

Gene-Driven Future: Breakthroughs and Applications of Marker-Assisted Selection in Tree Breeding

Yufen Wang, Lianming Zhang ✉

Traditional Chinese Medicine Research Center, Cuixi Academy of Biotechnology, Zhuji, 311800, Zhejiang, China

✉ Corresponding email: lianming.zhang@cuixi.org

Molecular Plant Breeding, 2024, Vol.15, No.3 doi: [10.5376/mpb.2024.15.0014](https://doi.org/10.5376/mpb.2024.15.0014)

Received: 18 Apr., 2024

Accepted: 27 May, 2024

Published: 28 Jun., 2024

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Preferred citation for this article:

Wang Y.F., and Zhang L.M., 2024, Gene-driven future: breakthroughs and applications of marker-assisted selection in tree breeding, Molecular Plant Breeding, 15(3): 132-143 (doi: [10.5376/mpb.2024.15.0014](https://doi.org/10.5376/mpb.2024.15.0014))

Abstract Marker-assisted selection (MAS) is a transformative method in tree breeding, combining traditional breeding techniques with modern genetic tools to enhance desirable traits such as growth rate, wood quality, and disease resistance. This study systematically examines the progress, applications, challenges, and future prospects of MAS in tree breeding. Technological advancements, including high-throughput sequencing and genomic selection, have significantly improved the precision and efficiency of MAS. Key achievements include the development of tree varieties that are disease-resistant, fast-growing, and produce high-quality wood. However, MAS still faces technical, biological, and socioeconomic challenges that must be addressed. Integrating emerging technologies such as CRISPR gene editing, synthetic biology, big data analysis, and remote sensing holds promise for further advancements. By leveraging these advancements, MAS can make significant contributions to developing high-quality tree varieties, promoting environmental conservation, and improving resource management.

Keywords Marker-assisted selection; Genomic selection; Tree breeding; Genomics; Disease resistance; Genetic gain

1 Introduction

Tree breeding has long been a cornerstone of forestry, aimed at improving traits such as growth rate, wood quality, and disease resistance. Traditional tree breeding methods involve recurrent cycles of selection, mating, and testing, which are time-consuming and labor-intensive due to the long generation intervals of trees (Grattapaglia et al., 2018). The breeding cycle for forest trees can span decades, making the process of genetic improvement particularly challenging (Lebedev et al., 2020).

Genetic improvement in trees plays a critical role in addressing global challenges such as climate change, deforestation, and increasing demand for wood and non-wood forest products. Enhanced tree varieties contribute to sustainable forestry practices, carbon sequestration, and ecosystem services. Improved disease resistance and adaptability to changing environmental conditions help mitigate the impacts of biotic and abiotic stresses, ensuring forest health and productivity. Furthermore, genetic advancements in trees can lead to higher economic returns for forest industries and communities reliant on forestry (Grattapaglia et al., 2018; Lebedev et al., 2020; Degen and Müller, 2023)

Marker-Assisted Selection (MAS) represents a revolutionary approach in the field of tree breeding. MAS leverages molecular markers—specific DNA sequences associated with particular traits—to accelerate the breeding process. By identifying and selecting for these markers, breeders can predict and enhance desired characteristics in seedlings with greater precision and efficiency compared to conventional methods. This technique reduces the time required to achieve genetic gains and improves the accuracy of selection, thereby expediting the development of superior tree varieties (Grattapaglia et al., 2018; Kumawat et al., 2020; Moriguchi et al., 2020; Degen and Müller, 2023). Despite its potential, the application of MAS in tree breeding has been limited by the complex genetic architecture of many traits and the high cost of genotyping (Grattapaglia et al., 2018; Degen and Müller, 2023).

The aim of this study is to explore the breakthroughs and applications of molecular marker-assisted selection (MAS) in tree breeding. By synthesizing current research and developments, this study highlights the potential of MAS to revolutionize tree breeding practices. It provides breeders, researchers, and policymakers with

information on the advancements and practical applications of MAS, contributing to the development of genetically superior tree varieties that meet economic and ecological demands.

2 Fundamentals of Marker-Assisted Selection

2.1 Definition and principles of MAS

Marker-Assisted Selection (MAS) is a modern plant breeding technique that utilizes molecular markers to select plants with desirable traits. This approach is grounded in the principles of genetics, where specific DNA sequences (markers) are associated with particular traits. Unlike traditional breeding methods, which rely on phenotypic selection, MAS allows for the identification of specific genes or genomic regions associated with traits of interest, thereby accelerating the breeding process and increasing its precision. The principles of MAS involve the identification of markers linked to traits, the development of marker-trait associations, and the use of these markers to select plants that carry the desired genetic traits (Boopathi, 2020; Kumawat et al., 2020; Hasan et al., 2021).

2.2 Types of markers used in MAS

2.2.1 Molecular markers

Molecular markers are segments of DNA that are associated with a particular location within the genome. They are used to identify genetic differences between individuals. Common types of molecular markers include Simple Sequence Repeats (SSRs), Single Nucleotide Polymorphisms (SNPs), and Sequence Tagged Sites (STS). These markers are highly polymorphic, co-dominant, and reproducible, making them ideal for use in MAS (Hasan et al., 2021; Darmanov et al., 2022).

2.2.2 DNA markers

DNA markers are specific sequences within the genome that can be used to identify individuals or species and to associate genetic variation with phenotypic traits. Examples of DNA markers used in MAS include SSRs, SNPs, and Genotyping by Sequencing (GBS). These markers are used to create genetic maps and to identify Quantitative Trait Loci (QTLs) associated with important traits such as disease resistance, yield, and quality (Kumawat et al., 2020; Hasan et al., 2021).

2.3 Advantages of MAS over traditional breeding methods

MAS is a powerful tool that leverages molecular and DNA markers to enhance the efficiency, accuracy, and speed of plant breeding programs, offering significant advantages over traditional methods. It significantly reduces the time required to develop new varieties by allowing for the early selection of desirable traits. This is particularly important in tree breeding, where long generation times can slow down the breeding process (Grattapaglia et al., 2018; Moriguchi et al., 2020; Degen and Müller, 2023). MAS increases the accuracy of selection by targeting specific genes or genomic regions, thereby reducing the influence of environmental factors on phenotypic selection (Boopathi, 2020; Hasan et al., 2021). MAS can be used to pyramid multiple genes for complex traits, enhancing the overall genetic gain and improving the efficiency of breeding programs (Osei et al., 2018; Kumawat et al., 2020; Darmanov et al., 2022). MAS is cost-effective in the long run, as it reduces the need for extensive field trials and phenotypic evaluations (Hasan et al., 2021).

3 Breakthroughs in Marker-Assisted Selection

3.1 Technological advances in MAS

3.1.1 High-throughput sequencing

High-throughput sequencing technologies have revolutionized the field of marker-assisted selection (MAS) by enabling the rapid and cost-effective sequencing of entire genomes. This advancement has facilitated the identification of numerous single nucleotide polymorphisms (SNPs) and other genetic markers that are crucial for MAS. For instance, the development of high-throughput sequencing has allowed for the precise mapping of quantitative trait loci (QTLs) and the identification of gene families involved in disease resistance in forest trees (Younessi-Hamzekhanlu and Gailing, 2022). Additionally, the integration of high-throughput sequencing with other genomic tools has enhanced the accuracy and efficiency of MAS in various plant breeding programs (Salgotra and Stewart, 2020; Hasan et al., 2021).

3.1.2 Genomic selection

Genomic selection (GS) represents a significant technological advancement in MAS, utilizing genome-wide markers to predict complex phenotypes. This approach has the potential to accelerate breeding cycles, increase selection intensity, and improve the accuracy of breeding values. GS has been particularly impactful in tree breeding, where long breeding cycles and complex genetic architectures pose significant challenges. Studies have shown that GS can outperform traditional MAS, especially when large populations are genotyped, and advanced computational models are employed (Grattapaglia et al., 2018; Sandhu et al., 2022; Degen and Müller, 2023).

The study by Degen and Müller (2023) compared the effectiveness of advanced marker-assisted selection (MAS) and the widely used genomic selection (GS) in tree breeding programs. The research utilized a new software, "SNPscan breeder", to simulate simple tree breeding procedures and compare the impact of different selection criteria on genetic gain and inbreeding. The results indicated that GS outperformed other methods in nearly all simulated scenarios, especially when using the gBLUP method. MAS based on GWAS results only surpassed GS when the population used to estimate allele effects was very large (around 10 000 individuals) and the individuals had no kinship. Furthermore, GS increased inbreeding more than progeny testing and GWAS-based selection, which led to a stronger reduction in genetic diversity. The article discussed the practical implications of these findings for tree breeding programs and summarized the potential of GS in forest breeding and improvement, noting that MAS could become more relevant in the future as sequencing costs decrease (Figure 1).

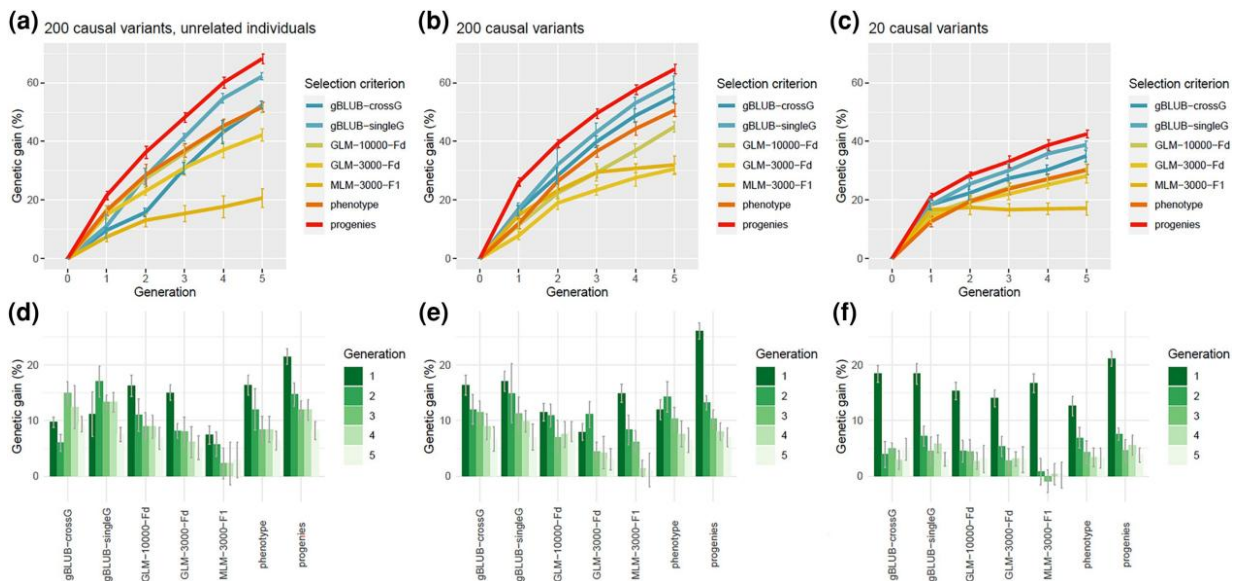


Figure 1 Genetic gains achieved by different selection criteria over 5 generations in 3 simulated breeding populations (Adopted from Degen and Müller, 2023)

Image caption: a-c) Average cumulative genetic gains ($n = 10$) over 5 breeding cycles are shown for selection based on gBLUP, i.e. GS (blue), GWAS, i.e. MAS (green and yellow), phenotypes (orange), and progeny tests (red); d-f) Average genetic gains ($n = 10$) per breeding cycle (generation) are shown for the different selection criteria. Error bars represent the standard deviation of the mean; the 3 simulated breeding populations exhibit different genetic architectures, with 200 a, b, d, e) vs 20 c, f) causal variants, and different levels of kinship, with unrelated individuals a, d) vs average kinship values of approximately 0.04 b, c, e, f) (Adopted from Degen and Müller, 2023)

Figure 1 compares genetic gains under different selection criteria over five breeding cycles. Different colors distinguish genomic selection (GS, blue), marker-assisted selection based on GWAS (MAS, green and yellow), phenotypic selection (orange), and progeny testing (red). The results indicate that selection based on progeny testing achieved the highest genetic gains across all test scenarios, with over 20% gain in the first breeding cycle and cumulative gains ranging from 40% to 70% over five breeding cycles. In contrast, MAS based on different GWAS analyses performed the worst, resulting in the lowest genetic gains.

3.2 Significant achievements in tree breeding using MAS

3.2.1 Disease resistance

One of the significant achievements in tree breeding using MAS is the development of disease-resistant tree varieties. By identifying and selecting genetic markers associated with disease resistance, breeders have been able to produce trees that are less susceptible to pathogens, thus reducing the need for chemical treatments and enhancing sustainability. For example, MAS has been effectively used to develop disease-resistant varieties of *Cryptomeria japonica* by targeting the *MALE STERILITY 1 (MSI)* gene (Moriguchi et al., 2020).

Moriguchi et al. (2020) applied marker-assisted selection (MAS) technology in Japanese cedar (*Cryptomeria japonica*) to effectively identify trees carrying the male sterility gene (*MSI*). In two families constructed through artificial crossing, markers closely linked to the *MSI* gene were successfully identified. Additionally, the study used MAS technology to screen 650 trees, significantly reducing the time and labor required to select suitable breeding materials. This provides an effective tool for future tree breeding and has potential value in addressing issues related to allergic pollinosis.

3.2.2 Growth and yield improvement

MAS has also contributed to significant improvements in the growth and yield of tree species. By selecting for genetic markers associated with rapid growth and high yield, breeders have been able to develop tree varieties that meet the increasing demands for wood and other forest products. This has been particularly effective in species such as Eucalyptus, where MAS has facilitated the rapid identification of high-yielding genotypes (Degen and Müller, 2023).

3.2.3 Wood quality enhancement

Enhancing wood quality is another area where MAS has made substantial contributions. By identifying markers linked to desirable wood properties, such as density and fiber length, breeders have been able to select for trees that produce higher quality wood, which is essential for various industrial applications. This has led to the development of tree varieties with superior wood characteristics, benefiting both the timber and pulp industries (Grattapaglia, 2022).

3.3 Case studies

The integration of advanced genomic technologies and MAS has led to significant breakthroughs in tree breeding, enhancing disease resistance, growth, yield, and wood quality. These advancements underscore the potential of MAS to drive the future of tree breeding and forestry.

3.3.1 Case 1: disease resistance in apple trees

Apple breeding programs have successfully used MAS to develop disease-resistant varieties. Patocchi et al. (2020), through the international collaboration project VINQUEST, successfully utilized marker-assisted selection (MAS) to develop new apple varieties with durable resistance to apple scab by incorporating multiple resistance genes (*Rvi5*, *Rvi11*, *Rvi12*, *Rvi14*, and *Rvi15*). The research strategy involved combining multiple resistance genes within a single variety to create a "gene pyramid," enhancing the stability and durability of resistance. Analysis of data from 14 countries revealed that while some genes like *Rvi1*, *Rvi3*, and *Rvi8* were often overcome, genes such as *Rvi5*, *Rvi11*, *Rvi12*, *Rvi14*, and *Rvi15* exhibited excellent disease resistance stability. The outcomes of this study will enhance the efficiency of apple breeding, reduce pesticide use, and promote sustainable agricultural development (Figure 2).

Figure 2 provides a visual assessment of the resistance performance of different apple resistance genes across multiple test locations and years, aiding in the evaluation and selection of genes with high disease resistance. Each box plot represents the distribution of resistance scores for a specific resistance gene across all test locations and years. The thick black line indicates the median, the box encompasses 50% of the data, and the whiskers cover most of the extreme values. From the figure, it can be observed that some genes, such as *Rvi11* and *Rvi15*, have generally low resistance scores, indicating strong disease resistance. In contrast, genes like *Rvi1* and *Rvi3* have higher resistance scores, suggesting weaker resistance that is more easily overcome by pathogens.

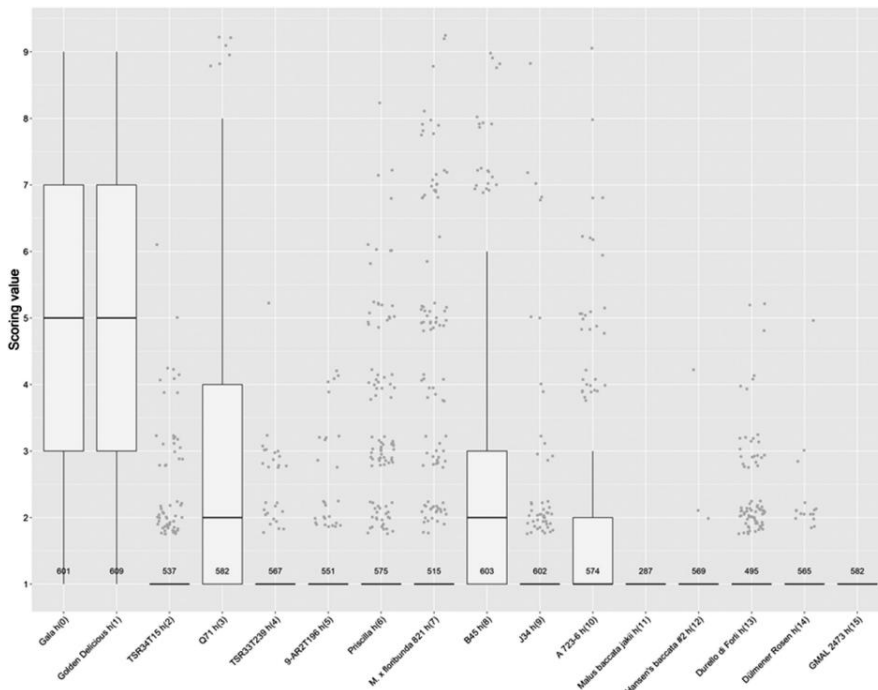


Figure 2 Box plot of the scores observed over all years and sites for each of the 16 differential hosts (Adopted from Patocchi et al., 2020)

Image caption: Severity class 1: No visible lesions; class 2: one or very few lesions detected upon close scrutiny of the tree ($\pm 1\%$ of leaves affected); class 3: immediately apparent lesions in general clustered in a few parts of the tree (1 to 5% of leaves affected); class 4: intermediate; class 5: numerous lesions widespread over a large part of the tree ($\pm 25\%$); class 6: intermediate; class 7: severe infection with half of the leaves badly infected by multiple lesions ($\pm 50\%$); class 8: intermediate ($\pm 75\%$); class 9: tree completely affected with (nearly) all the leaves badly infected by multiple lesions ($>90\%$). The bold horizontal line represents the median value. The boxes cover 50% of the middle values while the whiskers each cover 25% of the more divergent values. The dots (outliers) are defined as values located at a distance from the median that is greater than two times the standard deviation (Adopted from Patocchi et al., 2020)

3.3.2 Case 2: accelerating eucalyptus breeding

Simiqueli et al. (2023) investigated the practical effectiveness of cross-generational genomic selection (GS) in a recurrent reciprocal selection (RRS) breeding program for hybrid Eucalyptus. The research team employed GBLUP and HBLUP models, utilizing genomic data from approximately 16 000 SNPs to predict the growth volume of G1 and G2 hybrid Eucalyptus seedlings. The results showed that the realized predictive ability (RPA) could exceed 0.80 as the genetic relationship between G1 and G2 increased. Additionally, when the training set included direct parents, the RPA of the GBLUP model exceeded 0.70. This study validated the potential of genomic selection in Eucalyptus breeding, particularly in enhancing genetic gain by shortening breeding cycles and increasing selection intensity, thereby optimizing genotype costs. These findings have significant implications for other plant breeding programs, especially in addressing climate change and promoting sustainable forestry management (Figure 3).

Figure 3 illustrates the realized predictive ability (RPA) of different genomic selection models in predicting the mean annual increment (MAI) of G2 hybrid Eucalyptus seedlings. The figure compares three models: GBLUP_G, GBLUP_G+D, and HBLUP, each trained with different datasets. The results indicate that when G1 parents (PARENTS), which are genetically closer to the G2 generation, are used as the training set, all three models show generally higher RPA. Notably, the GBLUP_G model performs best, with RPA values approaching or exceeding 0.80, demonstrating high predictive accuracy. Additionally, the choice of the training dataset significantly impacts predictive ability, underscoring the importance of selecting training data that are closely related to the individuals being predicted to enhance model accuracy.

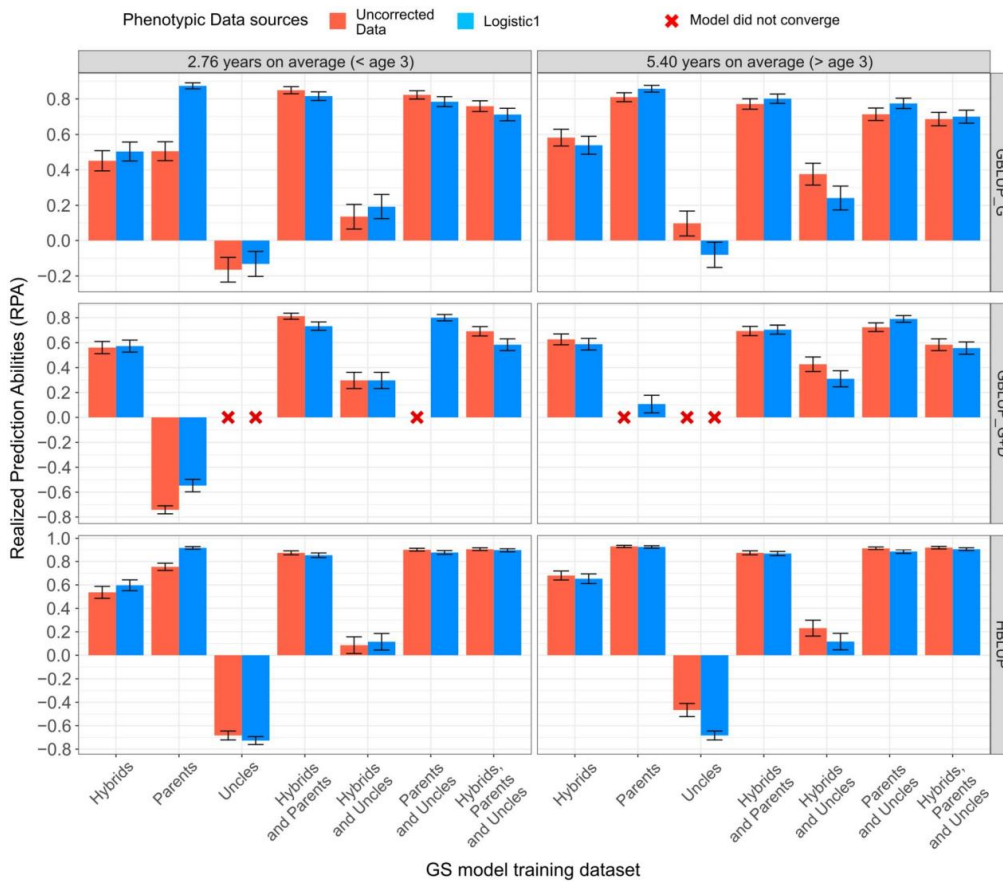


Figure 3 Realized genomic predictive abilities for mean annual increment (MAI) in tree growth at ages 3 and 6 years (Adopted from Simiqueli et al., 2023)

Image caption: estimated with an additive (GBLUP_G), an additive + dominance (GBLUP_G+D) model, and an additive HBLUP model, trained with different training datasets (Adopted from Simiqueli et al., 2023)

3.3.3 Case 3: growth improvement in rubber

Francisco et al. (2021) conducted an in-depth exploration of the genetic mechanisms underlying rubber tree growth using a multi-omics approach, including genome-wide association studies (GWAS) and RNA sequencing. The research team employed molecular marker-assisted selection (MAS) techniques to identify key genes and molecular markers that influence rubber tree growth and yield, which are closely associated with important agronomic traits such as growth rate and stress resistance (Figure 4).

By establishing gene co-expression networks and enzyme network models, the study revealed the molecular networks involved in the phenotypic formation of rubber trees, providing new insights into gene function. These findings not only aid scientists in screening rubber trees with superior genetic traits and accelerating the breeding process but also enable precise genetic improvement of rubber trees using MAS techniques. This includes enhancing rubber yield and improving rubber quality.

The outcomes of this study are significant for the genetic improvement of rubber trees, allowing breeders to select and cultivate high-yield and high-quality rubber tree varieties that are well-adapted to different environmental conditions in a shorter time frame. This approach can effectively increase the production efficiency and economic value of rubber trees, positively impacting the sustainable development of the rubber industry.

4 Applications of Marker-Assisted Selection in Tree Breeding

The application of marker-assisted selection in tree breeding has revolutionized the process of developing disease-resistant, fast-growing, high-yielding, and superior wood quality tree varieties. The integration of advanced genomic tools and techniques continues to enhance the efficiency and precision of tree breeding programs, ensuring the sustainable management and conservation of forest resources.

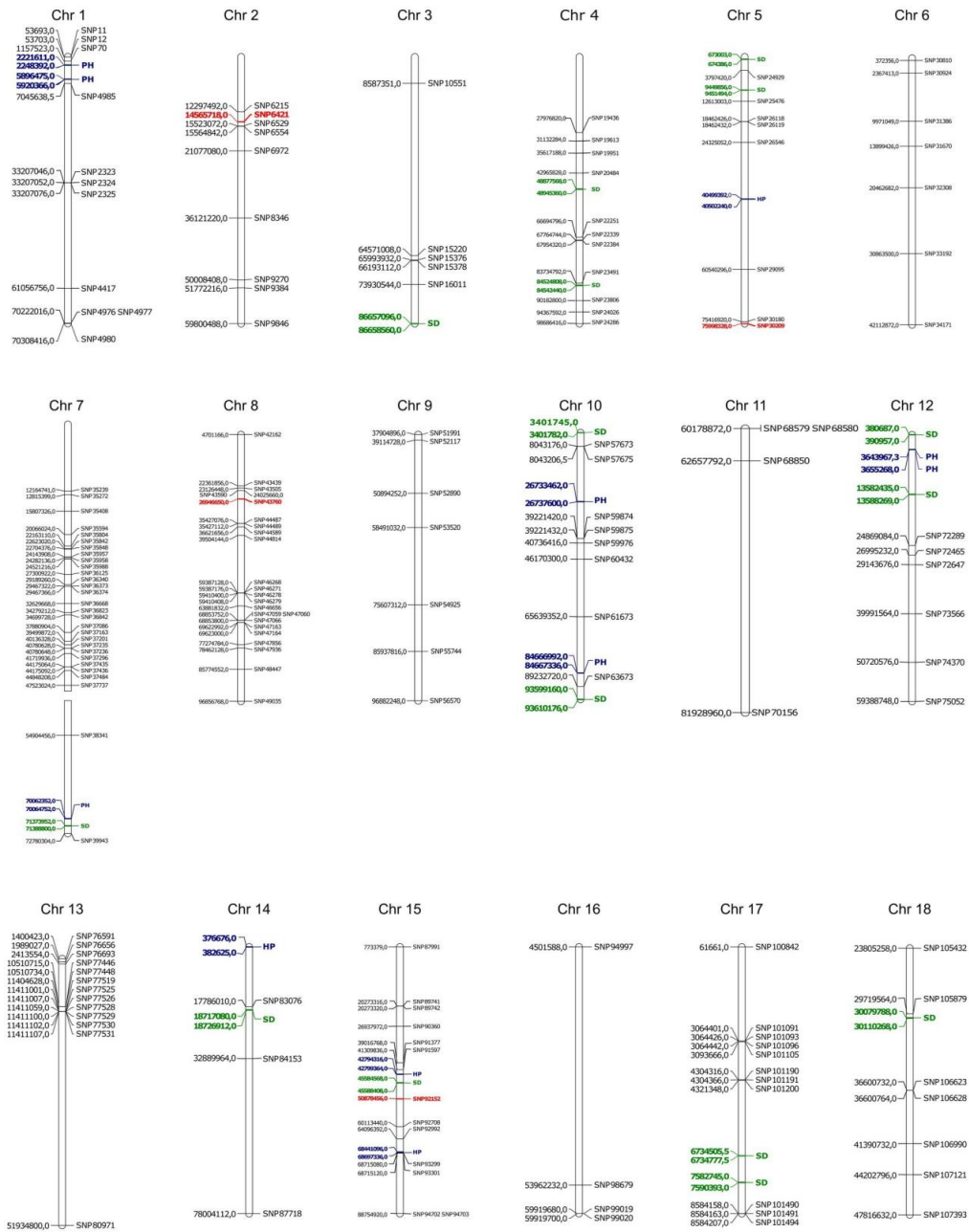


Figure 4 Physical position of snpsGWAS (Adapted from Francisco et al., 2021)

In the rubber tree genome, the physical locations of quantitative trait loci (QTLs) associated with plant height (PH) and stem diameter (SD) were identified through genome-wide association studies (GWAS). In the figure, different types of SNPs and QTLs are marked with distinct colors: snpsGWAS are marked in red, snpsLD in black, QTLs related to plant height in blue, and QTLs related to stem diameter in green. This color differentiation clearly displays the distribution of these genetic markers across the 18 chromosomes of the rubber tree and their relative positions on the genetic map. This provides a visual foundation for further gene function analysis and breeding research. The figure effectively reveals the connections between multiple genetic markers and important agronomic traits (Adapted from Francisco et al., 2021)

4.1 Enhancing disease resistance

4.1.1 Identification of resistance genes

Marker-assisted selection (MAS) has significantly advanced the identification of resistance genes in tree breeding. Genomics and transcriptomics studies using next-generation sequencing (NGS) methods have revealed the architecture of resistance to various diseases, exploiting natural genetic diversity to select elite genotypes with high resistance to diseases (Younessi-Hamzekhanlu and Gailing, 2022). Quantitative trait loci (QTL) mapping and genome-wide association studies (GWAS) have identified several QTLs related to disease resistance traits and

gene families, such as NB-LRR, WRKY, bZIP, and MYB, which are crucial for developing disease-resistant tree varieties (Younessi-Hamzekhanlu and Gailing, 2022). The use of functional markers (FMs) closely associated with phenotypic traits further enhances the precision of selecting resistance genes (Salgotra and Stewart, 2020).

4.1.2 Breeding for multi-pathogen resistance

Breeding for multi-pathogen resistance involves the pyramiding of multiple resistance genes into a single genotype. This approach has been successfully applied in various crops and can be adapted for tree breeding. For instance, molecular marker-assisted gene pyramiding has been used to combine resistance genes for different pathogens, enhancing the overall disease resistance of the plant (Zheng et al., 2022). Genomics-assisted breeding also facilitates the selection of multi-disease resistance (MDR) QTLs, which are essential for developing tree varieties resistant to multiple pathogens (Miedaner et al., 2020).

4.2 Improving growth rates and yield

4.2.1 Selecting for fast-growing varieties

MAS has been instrumental in selecting fast-growing tree varieties by identifying and utilizing markers linked to growth rate traits. The integration of genomic selection (GS) methods, which use information from all markers across the genome, has further accelerated the breeding process by predicting the performance of individuals for specific traits, including growth rates (Younessi-Hamzekhanlu and Gailing, 2022). This approach allows for the rapid selection of fast-growing genotypes, thereby reducing the breeding cycle time.

4.2.2 Yield optimization strategies

Yield optimization in tree breeding involves the selection of genotypes with superior yield traits. MAS enables the identification of markers associated with high yield traits, facilitating the selection of high-yielding varieties. The use of QTL mapping and GWAS has identified several marker-trait associations that are crucial for yield improvement (Kumawat et al., 2020). Additionally, the application of GS methods enhances the accuracy and efficiency of selecting high-yielding genotypes, thereby optimizing yield in tree breeding programs (Younessi-Hamzekhanlu and Gailing, 2022).

4.3 Enhancing wood quality

4.3.1 Traits affecting wood quality

Wood quality is influenced by various traits, including wood density, fiber length, and lignin content. MAS has enabled the identification of markers associated with these traits, facilitating the selection of superior wood quality genotypes. Functional markers (FMs) that are closely linked to wood quality traits have been developed, allowing for precise selection and breeding of trees with desirable wood properties (Salgotra and Stewart, 2020).

4.3.2 Breeding programs for superior wood traits

Breeding programs aimed at enhancing wood quality have benefited from the integration of MAS and GS methods. By identifying and utilizing markers linked to superior wood traits, breeders can develop tree varieties with enhanced wood quality more efficiently. The use of high-throughput markers and genomic selection models has significantly increased the speed and accuracy of breeding programs focused on wood quality improvement (Salgotra and Stewart, 2020; Younessi-Hamzekhanlu and Gailing, 2022).

5 Challenges and Limitations of Marker-Assisted Selection

While MAS holds great promise for accelerating tree breeding programs, several technical, biological, and socio-economic challenges must be addressed to fully realize its potential. Addressing these challenges will require concerted efforts from researchers, breeders, and policymakers to develop more efficient, cost-effective, and widely accepted MAS methodologies.

5.1 Technical challenges

5.1.1 Marker density and coverage

One of the primary technical challenges in marker-assisted selection (MAS) is ensuring adequate marker density and coverage across the genome. In conifers, for instance, the rapid decrease in linkage disequilibrium and the

limited genomic information available make it difficult to develop effective markers. This issue is compounded by the diverse genetic backgrounds among breeding material collections, which further complicates the development of a comprehensive linkage map (Moriguchi et al., 2020).

5.1.2 Cost and resource requirements

The cost and resource requirements for MAS are significant barriers to its widespread adoption. The process of developing and validating molecular markers, constructing linkage maps, and conducting genotyping is both time-consuming and expensive. For example, the breeding cycle for forest trees can take 20~30 years, making the cost-benefit analysis crucial before implementing genomic selection. Additionally, the need for high-throughput phenotyping methods to complement genotyping efforts adds to the overall resource burden (Lebedev et al., 2020).

5.2 Biological challenges

5.2.1 Genetic complexity of traits

The genetic complexity of traits is another major challenge in MAS. Many traits of interest in tree breeding, such as fruit size, weight, and sugar content, are controlled by multiple genes and are influenced by environmental factors. This complexity makes it difficult to identify and utilize molecular markers that can reliably predict these traits. The translation of trait loci and whole-genome sequences into diagnostic genetic markers that are effective and affordable remains a significant hurdle (Mori and Cipriani, 2023).

5.2.2 Gene-environment interactions

Gene-environment interactions further complicate the application of MAS in tree breeding. Environmental variability plays a crucial role in the heritability evaluations of important traits, making it challenging to achieve consistent results across different environments. Although vegetative propagation allows for the production of clonal replicates to evaluate environmental effects, the space and labor required for these phenotypic surveys slow down the breeding process (Mori and Cipriani, 2023).

5.3 Socio-economic and regulatory challenges

5.3.1 Acceptance by stakeholders

The acceptance of MAS by stakeholders, including breeders, farmers, and regulatory bodies, is a significant socio-economic challenge. There is often skepticism about the reliability and benefits of MAS, particularly when compared to traditional breeding methods. Educating stakeholders about the advantages and potential of MAS is essential for its broader adoption (Kumawat et al., 2020).

5.3.2 Intellectual property issues

Intellectual property issues also pose a challenge to the implementation of MAS. The development of molecular markers and the associated technologies often involve significant investment, leading to concerns about patenting and proprietary rights. These issues can create barriers to the sharing of genetic resources and technologies, hindering collaborative efforts in tree breeding (Kumawat et al., 2020).

6 Future Perspectives and Emerging Trends

6.1 Integration of MAS with other biotechnologies

6.1.1 CRISPR and gene editing

The integration of Marker-Assisted Selection (MAS) with CRISPR and other gene-editing technologies holds significant promise for the future of tree breeding. CRISPR/Cas9 technology allows for precise modifications at specific genomic locations, which can be used to introduce or enhance desirable traits identified through MAS. This combination can accelerate the breeding process by directly targeting and modifying genes associated with important traits such as disease resistance, growth rate, and wood quality (Degen and Müller, 2023). The convergence of these technologies can potentially overcome the limitations of traditional breeding methods, such as long breeding cycles and complex trait inheritance (Grattapaglia et al., 2018).

6.1.2 Synthetic biology approaches

Synthetic biology offers another frontier for the integration with MAS. By designing and constructing new biological parts, devices, and systems, synthetic biology can create novel traits that are not found in nature. When combined with MAS, synthetic biology can enhance the precision and efficiency of tree breeding programs. For instance, synthetic promoters and regulatory elements can be used to control the expression of genes identified through MAS, leading to improved trait performance under various environmental conditions (Moriguchi et al., 2020; Hasan et al., 2021). This approach can also facilitate the development of trees with enhanced resilience to climate change and emerging pests and diseases (Grattapaglia et al., 2018).

6.2 Precision tree breeding

6.2.1 Big data and machine learning

The advent of big data and machine learning technologies is revolutionizing precision tree breeding. By leveraging large datasets from genomic, phenotypic, and environmental sources, machine learning algorithms can identify complex patterns and predict breeding outcomes with high accuracy. This can significantly enhance the efficiency of MAS by providing more accurate selection criteria and reducing the time required for breeding cycles (Grattapaglia et al., 2018). The integration of big data analytics with MAS can also help in the identification of novel genetic markers and the optimization of breeding strategies (Degen and Müller, 2023).

6.2.2 Remote sensing and phenotyping

Remote sensing technologies, including drones and satellite imagery, combined with high-throughput phenotyping platforms, are transforming the way phenotypic data is collected in tree breeding programs. These technologies enable the rapid and non-destructive assessment of a wide range of traits across large populations, providing valuable data that can be integrated with MAS (Degen and Müller, 2023). This approach not only improves the accuracy of phenotypic measurements but also allows for the monitoring of tree performance under different environmental conditions, facilitating the selection of trees with superior adaptability and resilience (Grattapaglia et al., 2018).

6.3 Policy and regulatory frameworks

6.3.1 International collaborations

International collaborations are essential for the advancement of MAS and its integration with other biotechnologies in tree breeding. Collaborative efforts can facilitate the sharing of resources, knowledge, and technologies, thereby accelerating the development and adoption of innovative breeding strategies (Degen and Müller, 2023). Joint research initiatives and cross-border partnerships can also help address global challenges such as climate change, biodiversity loss, and food security by developing tree varieties that are resilient and sustainable (Grattapaglia et al., 2018).

6.3.2 Developing standardized protocols

The development of standardized protocols for MAS and its integration with other biotechnologies is crucial for ensuring consistency, reliability, and reproducibility in tree breeding programs. Standardized protocols can facilitate the comparison of results across different studies and breeding programs, thereby enhancing the overall efficiency and effectiveness of MAS (Degen and Müller, 2023). These protocols should encompass all aspects of the breeding process, including marker development, genotyping, phenotyping, data analysis, and regulatory compliance (Grattapaglia et al., 2018). Establishing such standards will also support the broader adoption of MAS and related technologies in tree breeding.

7 Concluding Remarks

Marker-Assisted Selection (MAS) has revolutionized tree breeding by providing a precise and efficient method for selecting desirable traits. Key advancements include the identification and utilization of genetic markers linked to important traits such as disease resistance, growth rate, and wood quality. Technological advances, such as high-throughput sequencing and genomic selection, have further enhanced the capabilities of MAS. Despite these advancements, challenges remain, including technical issues related to marker density and cost, biological complexities of genetic traits, and socio-economic hurdles. However, the integration of MAS with other

biotechnologies like CRISPR and synthetic biology, along with precision breeding tools such as big data and remote sensing, holds promise for the future of tree breeding.

The future of tree breeding with MAS looks promising as it continues to integrate with cutting-edge biotechnologies. CRISPR and other gene editing tools will enable more precise modifications, enhancing traits such as disease resistance and growth. Synthetic biology will introduce new capabilities for creating novel genetic constructs, further expanding the possibilities of tree improvement. Precision breeding technologies, including machine learning and remote sensing, will refine the selection process, making it faster and more accurate. These advancements will not only improve the efficiency of tree breeding programs but also contribute to sustainable forestry practices and environmental conservation.

To fully realize the potential of MAS in tree breeding, continued research and collaboration are essential. Researchers should focus on optimizing strategies for updating prediction models and integrating validated functional genomics data to improve prediction accuracy. Collaborative efforts between geneticists, breeders, and bioinformaticians will be crucial for addressing the challenges associated with the complex genetic architectures of trees and other crops. Furthermore, international collaboration and data sharing will be vital for building comprehensive genomic databases and developing robust breeding programs that can adapt to changing environmental conditions. By fostering a collaborative research environment, the tree breeding community can accelerate the development of innovative solutions and ensure the sustainable improvement of tree species for future generations.

MAS has already made significant contributions to tree breeding, and its future looks bright with the continued integration of new technologies and collaborative efforts. These advancements will not only enhance the efficiency and effectiveness of tree breeding programs but also contribute to global efforts in forestry conservation and resource management.

Acknowledgments

The authors extend sincere thanks to the peer reviewers for their valuable feedback.

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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