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Accelerating the Process of Tree Breeding: A Review and Progress of GWAS Applications in Forest Trees

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Abstract This study reviews and prospects the application of Genome-wide Association Studies (GWAS) in forest tree breeding. With the rapid development of molecular biology and genomics, GWAS has become an essential tool for deciphering the relationship between genetic variation and trait expression in trees. This research introduces the basic principles and methods of GWAS technology and discusses its successful application in the field of plant breeding, showcasing the potential of GWAS in identifying genetic markers related to important agronomic traits such as crop yield, quality, and disease resistance. The study focuses on the special considerations and challenges of GWAS in tree breeding, including the long lifespan of trees, their large genomes, and genetic diversity, and elucidates the application of GWAS in identifying genetic markers related to important traits in trees, using actual case studies. The application of GWAS in tree breeding not only improves the efficiency and accuracy of breeding but also provides new strategies and methods for protecting genetic resources and adapting to environmental changes.

Keywords Genome-wide Association Studies (GWAS); Forest trees; Breeding process; Genetic markers; Technical challenges

Tree breeding, a science deeply rooted in human history, has become the core of modern forestry research. Since ancient times, trees have provided indispensable resources for humans, such as timber and pulp, and played a crucial role in maintaining global ecological balance and biodiversity (Ahmar et al., 2021). In terms of coping with climate change, protecting soil and water sources, and maintaining a balanced biosphere, the role of trees is not to be underestimated. However, with the rapid changes in the global environment and the increasing human demand for forest products, tree breeding is facing unprecedented challenges.

Traditional tree breeding methods, such as selective breeding, controlled hybridization, and grafting, rely on long-term selection and hybridization experiments, but are limited by the long lifespan of trees and their genetic diversity (Whetten et al., 2023). These methods are inefficient in improving tree quality, adaptability, and stress resistance, making it difficult to rapidly adapt to environmental changes and market demands. To overcome these limitations, modern genetic technologies, especially Genome-wide Association Studies (GWAS), have provided new perspectives for tree breeding.

GWAS utilizes high-throughput sequencing techniques to analyze genomic variations and explore their associations with specific traits in trees, revealing the genetic factors influencing these traits. This method has achieved significant results in elucidating the genetic basis of crops and human diseases. For example, in crops, GWAS has been successfully applied to genetic improvement of wheat, rice, and corn. In wheat, through GWAS analysis, researchers have successfully identified multiple genetic markers associated with important traits such as yield, quality, and stress resistance (Saini et al., 2022). In human diseases, the application of GWAS has also made significant progress, identifying many important gene variations associated with diseases such as diabetes, cardiovascular diseases, and cancer (Mills and Rahal, 2020). The application of GWAS in tree breeding is also becoming increasingly widespread, particularly in the genetic improvement of trees, showing great potential. Breeders can use GWAS to identify genetic markers associated with important traits such as growth rate, wood quality, and disease resistance, thereby accelerating the breeding process and cultivating tree species with stronger adaptability, faster growth, and better disease resistance (Sawitri et al., 2020).

This study will delve into the application of GWAS in tree breeding, reviewing its developmental history in tree genetics research, analyzing current achievements and challenges, and prospecting future directions. As global environmental changes and the demand for sustainable forestry increase, integrating traditional breeding techniques with modern molecular biology methods to develop tree species that are more adaptable to environmental changes and more economically valuable is becoming increasingly important. Through this comprehensive overview, not only can scientific researchers gain a comprehensive perspective on tree breeding and GWAS applications, but forestry managers and policymakers can also obtain practical references to promote the development of sustainable forestry and the rational utilization of forest resources. Furthermore, this study emphasizes the potential of GWAS in addressing the protection and sustainable utilization of tree genetic diversity. As the impact of global climate change on forest ecosystems intensifies, developing tree species with stronger resistance to adverse environments has become crucial. The application of GWAS technology provides new avenues for identifying and cultivating these tree species. This not only helps to improve the productivity and economic value of trees but also plays a crucial role in maintaining biodiversity and a healthy ecosystem.

The role and potential of GWAS in tree breeding cannot be underestimated. It not only complements traditional breeding methods but also holds significant importance for improving the efficiency and adaptability of tree breeding, protecting genetic diversity, and promoting sustainable forestry development in the new era. With the advancement of science and technology, future tree breeding will continue to progress toward higher efficiency and sustainability based on the integration of traditional experience and modern biotechnology.

1 History and Current Status of Tree Breeding

As a science, tree breeding has a long and rich history. From initial selective breeding to modern gene editing, tree breeding has undergone a transformation from experience to science. Over centuries, the core goal of tree breeding has always been to improve the productivity, adaptability, and disease resistance of trees. Nevertheless, with rapid global environmental changes and the increasing human demand, tree breeding is facing unprecedented challenges and opportunities.

1.1 Review of traditional tree breeding methods

The history of tree breeding can be traced back several centuries, when the methods were mainly based on natural selection and human selection. In natural selection, the tree species best adapted to the environment naturally propagated. Human selection, on the other hand, involved the selection of specific traits in trees for breeding, such as selecting trees with fast growth and good wood quality. Although simple, these methods were often limited by the long lifespan of trees and their complex genetic backgrounds.

In the early 20th century, with the development of Mendelian genetics principles, tree breeding began to incorporate scientific hybridization experiments, including controlled hybridization to combine the desirable traits of different tree species, such as combining the fast growth of one species with the disease resistance of another (He et al., 2023). Other methods included population selection, grafting, and propagation techniques for tree improvement and breeding.

1.2 Application of modern biotechnology in tree breeding

Entering the 21st century, advances in genomics and bioinformatics have provided new perspectives for tree breeding. With the rapid development of molecular biology and genetic engineering technologies, modern biotechnology has become an important tool for tree breeding. Techniques such as marker-assisted selection (MAS), genome editing (e.g., CRISPR-Cas9), and tissue culture have enabled breeders to manipulate and improve the genetic traits of trees more precisely and efficiently.

For example, through MAS, breeders can identify and select individuals carrying beneficial genetic traits at the seedling stage, greatly shortening the breeding cycle (Hasan et al., 2021). Genome editing techniques provide the possibility of precisely modifying target genes at the molecular level, offering new avenues for creating tree species with specific traits.

1.3 Major challenges and demands facing tree breeding

Despite the revolutionary progress brought about by modern technologies, tree breeding still faces numerous challenges. The long lifespan of trees means that any breeding improvements take a long time to manifest. The genetic diversity of trees and their complex environmental adaptation also require breeding strategies to consider the protection and sustainability of genetic resources. With the intensification of global climate change and environmental degradation, tree species resistant to adverse conditions (such as drought, pests, and diseases) are becoming increasingly important. Simultaneously, the societal demand for eco-friendly and sustainable forest products is growing, requiring tree breeding to not only improve yield and quality but also consider environmental impact and ecological balance.

Tree breeding is in a period of transition. The combination of traditional breeding techniques and modern biotechnology provides new opportunities for improving tree quality, adaptability, and ecological sustainability. Future tree breeding will increasingly rely on scientific research and technological innovation to meet the growing human demand for forest resources while protecting and maintaining the health and diversity of natural ecosystems.

2 Overview of GWAS Technology

Genome-wide Association Studies (GWAS) is a revolutionary genetic method that has demonstrated tremendous potential in numerous fields of biology. GWAS helps scientists unravel how genetic variations influence the phenotypic traits of organisms by analyzing the associations between polymorphic loci across the genome and specific traits. This method has achieved significant results in crop improvement and human disease research, providing new perspectives and tools for tree research.

2.1 Principles and methods of GWAS technology

Genome-wide Association Studies (GWAS) is a method to study the relationship between genetic variations and phenotypic traits. Its core principle is to identify genetic markers (such as single nucleotide polymorphisms or SNPs) associated with a specific phenotype (such as a disease or biological trait) across a large number of individuals (Figure 1). GWAS typically involves scanning thousands to millions of genetic loci to find SNPs that are significantly associated with the phenotype of interest (Uffelmann et al., 2021).

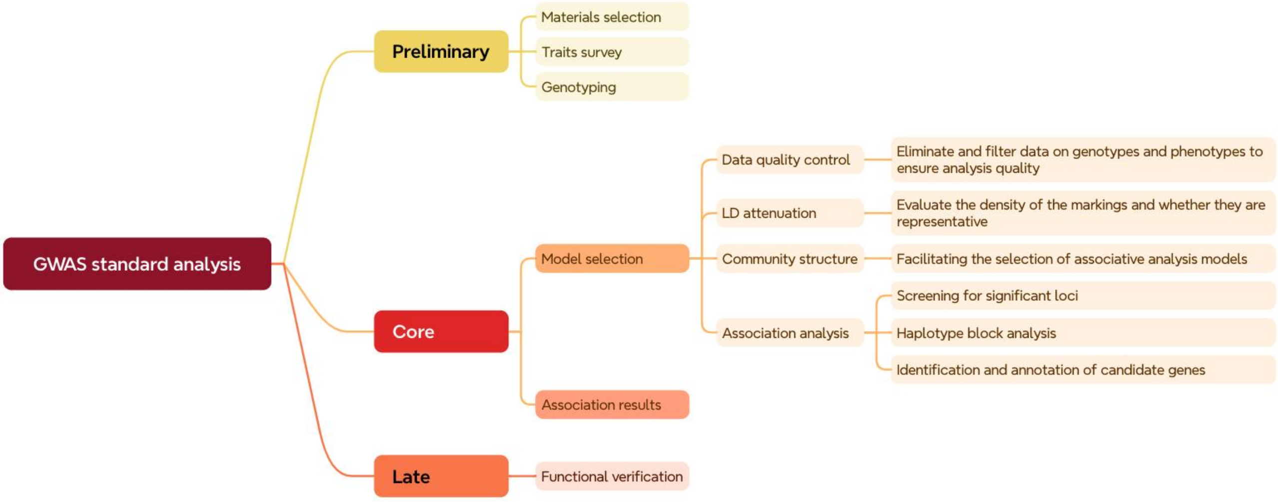

Figure 1 Standard analysis flow for GWAS (Genome-wide Association Studies)

To conduct a GWAS, a sufficiently large sample size is required, which helps improve the accuracy of detecting associations between genetic variations and phenotypes. The samples undergo high-throughput genome sequencing to generate a large amount of genetic data. This data contains thousands to millions of SNPs distributed across the entire genome. Statistical methods are then used to analyze the associations between these SNPs and the specific trait being studied. If the variation frequency of a particular SNP is significantly different between individuals with the specific phenotype and the general population, that SNP is likely associated with the phenotype.

The advantage of this method is that it does not rely on prior genetic knowledge and can discover novel genetic variations associated with traits across broad genomic regions. GWAS can also handle complex traits, which are those influenced by multiple genes as well as gene-environment interactions.

2.2 Applications of GWAS in plant breeding

In plant breeding, the application of GWAS technology has primarily focused on identifying genetic markers associated with important agronomic traits. These traits span yield, disease resistance, stress tolerance (such as drought and salt stress), and nutritional quality. For instance, in a study on spring barley and winter wheat, Tsai et al. (2020) conducted genotypic and phenotypic analyses on 1 317 spring barley and 1 325 winter wheat accessions. In spring barley, GWAS identified QTLs associated with resistance to powdery mildew and leaf rust, as well as multiple SNPs related to yield. In winter wheat, GWAS revealed SNPs associated with quality traits such as grain moisture and starch content.

Gutiérrez et al. (2023) conducted a genome-wide association study on 100 faba bean accessions from different geographic origins to identify traits related to drought tolerance. They identified 29 single nucleotide polymorphism (SNP) markers significantly associated with traits under drought conditions and performed genome analysis on the surrounding sequences of these markers to search for potential candidate genes. The study found that 3 SNPs associated with chlorophyll content corresponded to unknown proteins, suggesting the existence of new genes related to drought tolerance in faba beans, providing a basis for molecular-assisted breeding in faba beans.

These studies not only deepened the understanding of the genetic basis of crops but also provided powerful tools for molecular breeding in practice. By utilizing the specific genetic markers discovered through GWAS, marker-assisted selection (MAS) techniques can more efficiently breed crops to improve yield and quality; furthermore, GWAS provides precise target genes for CRISPR/Cas9, further promoting directional improvement of crop traits. These advancements have not only increased the efficiency of crop breeding but also provided new strategies for coping with climate change and environmental pressures.

2.3 Special considerations and challenges of GWAS in tree research

Although GWAS has achieved tremendous success in other fields, applying this technology to tree research requires considering some unique challenges. Firstly, the long lifespan and large genome sizes of trees present difficulties for genome sequencing and genetic analysis. Furthermore, the genetic diversity of tree populations is typically greater than that of crop populations, requiring larger sample sizes to ensure the accuracy and representativeness of the study. The growth and development of trees are also greatly influenced by the environment, meaning that gene-environment interactions must be considered when analyzing the associations between genes and traits. Therefore, unlike crop breeding focused on specific environments, tree breeding needs to consider the effects of genes across broader and more diverse environmental conditions.

GWAS provides a powerful tool for tree genetics research and breeding, although challenges exist, its potential is immense and worth further exploration and application. Through this method, a better understanding of tree genetic diversity can be gained, providing a theoretical basis for cultivating tree species that are more adaptable to environmental changes and have higher economic value.

3 Applications of GWAS in Tree Breeding

With the advancement of genomics and bioinformatics technologies, Genome-wide Association Studies (GWAS) has become an important tool in tree breeding research. Through GWAS, breeders can identify genetic markers influencing important tree traits, thereby accelerating the breeding process and promoting the protection and utilization of genetic resources.

3.1 Progress in the application of GWAS in tree breeding research

The application of Genome-wide Association Studies (GWAS) in tree breeding is a relatively new field, but significant progress has been made. This technique has been primarily applied to exploring the genetic basis of wood property traits, particularly in major timber species such as eucalyptus, poplar, and various coniferous trees (Table 1) (Du et al., 2018).

Porth et al. (2013) conducted a genome-wide association study on 334 unrelated black cottonwood (*Populus trichocarpa*) individuals and discovered 141 significant single nucleotide polymorphisms (SNPs) associated with cell wall traits. Furthermore, Resende et al. (2017) applied regional heritability mapping (RHM) to 768 hybrid eucalyptus trees, showing that complex traits in eucalyptus are controlled by multiple rare-effect alleles. These studies revealed the potential of GWAS in elucidating wood composition and wood property traits.

Another research direction is to explore the effects of rare alleles and major structural variations on GWAS. For example, Fahrenkrog et al. (2017) conducted a GWAS on wood composition traits in 391 unrelated eastern cottonwood (*Populus deltoides*) individuals and discovered multiple low-frequency SNPs associated with bioenergy traits.

The applications of GWAS have also extended to coniferous tree species, despite their typically large genomes. For instance, Uchiyama et al. (2013) conducted a genome-wide association study on 367 unrelated Japanese cedar (*Cryptomeria japonica* D. Don) individuals and discovered six new QTLs associated with wood property traits and the number of male strobili.

These studies demonstrate that GWAS is a powerful tool for unveiling the genetic basis of tree traits and providing valuable information for future molecular breeding. However, this field still faces challenges, including optimizing GWAS design, exploring the effects of rare alleles, and developing high-throughput phenotyping technologies.

Table 1 Summary of Genome-wide Association Studies (GWAS) of wood property traits in main timber species

Phenotype	Species	Sample size	No. of markers	Method	Reference
Growth and wood properties	*Eucalyptus globulus*	303	7 680 [Diversity Array Technology markers (DArT)]	General linear model (GLM) and unified mixed model (UMM)	Cappa et al., 2013
Wood density, stiffness, microfibril angle, and ring width	*Picea glauca*	1694	7 434 (SNPs)	Mixed linear model (MLM)	Lamara et al., 2016
16 wood chemistry/ultrastructure traits	*Populus trichocarpa*	334	29 233 (SNPs)	GLM	Porth et al., 2013
Lignin percentage, Lignin S:G ratio, 5-carbon sugars, and 6-carbon sugars	*Populus deltoides*	391	334 679 (consensus SNPs), 185 526 (Common SNPs), 76 804 (functional SNPs)	Single-variant and multiple-variant associations on GLM	Fahrenkrog et al., 2017
Basic wood density (BWD), bleached pulp, pulp yield (SPY), and pulp bleaching content	*Eucalyptus grandis* × *Eucalyptus urophylla*	768	24 806 (SNPs)	GWAS and regional heritability mapping	Resende et al., 2017
17 wood-quality traits	Norway spruce	517	178 101 (SNPs)	Multilocus LASSO Penalized regression	Baison et al., 2018
Seven wood properties	*Populus tomentosa*	435	5 482 (InDels)	MLM and Kempthorne model	Gong et al., 2017

Note: Diversity Array Technology (DArT) markers (Source: Du et al., 2018)

3.2 Identification of genetic markers related to important tree traits

One important application of Genome-wide Association Studies (GWAS) in tree breeding is the identification of genetic markers associated with economically and ecologically important traits. These traits include growth rate, wood quality, stress tolerance (such as drought resistance and pest resistance), among others. For example, Bai et al. (2020) utilized GWAS techniques to identify key genes in the pine genome associated with disease resistance, growth rate, and wood density. Through such analysis, breeders can more accurately identify genomic regions influencing important traits and perform effective genetic selection during the breeding process.

Resende et al. (2017) discovered genetic markers associated with wood fiber length and density in eucalyptus through GWAS. These findings not only deepened the understanding of tree genetic diversity but also provided crucial information for formulating tree breeding strategies. By selectively breeding individuals carrying favorable genetic variations, breeders can cultivate tree varieties with stronger adaptability, faster growth rates, and better stress resistance. Furthermore, GWAS has revealed some rare genetic variations in tree populations that significantly impact certain tree traits. The discovery of these rare variations provides important information for protecting tree genetic diversity and genetic resources, as well as valuable genetic resources for future breeding projects.

The application of GWAS in tree breeding has provided new insights into understanding the genetic mechanisms of trees and laid the foundation for cultivating tree species that are better adapted to environmental changes and more economically valuable. As technology advances, the future application of GWAS in tree breeding will become more widespread, providing more precise and efficient methods for tree genetic improvement and resource management.

3.3 Protection of tree genetic diversity and genetic resources

The application of GWAS in tree breeding is not only significant for breeding purposes but also plays an important role in the protection of tree genetic diversity and genetic resources. The genetic diversity within tree populations is key to their ability to adapt to environmental changes and resist pests and diseases. Through GWAS, a better understanding of the genetic variation within tree populations can be gained, guiding the formulation of conservation strategies. For example, GWAS can help identify rare or endangered tree species with unique genetic characteristics, providing scientific support for the conservation of these species (Funk et al., 2019). Additionally, an in-depth understanding of genetic resources can promote the sustainable utilization of tree germplasm, providing valuable genetic resources for future breeding projects.

The application of GWAS in tree breeding not only improves the efficiency and accuracy of breeding but also provides important support for the protection and sustainable utilization of tree genetic resources. As technology advances and research deepens, GWAS is expected to play an increasingly important role in tree breeding and forest resource management.

4 Case Study

4.1 Case study of GWAS in forest trees: The case of Qinghai spruce (*Picea crassifolia* Kom.)

Qinghai spruce (*Picea crassifolia* Kom.) is an important high-altitude tree species, mainly distributed in the eastern and central parts of the Qinghai-Tibet Plateau in China. As a tree species adapted to high altitudes, *Picea crassifolia* plays a crucial role in the ecosystem, serving as an important water conservation species and a vital component of biodiversity. Furthermore, *Picea crassifolia* also has high economic value, with its timber being used for construction and furniture manufacturing.

Zhou et al. (2022) studied the earlywood tracheid properties of *Picea crassifolia* Kom., which have a significant impact on wood quality and processing performance. Earlywood is the initial portion of wood formed within an annual ring, typically lighter and lower in density, influencing the physical and mechanical properties of wood. The researchers conducted phenotypic and genotypic analyses on 106 *Picea crassifolia* Kom. clones and performed genome-wide association analysis using specific-locus amplified fragment sequencing (SLAF-seq) technology to identify single nucleotide polymorphisms (SNPs) and candidate genes associated with earlywood tracheid properties. The researchers characterized 14 earlywood tracheid traits phenotypically, then used SLAF-seq technology to sequence the *Picea crassifolia* Kom. genome, obtaining a large number of SNP markers. Through GWAS analysis, they identified SNPs significantly associated with earlywood tracheid properties and further screened for candidate genes in the surrounding regions.

4.2 Analysis of the methods, findings, and impact on breeding

This study employed methods including high-throughput sequencing, complex statistical analysis, and genome-wide association studies. The results revealed multiple SNPs and candidate genes significantly associated with earlywood tracheid properties in Qinghai spruce (Zhou et al., 2022). These findings not only provide new insights into understanding the genetic basis of tracheid development in Qinghai spruce but also offer important molecular markers for future tree breeding efforts. These molecular markers can be used to guide the breeding process, improving efficiency and accuracy. Moreover, the methods and results of this study provide valuable experience for other tree species, particularly those growing at high altitudes and in harsh environments. By gaining a deeper understanding of the genetic characteristics of these trees, more effective genetic improvement can be achieved to address climate change and other environmental challenges.

This case study demonstrates the potential of GWAS in tree breeding, particularly in elucidating the genetic mechanisms of complex traits and assisting breeding decisions. The study has direct implications for Qinghai spruce breeding and provides methodological insights and approaches for genetic improvement in other tree species.

5 Challenges and Future Directions

Tree breeding, a field encompassing genetics, ecology, and biotechnology, among other disciplines, is facing multifaceted challenges. At the same time, with the advancement of science and technology and global environmental changes, this field is also presenting new research directions and technological trends.

5.1 Challenges in technology and data analysis

Tree breeding faces numerous challenges in terms of technology and data analysis. On one hand, the long lifespan of trees and their complex genome structures present difficulties for gene sequencing and genetic analysis. Compared to annual crops, the manifestation of tree traits requires a longer observation period, prolonging the breeding cycle and increasing research complexity (Chen et al., 2022). Furthermore, the high genetic diversity and large genome sizes of trees require more efficient sequencing technologies and more complex data processing methods.

In data analysis, the need to process large-scale genomic data places higher demands on bioinformatics capabilities. Analyzing the relationships between genes and traits requires advanced statistical methods and computational tools to process and interpret vast amounts of genomic data. Moreover, the genetic differences between different tree populations and the diversity of environmental conditions make it more challenging to draw accurate and generalizable conclusions from the data.

5.2 Impact of environmental changes on tree breeding

Global environmental changes, particularly climate change, have had a significant impact on tree breeding. Climate change-induced extreme weather events (such as droughts, floods, and temperature changes), as well as the occurrence and spread of pests and diseases, pose threats to the growth and distribution of trees (Czeszczewik et al., 2020). This requires tree breeders to not only focus on improving yield and wood quality but also emphasize the adaptability and stress resistance of tree species.

To address these challenges, tree breeding needs to develop new varieties that can adapt to environmental changes, such as drought-resistant, heat-tolerant, and disease-resistant species. This requires a deep understanding of the physiological and genetic responses of tree species to environmental stresses. Protecting tree genetic diversity is also crucial for coping with environmental changes, as genetic diversity is the foundation for trees to adapt to environmental changes and withstand pests and diseases.

5.3 Future research directions and technological development trends

Future tree breeding research will increasingly rely on genomics and molecular biology technologies. GWAS and gene editing techniques such as CRISPR/Cas9 will play a vital role in identifying genetic markers for important traits and directly improving tree traits. These techniques make the breeding process more precise and efficient, potentially significantly shortening the breeding cycle.

With the advancement of bioinformatics and data science, big data analysis will play an increasingly important role in tree breeding. By integrating genetic, phenotypic, and environmental data, researchers can gain a more comprehensive understanding of the growth, development, and environmental adaptation mechanisms of trees (Cao et al., 2022). The application of artificial intelligence and machine learning techniques will further enhance the efficiency and accuracy of data analysis. Simultaneously, with the growing awareness of sustainable forestry and ecological conservation, future tree breeding will place greater emphasis on environmental friendliness and ecological balance. This includes developing tree species better adapted to climate change, protecting tree genetic diversity, and developing more sustainable forestry management practices.

Facing challenges and opportunities, future tree breeding will be a multidisciplinary, high-tech, and comprehensive field, involving genetics, ecology, molecular biology, and information science, among others. With technological advancements and environmental changes, tree breeding will continue to evolve, contributing to sustainable forestry and the health of global ecosystems.

6 Conclusion

The application of Genome-wide Association Studies (GWAS) in tree breeding has demonstrated its tremendous potential and significance. As an efficient genetic analysis tool, GWAS enables breeders to identify genetic markers influencing important tree traits at the molecular level, including growth rate, wood quality, disease resistance, stress tolerance, and others. Through these genetic markers, breeding selection can be conducted more precisely, accelerating the breeding process and cultivating tree species that are better adapted to environmental changes and have higher economic value. In recent years, the application of GWAS has successfully identified gene loci associated with key traits in various tree species. This has not only deepened our understanding of the genetic mechanisms in trees but also provided new directions for tree breeding. Through GWAS, the precision and efficiency of tree breeding have been significantly improved, with the potential to bring a leap in forestry productivity in the near future.

Although GWAS is playing an increasingly important role in tree breeding, traditional breeding methods remain indispensable. Traditional methods, such as selective breeding and hybridization, based on long-term experience and practice, provide the foundation for maintaining the genetic diversity and adaptability of tree populations. To achieve optimal breeding outcomes, a combination of traditional breeding methods and modern biotechnology is necessary. Traditional methods provide the basic framework for breeding, while GWAS and other molecular techniques offer support and optimization at the molecular level. Future tree breeding will need to fully utilize GWAS, genome editing, and other advanced biotechnologies while maintaining traditional breeding techniques. This integrated approach will not only improve breeding efficiency but also ensure the sustainability and environmental friendliness of the breeding process.

The future development of tree breeding will increasingly depend on scientific advancements and adaptation to environmental changes. With the development of gene editing and other molecular techniques, tree breeding will become more precise and efficient. Gene editing technologies such as CRISPR/Cas9 will make it possible to directly improve tree traits, accelerating the process of developing new varieties. As the impacts of global climate change intensify, cultivating tree species adapted to environmental changes will become an important trend. This includes improving the tolerance of trees to drought, pests and diseases, and other adverse conditions. Furthermore, tree breeding will place greater emphasis on ecological and environmental protection, particularly in terms of preserving genetic diversity and promoting ecosystem health. The application of big data and artificial intelligence in tree breeding will also become more widespread. These technologies will help analyze and process large-scale genomic data, providing deeper insights and predictions for tree breeding.

The application of GWAS in tree breeding has demonstrated clear potential and value. With the advancement of science and technology, combined with traditional breeding methods and modern biotechnology, tree breeding will be able to more effectively adapt to environmental changes and market demands, making important contributions to the sustainable development of future forestry.

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