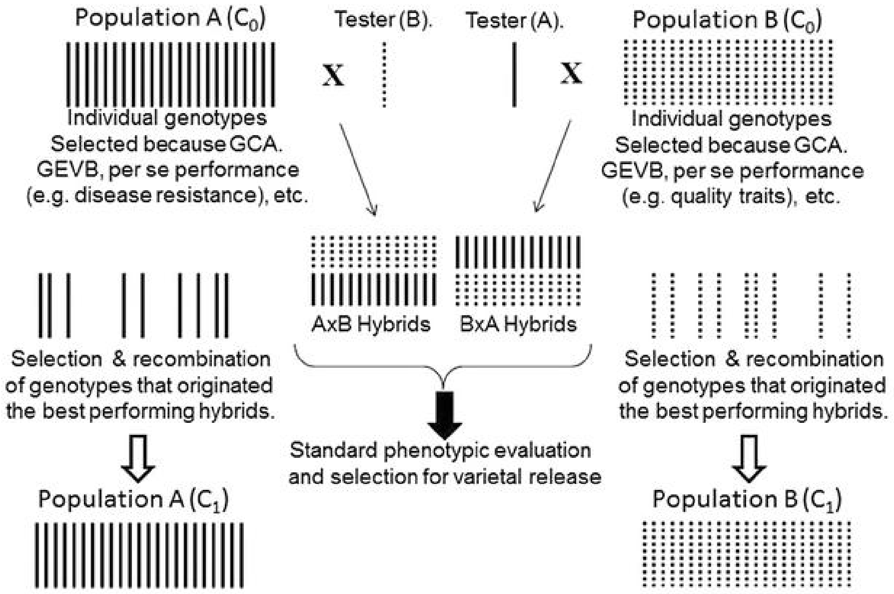

Figure 4 Illustration of a typical scheme of reciprocal recurrent selection of two heterotic populations. Hybrids are made through crosses of selected gentoypes from each population with a tester from the reciprocal population. Progenitors of the best hybrids are combined (within each population) to start a new cycle of selection (Ceballos et al., 2015)

4 Challenges and Opportunities for Implementing Marker-assisted Selection in Cassava

4.1 Technical challenges of genetic marker development

Implementing marker-assisted selection (MAS) offers significant advantages in cassava breeding, but it also faces several challenges and opportunities. The high genetic diversity of cassava, while providing a wide range of genetic resources for breeding, complicates the development and application of effective markers, particularly the technical challenges of genetic marker development (Amelework and Bairu, 2022).

A major challenge in implementing MAS in cassava is the complexity of the genetic background. The cassava genome contains a large number of repeats and a high degree of polymorphism, which makes it difficult to accurately identify genetic markers closely related to key agronomic traits. Many economic traits in cassava, such as yield, starch content, and stress resistance, are quantitative traits controlled by multiple genes (Amelework and Bairu, 2022). The genetic mechanism of MAS is complex and its interaction with the environment is significant, which further increases the difficulty of MAS.

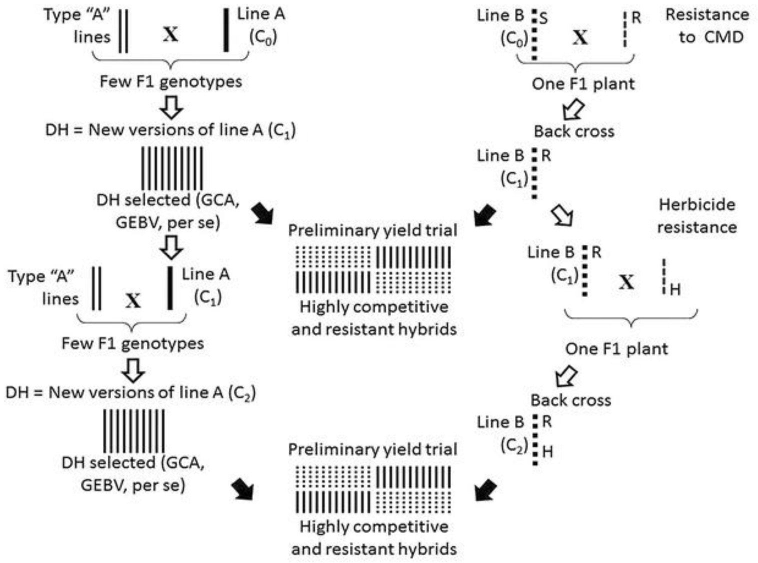

Figure 5 A breeding scheme for cassava based on the use of inbred progenitors from two heterotic populations. Solid black arrows indicate the between heterotic group crosses for production and evaluation of experimental hybrids. White arrows indicate within-population variation. Line A is gradually improved for its heterotic response when crossed with line B. On the other hand, line B is improved for resistance or quality traits (Ceballos et al., 2015)

From a technical point of view, the development of markers requires high-throughput sequencing and precise bioinformatics analysis. Although recent reductions in sequencing costs and advances in analytical techniques have facilitated marker development, precise mapping of quantitative trait loci (QTLS) in cassava still requires large-scale genomic data and complex statistical analyses. Moreover, the association analysis of markers and traits often requires a large amount of genetic and phenotypic data to ensure that the markers found have stable expression in different environments and populations.

4.2 Effective QTL identification and marker development

The genetic background of cassava is complex and contains a large number of repeated sequences, which makes the development and localization of genetic markers more difficult. Effective quantitative trait locus (QTL) identification is key to MAS success, but relies on high-density genetic linkage maps and large-scale phenotypic data, and the large size and high heterogeneity of cassava genomes require comprehensive analysis using high-throughput sequencing techniques (Chen et al., 2012). Not only is this costly, but the data processing is extremely complex.

Marker development requires ensuring stable associations between genetic markers and target traits, which requires extensive validation experiments, including field trials and repeated testing across environments. These tests need to consider the influence of environmental variation on trait expression to ensure the effectiveness of markers in different environments. Effective QTL identification in cassava also faces the problem of limited genetic resources (Chen et al., 2012), and although international collaborative projects have made progress in expanding available genetic resources, further resource and information sharing is needed.

4.3 From laboratory to field: Practical applications and limitations of marker-assisted selection

Marker-assisted selection (MAS) technology has attracted a lot of attention in cassava breeding because it can effectively accelerate the improvement of cassava agronomic traits. MAS uses molecular markers to directly select genetic variants associated with important traits, thereby improving the accuracy and efficiency of selection. This approach allows screening based on genetic information at the seedling stage, significantly reducing the amount and time required for maintenance in mature plants (Hasan et al., 2021), and is particularly beneficial for complex traits such as pest resistance and adaptability. In this way, MAS can save a lot of time and resources and accelerate the development of superior varieties.

However, there are still a series of problems that need to be solved when MAS is extended from the laboratory to the field application. The diversity of environmental factors may affect the stability of the association between markers and traits, making the performance of some markers inconsistent in different environments. The implementation of MAS technology requires expensive equipment and a high level of expertise, which is especially a significant economic burden for resource-limited regions (Hasan et al., 2021). Although cassava is rich in genetic diversity, detailed genotype data is still limited, which restricts the development of effective markers. Although some markers associated with important traits have been identified, the development of universally applicable and accurate markers, especially for polygenic controlled traits, remains challenging.

5 Future Prospects and Research Directions

5.1 Scientific and technical challenges

Marker-assisted selection (MAS) has shown great potential in cassava breeding, but it still faces a series of scientific and technical challenges in its practical application. The genetic complexity of cassava poses a major scientific challenge, with many important agronomic traits, such as drought resistance, yield and disease resistance, often controlled by multiple genes, complicating accurate selection by a single molecular marker (Ceballos et al., 2015). The association between marker and trait may be unstable due to environmental variation, and the correlation of the same genetic marker may be very different in different growth conditions and varieties, and the limitations of existing genetic resources and genetic information also restrict the discovery and utilization of effective markers.

High-throughput genotyping capability in MAS implementation is one of the major challenges. For experimental Settings with limited resources, the equipment and technology required to acquire and process large amounts of genotype data are relatively large, and data management and analysis is also a technical challenge, requiring complex bioinformatics tools and a high level of expertise to effectively process genetic markers, genomic information and phenotypic data (Ceballos et al., 2015). Even when candidate markers are identified, their practical application in the field is subject to rigorous validation, a process that is often time-consuming and expensive, especially when it comes to demonstrating the versatility and reliability of markers in different environments.

5.2 Key areas and potential breakthroughs for future research

The application of marker-assisted selection (MAS) in cassava breeding shows great potential, and future research will be carried out around several key areas to achieve more scientific and technological breakthroughs. With the reduction in cost and availability of high-throughput sequencing technologies, cassava MAS studies will be able to more widely employ genome-wide association studies (GWAS) and genome selection (GS) techniques, which can reveal the genetic basis controlling complex traits (Ceballos et al., 2015). Accurate phenotyping techniques, especially image-based phenotyping techniques, will enable more accurate measurement of traits and help researchers better understand the relationship between trait expression and environmental factors.

In terms of gene function analysis, the future MAS will focus on verifying the function of specific genes through gene editing technologies such as CRISPR/Cas, which will provide direct evidence for function-based breeding. The application of information technology will be particularly critical for MAS research, and the development of advanced bioinformatics tools and databases will help researchers effectively manage and analyze large amounts of genetic and phenotypic data, improving the accuracy and efficiency of cassava breeding (Ceballos et al., 2015).

Interdisciplinary and international collaboration will also be an important driver of MAS research in the future. By integrating multidisciplinary knowledge and technology, as well as strengthening the collaboration of research teams on a global scale, the progress and application of MAS technology can be accelerated. However, given the sustainability and social acceptance of the breeding technology, future research will also need to assess the economic feasibility, environmental impact of MAS technology, and establish communication and collaboration with policymakers, farmers and consumers to ensure widespread acceptance and application of the technology.

5.3 Impact of policy and financial support on MAS implementation

Policy and financial support play a key role in driving the implementation and application of mark-assisted selection (MAS) techniques in cassava breeding. Appropriate policies can stimulate research and technological innovation, especially by supporting basic science research and technology development projects, governments and international organizations can promote gene exploration and marker development for key agronomic traits (Slater et al., 2013). Education and training policies are essential to enhance the professional capacity of breeders and agricultural technicians, which directly affects the success rate of MAS technology from theory to field application.

Financial support is also essential for the research, development, dissemination and commercialization of MAS technologies. Research funds can be used to purchase advanced equipment, hire professionals and conduct the necessary field trials, which are the basis for MAS technology development (Slater et al., 2013). Financial support for technology transfer and commercialization ensures that research results can be effectively translated into practical applications, including large-scale production and marketing. Continued financial support is also key to ensuring the long-term application and renewal of MAS technologies, which can fund activities such as continuous improvement of genetic resources and resistance monitoring.

6 Concluding Remarks

Marker-assisted selection (MAS) has shown significant promise in the improvement of cassava (*Manihot esculenta* Crantz), a staple crop with immense importance in tropical and subtropical regions. The development of molecular genetic markers, particularly simple sequence repeats (SSRs), has been pivotal in advancing cassava breeding programs. SSR markers have been extensively developed and characterized, providing a foundation for the construction of molecular genetic maps of cassava (Mba et al., 2001; Okogbenin et al., 2006; Kunkeaw et al., 2010). These maps facilitate the identification of quantitative trait loci (QTL) controlling traits of agronomic interest, thereby reducing the time and cost of mapping and increasing the efficiency of MAS (Okogbenin et al., 2006; Pootakham et al., 2014).

The practical application of MAS in cassava breeding has led to the development of varieties with enhanced resistance to cassava mosaic disease through the introgression of the *CMD2* gene from Latin American germplasm into African varieties (Okogbenin et al., 2007). This has significantly broadened the genetic base in Africa, improving the potential value of Latin American germplasm for African cassava breeding programs (Okogbenin et al., 2007). Additionally, MAS complements phenotypic screening, increasing the selection efficiency for CMD-resistant genotypes in African cassava populations (Olasanmi et al., 2021).

The use of high-density SNP markers has further refined the understanding of genetic diversity and population structure in cassava, which is crucial for germplasm conservation and breeding (Adu et al., 2021). Economic impact analyses have demonstrated that MAS can save at least four years in the breeding cycle for pest-resistant varieties, with potential net benefits ranging from $34 to $800 million, depending on the country and the constraint addressed (Rudi et al., 2010).

Despite these advancements, continuous research and collaboration are essential to realize the full potential of MAS in cassava breeding. The integration of novel biotechnological tools, such as doubled haploids and genomic selection, could further enhance the efficiency of cassava improvement (Ceballos et al., 2012). The development of more efficient genotyping approaches, coupled with the cassava genome sequence, promises to increase the impact of biotechnology tools on cassava improvement (Ceballos et al., 2012).

Collaborative efforts are also needed to address bottlenecks in cassava breeding, such as the limited investment in research and the challenges in efficient and reliable phenotyping (Ceballos et al., 2012). International collaboration can facilitate the sharing of genetic resources, molecular markers, and breeding techniques, thereby accelerating the development of improved cassava varieties that can meet the growing demands for food security and industrial use.

In conclusion, MAS in cassava has already demonstrated practical results in disease resistance and genetic improvement, with significant economic impacts. However, the importance of ongoing research, particularly in the application of advanced biotechnological tools and international collaboration, cannot be overstated for the wider application and success of MAS in cassava breeding programs.

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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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