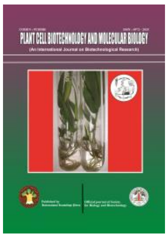

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A Review on Balancing Genomic Selection Efforts for Allogamous Plant Breeding

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Genomic selection (GS) represents a paradigm shift in allogamous plant breeding, leveraging genome-wide marker data to predict the genetic potential of breeding candidates with unprecedented accuracy. This comprehensive review explores the evolution, principles, and applications of GS, highlighting its transformative impact on breeding efficiency and crop improvement. GS uses dense SNP markers to capture the genetic architecture of complex traits, surpassing traditional marker-assisted selection in predictive power. The integration of GS in breeding programs for crops like maize and perennial ryegrass has demonstrated significant gains in traits such as yield, disease resistance, and stress tolerance. Despite its advantages, GS faces challenges including high genotyping costs, the need for large training populations, and the complexity of genetic architectures. Economic constraints and ethical concerns about genetic diversity and data access also pose barriers. Emerging technologies such as AI, machine learning, high-throughput phenotyping, and genome editing hold promise for enhancing GS's accuracy and efficiency. Future strategies should focus on optimizing resource allocation, integrating GS with conventional breeding methods, and fostering collaborative efforts for data sharing and capacity building. The long-term impact of GS is profound, potentially accelerating breeding cycles, enhancing genetic diversity, and developing climate-resilient crops. Collaborative initiatives and open-access genomic resources will be crucial in overcoming current limitations and ensuring that GS benefits global agriculture. As GS continues to evolve, it promises to drive sustainable agricultural practices and improve food security, meeting the challenges posed by climate change and a growing global population. This review underscores the critical role of GS in modern plant breeding and its potential to revolutionize crop improvement.

Keywords: Genomic selection; plant breeding; genetic potential; breeding efficiency; crop improvement; genetic architecture; Genetic gains; crop heterosis.

1. INTRODUCTION

Genomic selection (GS) is a revolutionary approach in plant and animal breeding that leverages genome-wide genetic markers to predict the genetic value of individuals within a breeding population. Unlike traditional marker-assisted selection, which relies on a few markers associated with specific traits, GS uses dense markers covering the entire genome, enabling the prediction of complex traits influenced by numerous genes with small effects. The importance of GS lies in its ability to enhance breeding efficiency, reduce the time required for developing new cultivars, and increase the precision of selection. By utilizing genomic information, breeders can make more informed decisions, leading to faster development of superior varieties with desirable traits such as disease resistance, drought tolerance, and improved nutritional content [1]. The adoption of GS in plant breeding has shown substantial promise, particularly in crops with long breeding cycles. For instance, in perennial crops like trees and vines, where traditional breeding can take decades, GS offers a means to significantly shorten the breeding cycle. Studies have demonstrated that GS can reduce the breeding cycle of perennial ryegrass from 15 years to 7 years, highlighting its transformative potential. Similarly, in annual crops like maize and wheat, GS has led to accelerated genetic gains and increased yield stability under various environmental conditions [2]. The integration of GS into breeding programs is expected to play a pivotal role in meeting the global demand for food security in the face of climate change and a growing population.

Allogamous plant breeding refers to the breeding of plants that predominantly undergo cross-pollination, meaning that they rely on the exchange of genetic material between different individuals to produce offspring. This genetic exchange leads to high levels of heterozygosity and genetic diversity within allogamous species, which is advantageous for adaptability and resilience to environmental stresses. Common allogamous crops include maize (Zea mays), alfalfa (Medicago sativa), and many forage grasses. The breeding strategies for these crops often focus on exploiting heterosis, or hybrid vigor, to produce high-yielding and robust hybrids [3].

The process of breeding allogamous plants typically involves the creation of hybrid populations through controlled pollinations, followed by selection of superior individuals based on phenotypic performance and, more recently, genomic data. The high genetic diversity inherent in allogamous populations poses both opportunities and challenges for breeders. On one hand, the genetic variability provides a rich resource for selecting traits of interest. On the other hand, the complex genetic architecture can make it difficult to achieve consistent improvements in targeted traits [4]. Traditional breeding methods in allogamous crops, such as recurrent selection and hybrid breeding, have been effective in improving traits like yield, disease resistance, and stress tolerance. However, these methods are time-consuming and resource-intensive. The introduction of GS into allogamous plant breeding programs has the potential to overcome these limitations by enabling the selection of superior individuals at an early stage, thus speeding up the breeding cycle and improving the precision of selection. For example, in maize, the implementation of GS has been shown to increase the rate of genetic gain per unit time by approximately 30% compared to traditional methods [5].

1.1 Objectives of the Review

The primary objective of this review is to provide a comprehensive analysis of the current state of genomic selection in allogamous plant breeding, highlighting the advancements, challenges, and future prospects. This review aims to: By providing a detailed overview of the theoretical foundations and practical applications of GS, this review seeks to elucidate how GS can be effectively integrated into allogamous plant breeding programs. This review will analyze various case studies and empirical data to assess how GS has influenced the rate of genetic gain, breeding cycle duration, and overall breeding efficiency in allogamous crops. By examining the technical, economic, and ethical challenges faced by breeders, this review will provide insights into the barriers to the widespread adoption of GS and potential strategies to overcome these obstacles [6]. This review will discuss emerging technologies and methodologies that have the potential to further enhance the effectiveness of GS in allogamous plant breeding, such as machine learning algorithms, gene editing, and high-throughput phenotyping.

2. HISTORY

2.1 Evolution of Genomic Selection Techniques

The concept of genomic selection (GS) emerged in the early 2000s, revolutionizing the field of plant and animal breeding (Table 1). The foundational work laid the groundwork for GS by introducing the idea of using dense genome-wide marker information to predict the genetic value of individuals [7]. This approach marked a significant departure from traditional marker-assisted selection (MAS), which relied on a limited number of markers associated with specific traits. GS, on the other hand, leverages the entire genome, providing a more comprehensive and accurate prediction of an individual's genetic potential. In the subsequent years, advances in high-throughput genotyping technologies, such as single nucleotide polymorphism (SNP) arrays, drastically reduced the cost and time required to generate dense marker data. These technological advancements facilitated the widespread adoption of GS in both animal and plant breeding programs. The integration of high-performance computing and advanced statistical models further enhanced the accuracy and efficiency of GS. Statistical methods such as Best Linear Unbiased Prediction (BLUP) and Bayesian approaches became standard tools for genomic predictions, allowing breeders to handle large datasets and complex genetic architectures [8]. The application of GS in plant breeding began with major crops such as maize and wheat. Studies demonstrated that GS could accelerate the breeding cycle and increase the rate of genetic gain. For instance, GS could improve the prediction accuracy for grain yield in maize compared to traditional MAS. Similar results were observed in wheat, where GS was found to be more effective than phenotypic selection for complex traits like grain yield and disease resistance [9]. The evolution of GS also saw the development of different models to handle various breeding scenarios and genetic architectures. Models such as Genomic Best Linear Unbiased Prediction (GBLUP) and Bayesian Ridge Regression (BRR) became popular due to their robustness and flexibility in handling different types of data. The continuous refinement of these models and the incorporation of machine learning techniques have further improved the predictive power of GS, making it an indispensable tool in modern plant breeding.

2.2 Development of Allogamous Plant Breeding Methods

Allogamous plant breeding, which involves the breeding of cross-pollinated species, has a rich history characterized by the exploitation of genetic diversity and heterosis. The development of allogamous plant breeding methods can be traced back to the early 20th century (Table 2) [10]. Their work on maize (*Zea mays*) demonstrated the benefits of hybrid vigor, leading to the development of the first commercial hybrid maize varieties in the 1920s. The success of hybrid maize breeding prompted the adoption of similar methods in other allogamous crops. Techniques such as recurrent selection and synthetic variety development were employed to enhance genetic diversity and improve population performance. Recurrent selection, in particular, became a cornerstone of allogamous plant breeding. This method involves repeated cycles of selection and recombination to accumulate favorable alleles and improve the overall performance of a population [11]. The development of cytoplasmic male sterility (CMS) systems in the mid-20th century provided a practical means of producing hybrid seeds on a commercial scale. CMS systems, which prevent self-pollination, facilitated the production of hybrids by enabling controlled cross-pollination. This breakthrough had a profound impact on crops like maize, sorghum, and sunflower, leading to significant yield improvements and the widespread adoption of hybrid varieties [12]. In recent decades, molecular breeding techniques have been integrated into allogamous plant breeding programs to enhance the efficiency and precision of selection. Marker-assisted selection (MAS) was one of the first molecular techniques to be widely adopted. MAS allows breeders to select individuals carrying desirable alleles at specific loci, thereby accelerating the breeding process. For example, MAS has been successfully used in alfalfa breeding to select for traits such as disease resistance and forage quality [13]. The advent of genomic selection has further revolutionized allogamous plant breeding by providing a means to predict the genetic value of individuals based on genome-wide marker data. This approach has proven particularly valuable in allogamous species, where high levels of heterozygosity and genetic diversity can complicate traditional breeding methods. Studies have shown that GS can enhance the rate of genetic gain and reduce the time required for developing new varieties in crops like maize and ryegrass [14].

2.3 Key Milestones in Genomic Selection for Allogamous Plants

The integration of genomic selection into allogamous plant breeding has been marked by several key milestones that have demonstrated its potential to transform breeding practices. One of the earliest milestones was the application of GS in maize breeding by the International Maize and Wheat Improvement Center (CIMMYT). In a landmark study, demonstrated that GS could significantly improve the accuracy of predicting grain yield and other complex traits in maize. This study provided a proof-of-concept for the application of GS in allogamous crops and paved the way for its adoption in other species. Another significant milestone was the implementation of GS in perennial ryegrass (Lolium perenne), a forage crop with a long breeding cycle. GS could reduce the breeding cycle of ryegrass from 15 years to 7 years, highlighting its potential to accelerate breeding programs for perennial crops [15]. This study demonstrated the feasibility of using GS in species with complex and long breeding cycles, encouraging its adoption in other perennial crops. The development of high-throughput phenotyping platforms has also been a critical milestone in the evolution of GS. These platforms enable the collection of large-scale phenotypic data, which is essential for training accurate genomic prediction models. For example, high-throughput phenotyping has been used to measure traits such as biomass and grain yield in maize, providing valuable data for GS models. The integration of phenotypic and genomic data has improved the accuracy and efficiency of GS, making it a more powerful tool for allogamous plant breeding. The widespread adoption of GS in commercial breeding programs represents another key milestone. Companies such as DuPont Pioneer and Monsanto have integrated GS into their maize breeding pipelines, leading to faster development of new hybrids with improved yield and stress tolerance [16]. The success of these commercial applications has demonstrated the practical benefits of GS and encouraged its adoption in other allogamous crops. In recent years, the use of machine learning algorithms and advanced statistical models has further enhanced the predictive power of GS. Techniques such as

Table 1. Evolution of genomic selection techniques in genetics and plant breeding

Era/Year	Technique/Approach	Description	Application in Plant Breeding
Pre-2000	Marker-Assisted Selection (MAS)	Utilization of molecular markers (RFLPs, AFLPs, SSRs) linked to Quantitative Trait Loci (QTLs) for selecting desirable traits without waiting for the plant to fully mature.	Effective for introgression of major genes (e.g., disease resistance) into elite cultivars.
2000-2005	Single Nucleotide Polymorphisms (SNPs)	Development of SNP markers enabled the identification of thousands of markers spread across the genome, providing more precise selection strategies.	Used in high-density mapping and genetic diversity studies for trait-linked marker identification.
2005-2010	Genomic Selection (GS)	Prediction models built on whole-genome marker data to estimate breeding values, facilitating early selection of breeding lines before phenotyping.	Improved selection accuracy for complex traits such as yield, stress tolerance, and quality traits.
2010-2015	Genotyping-by-Sequencing (GBS)	NGS-based approach generating large numbers of genome-wide markers quickly, with reduced cost and minimal reference genome information.	Enabled trait mapping and genomic selection for polygenic traits in non-model crops.
2015-2020	Whole Genome Sequencing (WGS)	Comprehensive sequencing of entire plant genomes to detect all variants, including structural variants, rare SNPs, and copy number variations associated with complex traits.	Accelerated identification of causal variants and marker development for breeding programs.
2020-Present	Machine Learning and AI-driven Genomic Selection	Advanced computational techniques for integrating complex genomic and phenotypic data to improve prediction accuracy of breeding values.	Enhanced selection strategies for improving yield stability and stress adaptation.
Future Trends	CRISPR-based Genomic Selection	Gene-editing technologies like CRISPR/Cas for direct manipulation of target genes identified through genomic selection models to produce desired phenotypes rapidly.	Creation of precise allelic variants to speed up breeding cycles and reduce linkage drag.

Table 2. Development of allogamous plant breeding methods

Era/Year	Method/Approach	Description	Application in Plant Breeding
1900-1930	Mass Selection	Selection of superior plants based on phenotypic traits from a diverse population and bulking their seeds for the next generation.	Improved population uniformity and maintained heterozygosity in open-pollinated crops.
1930-1950	Recurrent Selection	Systematic selection and recombination of superior individuals repeatedly over several generations to accumulate favorable alleles.	Enhanced genetic gain for quantitatively inherited traits such as yield and quality.
1950-1970	Hybrid Breeding	Crossing of genetically diverse parent lines to produce F1 hybrids exhibiting heterosis (hybrid vigor) for traits like vigor, yield, and adaptability.	Widely used in maize, sunflower, and other cross-pollinated crops to maximize yield potential.
1970-1990	Synthetic Varieties	Creation of synthetic varieties by intercrossing selected clones, inbred lines, or varieties to maintain heterozygosity and hybrid vigor over multiple generations.	Suitable for crops like forage grasses and legumes, offering better adaptability and stability.
1990-2005	Population Improvement	Refinement of recurrent selection methods to improve populations by increasing the frequency of desirable alleles through various breeding cycles.	Applied for improving complex traits such as disease resistance, stress tolerance, and yield stability.
2005-Present	Genomic-Assisted Breeding	Integration of molecular markers and genomic selection strategies for efficient selection of superior plants in large breeding populations.	Accelerated genetic gain through precise identification of favorable alleles, even for complex traits.
Future Trends	Biotechnological Approaches	Application of gene editing tools like CRISPR/Cas and transgenic technologies to modify specific genes responsible for allogamous crop traits.	Targeted modification of traits such as fertility, self-incompatibility, and pest resistance.

genomic-enabled prediction and deep learning have been employed to improve the accuracy of genomic predictions in complex breeding scenarios [17]. These innovations have opened new avenues for GS, enabling breeders to tackle complex traits and improve the efficiency of selection.

3. PRINCIPLES OF GENOMIC SELECTION

3.1 Genetic Basis and Mechanisms

Genomic selection (GS) is founded on the principle of using genome-wide marker data to predict the genetic potential of individuals within a breeding population. Unlike traditional marker-assisted selection (MAS), which focuses on a few markers linked to specific traits, GS employs dense single nucleotide polymorphism (SNP) markers distributed across the entire genome. This comprehensive approach captures the genetic architecture of complex traits influenced by many small-effect loci, providing a more accurate prediction of an individual's breeding value [18]. The genetic basis of GS lies in the quantitative genetics theory, where the genetic variance of a trait is partitioned into additive, dominance, and epistatic components. GS predominantly focuses on the additive genetic variance, which is the sum of the average effects of individual alleles. This is because additive genetic variance is the primary driver of response to selection in breeding programs. By estimating the effects of genome-wide markers, GS predicts the total additive genetic value of an individual, facilitating more precise selection decisions [19]. GS leverages linkage disequilibrium (LD) between markers and quantitative trait loci (QTLs). LD refers to the non-random association of alleles at different loci. When high LD exists between SNP markers and QTLs, the markers can effectively predict the genetic value of traits influenced by the QTLs. This relationship enables breeders to use marker information to predict phenotypic performance, even without direct phenotypic data for all individuals in the population. The implementation of GS involves the creation of a training population, which consists of individuals with known phenotypes and genotypes. The training population is used to develop a prediction model that estimates the effects of SNP markers on the trait of interest. This model is then applied to a selection population, for which only genotype data is available, to predict their genetic values. These predictions inform selection decisions, enabling breeders to choose individuals with the highest genetic potential for breeding [20].

3.2 Methodologies and Tools

Several methodologies and statistical models have been developed to implement GS effectively. The most commonly used methods include Best Linear Unbiased Prediction (BLUP), Genomic BLUP (GBLUP), and various Bayesian approaches. Each method has its strengths and limitations, and the choice of method depends on the specific breeding context and the nature of the trait being selected. BLUP is a traditional statistical method used in animal and plant breeding. It predicts breeding values by incorporating both fixed and random effects. When applied to GS, BLUP is extended to GBLUP, which uses genome-wide marker data to predict genetic values. GBLUP assumes that all markers have equal and small effects, making it suitable for traits controlled by many small-effect loci [21]. Bayesian methods, such as Bayesian Ridge Regression (BRR), BayesA, BayesB, and BayesCπ, offer flexible alternatives to GBLUP. These methods allow for different prior distributions of marker effects, accommodating varying genetic architectures. For instance, BayesB assumes that most markers have no effect, while a few have large effects, making it suitable for traits influenced by a few major QTLs and many small-effect loci [22]. Recently, machine learning algorithms have been integrated into GS to enhance prediction accuracy. Methods such as random forests, support vector machines, and neural networks can capture complex interactions between markers and traits. These techniques are particularly useful for traits with non-linear genetic architectures and can handle large datasets with high dimensionality.

3.3 Comparison with Traditional Breeding Methods

GS offers several advantages over traditional breeding methods, such as phenotypic selection and MAS. Traditional phenotypic selection relies solely on observable traits, which can be influenced by environmental factors and may not accurately reflect the genetic potential of an individual. This approach can be time-consuming and resource-intensive, especially for traits with low heritability or those that require long evaluation periods [23]. MAS, while more efficient than phenotypic selection, focuses on a limited number of markers associated with specific traits. This approach is effective for traits controlled by a few major QTLs but less so for complex traits influenced by many small-effect loci. MAS also requires prior knowledge of QTL positions and effects, which may not be available for all traits. GS uses genome-wide marker data to predict the genetic value of individuals, capturing the effects of many small-effect loci and providing a more comprehensive assessment of genetic potential. This genome-wide approach increases the accuracy of selection, especially for complex traits with polygenic inheritance [24]. Studies have demonstrated the superiority of GS over traditional methods in terms of prediction accuracy and genetic gain. For instance, GS increased the prediction accuracy for grain yield in maize compared to MAS. Similarly, GS outperformed phenotypic selection and MAS for several agronomic traits in wheat. These findings underscore the potential of GS to enhance breeding efficiency and accelerate genetic improvement. GS can reduce the breeding cycle duration by enabling early selection based on genomic predictions. This is particularly beneficial for perennial crops and those with long generation intervals, where traditional breeding methods can be slow and costly. By selecting individuals at an early stage, GS allows breeders to make faster progress in developing new varieties with desirable traits [25]. GS represents a significant advancement over traditional breeding methods, offering higher accuracy, efficiency, and flexibility in selecting for complex traits. Its ability to leverage genome-wide marker data and predict genetic values more accurately makes it a powerful tool for modern plant and animal breeding programs.

4. APPLICATIONS IN ALLOGAMOUS PLANT BREEDING

4.1 Case Studies of Successful Implementations

Genomic selection (GS) has been successfully implemented in several allogamous plant breeding programs, demonstrating its potential to enhance genetic gains and accelerate the development of improved varieties. One notable case is the application of GS in maize (Zea mays), an allogamous crop with significant economic importance. In a study GS was applied to maize breeding populations at the International Maize and Wheat Improvement Center (CIMMYT). The study showed that GS could predict grain yield and other complex traits with high accuracy, outperforming traditional phenotypic selection methods [26]. This success has led to the integration of GS into CIMMYT's maize breeding programs, resulting in faster genetic gains and more resilient varieties. Another successful implementation of GS is seen in perennial ryegrass (*Lolium perenne*), a key forage crop. The study utilized high-density SNP markers to predict traits such as biomass yield and disease resistance, achieving substantial improvements in prediction accuracy. This case highlights the potential of GS to expedite breeding cycles in perennial crops, which traditionally require long evaluation periods [27]. In the case of alfalfa (Medicago sativa), an important forage legume, GS has been used to enhance traits such as forage quality and disease resistance. The study demonstrated that GS could effectively identify superior genotypes at an early stage, reducing the time and cost associated with phenotypic evaluations. This implementation has shown that GS can be a valuable tool in improving the efficiency of breeding programs for forage crops.

4.2 Specific Traits Targeted in Different Crops

GS has been employed to target a wide range of traits in allogamous crops, reflecting the diverse breeding objectives across different species. In maize, for example, GS has been used to improve traits such as grain yield, drought tolerance, and disease resistance. The focus on grain yield is driven by the need to meet increasing global food demand, while drought tolerance and disease resistance are critical for ensuring crop resilience under changing climate conditions [28]. In perennial ryegrass, GS has targeted traits related to forage yield and quality, as well as abiotic and biotic stress tolerance. Biomass yield is a primary trait of interest due to its importance in forage production systems, while forage quality traits such as digestibility and protein content are essential for livestock nutrition. Studies have shown that GS can effectively predict these complex traits, facilitating the development of high-yielding and high-quality forage varieties. For alfalfa, GS has been applied to improve traits such as forage yield, nutritional quality, and resistance to diseases like anthracnose and root rot. The emphasis on nutritional quality traits, including crude protein content and fiber digestibility, reflects the importance of alfalfa as a high-quality forage crop for livestock. GS has proven effective in enhancing these traits, contributing to the overall productivity and sustainability of alfalfa production systems [29].

4.3 Impact on Breeding Efficiency and Crop Improvement

The implementation of GS in allogamous plant breeding programs has had a profound impact on breeding efficiency and crop improvement. One of the key advantages of GS is its ability to increase the accuracy of selection, particularly for complex traits controlled by many small-effect loci. Studies have consistently shown that GS outperforms traditional phenotypic selection and marker-assisted selection (MAS) in terms of prediction accuracy, leading to more effective breeding decisions [30]. By leveraging genome-wide marker data, GS enables early selection of superior genotypes, reducing the need for extensive phenotypic evaluations and shortening the breeding cycle. This is particularly beneficial for perennial crops and those with long generation intervals, where traditional breeding methods are time-consuming and costly. For instance, the use of GS in perennial ryegrass has significantly reduced the breeding cycle, allowing for more rapid development of improved varieties. GS also enhances the ability to simultaneously improve multiple traits, a critical aspect of modern plant breeding. Traditional breeding methods often struggle to balance selection for multiple traits, especially when they are negatively correlated. GS addresses this challenge by providing a comprehensive view of the genetic architecture of traits, enabling breeders to optimize selection strategies and achieve balanced genetic gains across multiple traits [31]. The integration of GS into breeding programs has also facilitated the development of more resilient crop varieties. By predicting traits such as drought tolerance and disease resistance with high accuracy, GS enables the selection of genotypes that can thrive under adverse environmental conditions. This is crucial for ensuring food security in the face of climate change and increasing global population. GS has proven to be cost-effective in the long run, despite the initial investment in genotyping and computational infrastructure. The efficiency gains achieved through GS, such as reduced breeding cycle duration and increased selection accuracy, offset the upfront costs and lead to higher returns on investment over time. This makes GS an economically viable option for both public and private breeding programs [32].

5. CHALLENGES AND LIMITATIONS

5.1 Technical and Practical Challenges

Despite the promise of genomic selection (GS) in plant breeding, several technical and practical challenges need to be addressed to fully realize its potential. One significant technical challenge is the need for high-density genotyping. The accuracy of genomic predictions relies on the availability of dense marker data covering the entire genome. While advancements in genotyping technologies have reduced costs, high-density genotyping remains expensive and may not be feasible for all breeding programs, particularly those with limited resources [33]. Another technical challenge is the complexity of genetic architectures underlying complex traits. Traits such as yield, drought tolerance, and disease resistance are often controlled by numerous small-effect loci, making it difficult to capture their genetic variance accurately. This complexity necessitates the use of sophisticated statistical models and large training populations to ensure robust genomic predictions. However, assembling and maintaining large, diverse training populations can be logistically challenging and resource-intensive. The integration of phenotypic and genotypic data also poses practical challenges. Accurate phenotyping is crucial for training genomic prediction models, but phenotypic data collection can be labor-intensive, time-consuming, and subject to environmental variability. High-throughput phenotyping platforms offer a solution but require significant investment in infrastructure and technology [34]. Managing and analyzing large-scale genomic and phenotypic datasets demand advanced computational tools and expertise, which may not be readily available in all breeding programs. Another practical challenge is the transferability of prediction models across different environments and breeding populations. Genomic prediction models trained in one environment or population may not perform well in another due to genotype-by-environment interactions and genetic differences among populations. This limitation necessitates the development of multi-environment and multi-population models, further complicating the implementation of GS [35].

5.2 Economic and Resource Constraints

The implementation of GS in plant breeding programs is constrained by economic and resource limitations. The initial investment required for genotyping, phenotyping, and computational infrastructure can be substantial. Small and resource-limited breeding programs may find it challenging to afford the high costs associated with these technologies [36]. While the cost of genotyping has decreased over time, it remains a significant barrier, particularly for programs in developing countries or those targeting orphan crops with limited commercial value. The cost-effectiveness of GS also depends on the scale of the breeding program. Large breeding programs with high turnover and significant investment in research and development can more easily absorb the costs of GS and benefit from its efficiency gains. In contrast, smaller programs may struggle to justify the high upfront costs and may not achieve the same economies of scale. The availability of skilled personnel and expertise is a critical resource constraint. Implementing GS requires expertise in quantitative genetics, bioinformatics, and data analysis. Training and retaining skilled personnel can be challenging, especially in regions with limited access to advanced education and training programs. This knowledge gap can hinder the adoption and effective implementation of GS in many breeding programs [37]. The long-term sustainability of GS also depends on continuous investment in research and development to improve genotyping technologies, statistical models, and phenotyping methods. Securing funding for such ongoing research can be challenging, particularly in the face of competing priorities and limited budgets in public and private sectors.

5.3 Ethics and Environment Considerations

The adoption of GS in plant breeding raises several ethical and environmental considerations. One ethical concern is the potential for reduced genetic diversity in breeding programs. The focus on selecting individuals with the highest genomic estimated breeding values (GEBVs) may lead to a narrowing of the genetic base, increasing the risk of genetic vulnerability to diseases and environmental changes [38]. Maintaining genetic diversity is crucial for the long-term sustainability and resilience of crop populations. Another ethical issue relates to the access and sharing of genomic data. The proprietary nature of genomic data and the concentration of genomic resources in a few large organizations can create disparities in access to technology and information. Ensuring equitable access to genomic tools and data is essential for fostering innovation and inclusivity in plant breeding [39]. Policies and frameworks that promote open access to genomic resources and collaborative research are necessary to address these disparities. Environmental considerations include the potential impact of GS on agroecosystems. The development of high-yielding, uniform crop varieties may lead to monocultures, which can have negative effects on biodiversity and ecosystem health. Monocultures are more susceptible to pests and diseases, requiring increased use of chemical inputs such as pesticides and fertilizers, which can have adverse environmental impacts [40]. Sustainable breeding practices that incorporate diverse and resilient crop varieties are needed to mitigate these risks. The use of genomic technologies also raises concerns about the unintended consequences of manipulating genetic information. While GS itself does not involve genetic modification, the precision and power of genomic tools may facilitate the development of genetically modified organisms (GMOs). The ethical and environmental implications of GMOs are subjects of ongoing debate, and regulatory frameworks must ensure the safe and responsible use of genomic technologies in plant breeding [41].

6. STRATEGIES FOR BALANCING GENOMIC SELECTION EFFORTS

6.1 Optimizing Resource Allocation

Efficient resource allocation is crucial for maximizing the benefits of genomic selection (GS) in plant breeding programs. One of the key strategies to optimize resource allocation is the use of cost-effective genotyping methods. High-density genotyping platforms, such as SNP arrays and next-generation sequencing, are essential for accurate genomic predictions, but they can be expensive. To mitigate costs, breeders can adopt genotyping-by-sequencing (GBS) and other reduced-representation sequencing methods that provide sufficient marker density at a lower cost. Combining low-cost genotyping with imputation techniques can help in achieving high marker density without the need for extensive genotyping [42]. Another strategy is to balance the size of the training population with the genotyping budget. While larger training populations generally lead to more accurate genomic predictions, they also require more resources. Optimal training population size can be determined based on the heritability of the trait, the genetic architecture, and the breeding program's budget. Simulation studies have shown that increasing the size of the training population enhances prediction accuracy up to a certain point, beyond which the gains diminish [43]. Breeders can use these insights to determine the most cost-effective training population size for their specific breeding goals.

Resource allocation can also be optimized by prioritizing traits that offer the highest return on investment. Traits with high economic value or those that are difficult to improve through conventional breeding methods should be given priority in GS efforts. For example, in maize breeding programs, traits such as drought tolerance and disease resistance are often prioritized due to their significant impact on yield and crop stability. By focusing on high-impact traits, breeders can maximize the efficiency and effectiveness of their GS programs. Leveraging existing genomic resources and data is another way to optimize resource allocation. Publicly available genomic data and reference genomes can be utilized to reduce the costs associated with de novo sequencing and marker development. Collaborative efforts and data sharing among breeding programs can further enhance the utility of existing resources and minimize redundant efforts [44].

6.2 Integrating Genomic Selection with Conventional Breeding

Integrating GS with conventional breeding methods can enhance the overall efficiency and effectiveness of plant breeding programs. One approach is to use GS to complement phenotypic selection. By using genomic predictions to select individuals in early generations, breeders can reduce the number of individuals that need to be phenotyped in later generations. This approach not only saves time and resources but also allows for the identification of superior genotypes that may not be distinguishable based on phenotype alone [45]. Another integration strategy is the use of GS in combination with marker-assisted selection (MAS). While GS provides genome-wide predictions, MAS focuses on specific markers linked to major genes or QTLs. Combining these methods can be particularly effective for improving traits controlled by a few major genes and many small-effect loci. For instance, MAS can be used to introgress major disease resistance genes, while GS can be used to select for yield and other complex traits [46]. Breeding schemes can also be optimized by incorporating GS into recurrent selection programs. In recurrent selection, individuals with the highest breeding values are selected and intermated to create the next generation. GS can enhance the efficiency of recurrent selection by providing more accurate estimates of breeding values and allowing for the selection of individuals at an early stage. This approach has been successfully implemented in maize and other crops, resulting in accelerated genetic gains [47].

Integrating GS with hybrid breeding programs offers another opportunity for enhancing breeding efficiency. In crops such as maize, hybrid vigor or heterosis is a major driver of yield improvements. GS can be used to predict the performance of hybrid combinations based on the genomic data of the parental lines. This allows breeders to identify the best hybrid combinations without extensive field testing, thus speeding up the development of superior hybrids [48].

6.3 Collaborative Efforts and Knowledge Sharing

Collaboration and knowledge sharing are essential for maximizing the benefits of GS in plant breeding. Collaborative breeding networks and consortia can pool resources, expertise, and data to address common challenges and achieve shared goals. For example, the Genomic Open-source Breeding Informatics Initiative (GOBII) aims to develop and deploy open-source tools for GS, facilitating data sharing and collaboration among public and private breeding programs. International collaborations can also enhance the utility of GS by enabling the sharing of diverse germplasm and environmental data. Breeding programs in different regions can benefit from each other's genomic resources and knowledge, leading to the development of varieties that are adapted to a wide range of environments. The International Wheat Genome Sequencing Consortium (IWGSC) and the International Maize and Wheat Improvement Center (CIMMYT) are examples of organizations that facilitate such collaborations, contributing to global food security [49]. Knowledge sharing through training and capacity-building initiatives is crucial for the widespread adoption of GS. Workshops, webinars, and online courses can provide breeders with the skills and knowledge needed to implement GS in their programs. Organizations such as the CGIAR and the Bill & Melinda Gates Foundation have been instrumental in supporting capacity-building efforts in developing countries, ensuring that breeders worldwide can benefit from advances in genomic technologies [50]. Data sharing platforms and repositories play a critical role in facilitating collaborative efforts. Public databases such as the National Center for Biotechnology Information (NCBI) and the European Nucleotide Archive (ENA) provide access to genomic data from a wide range of species. These platforms enable breeders to access and utilize existing data, reducing the need for redundant genotyping efforts. The development of interoperable data standards and formats is essential for ensuring that data can be easily shared and integrated across different platforms and breeding programs [51].

7. FUTURE

7.1 Emerging Technologies and Innovations

The future of genomic selection (GS) in allogamous plant breeding is poised for significant advancements driven by emerging technologies and innovations. One of the most promising technologies is the application of artificial intelligence (AI) and machine learning (ML) algorithms to enhance the accuracy and efficiency of genomic predictions. AI and ML can analyze large datasets to identify complex patterns and interactions among genetic markers, environmental factors, and phenotypic traits. These technologies have the potential to improve the predictive power of GS models and provide more accurate estimates of breeding values. Another emerging technology is the use of high-throughput phenotyping (HTP) platforms, which can rapidly and accurately measure phenotypic traits across large populations. HTP platforms, such as drones, ground-based sensors, and imaging systems, can collect data on traits like biomass, canopy temperature, and disease symptoms at various growth stages. Integrating HTP data with genomic information can enhance the accuracy of GS by providing precise phenotypic measurements that are crucial for training prediction models [52]. Advancements in genome editing technologies, particularly CRISPR/Cas9, also hold promise for the future of GS. Genome editing allows precise modification of specific genes associated with desirable traits, enabling the creation of new alleles that can be rapidly incorporated into breeding programs. Combining genome editing with GS can accelerate the development of improved varieties by directly targeting key genetic loci. This integration could lead to the production of crops with enhanced traits such as disease resistance, abiotic stress tolerance, and improved nutritional content. The use of multi-omics approaches, which integrate genomics, transcriptomics, proteomics, and metabolomics data, is another innovation that can transform GS. Multi-omics provides a comprehensive understanding of the molecular mechanisms underlying complex traits and can identify novel biomarkers for selection. By incorporating multi-omics data into GS models, breeders can improve the accuracy of predictions and uncover new targets for genetic improvement [53].

7.2 Potential Advances in Genomic Selection

Several potential advances in GS are expected to enhance its application in allogamous plant breeding. One such advance is the development of more sophisticated statistical models that can account for non-additive genetic effects, such as dominance and epistasis. Traditional GS models primarily focus on additive genetic variance, but incorporating non-additive effects can improve the accuracy of predictions for complex traits. Models such as Bayesian whole-genome regression and machine learning algorithms like deep learning can capture these complex interactions. Another advance is the use of environmental covariates in GS models to account for genotype-by-environment (GxE) interactions. GxE interactions play a significant role in the expression of many traits, particularly in allogamous crops that are often grown in diverse environments. By including environmental data in prediction models, breeders can improve the accuracy of GS across different environmental conditions and develop varieties that are resilient to climate change [54]. The implementation of GS in polyploid crops, such as wheat and sugarcane, presents another potential advance. Polyploidy complicates GS due to the presence of multiple sets of chromosomes, which affects the inheritance patterns and genetic architecture of traits. Recent developments in genotyping technologies and statistical models specifically designed for polyploid species can enhance the application of GS in these crops, leading to improved breeding outcomes. Advances in genotyping technologies, such as long-read sequencing and single-cell genomics, can also drive the future of GS. Long-read sequencing provides more accurate and contiguous genome assemblies, facilitating the identification of structural variants and complex genomic regions that are often missed by short-read sequencing. Single-cell genomics allows the study of gene expression and genetic variation at the cellular level, providing insights into the functional genomics of complex traits [55].

7.3 Long-term Impact on Allogamous Plant Breeding

The long-term impact of GS on allogamous plant breeding is expected to be profound, leading to significant improvements in breeding efficiency, genetic gain, and crop resilience. One of the key long-term impacts is the acceleration of breeding cycles. By enabling early and accurate selection of superior genotypes, GS can reduce the time required to develop new varieties. This is particularly important for perennial crops and those with long generation intervals, where traditional breeding methods are slow and costly. Another long-term impact is the enhancement of genetic diversity within breeding programs. While there are concerns that intense selection pressure from GS could reduce genetic diversity, strategies such as genomic mating and optimal contribution selection can be employed to maintain or even increase genetic diversity. These strategies ensure that breeding populations retain a broad genetic base, which is crucial for long-term adaptability and resilience to environmental changes [56]. GS is also expected to contribute to the development of climate-resilient crops. By accurately predicting traits associated with abiotic stress tolerance, such as drought and heat tolerance, GS can facilitate the selection of genotypes that are better adapted to changing climatic conditions. This will be essential for ensuring food security in the face of global climate change. The integration of GS with precision agriculture technologies can further enhance its long-term impact. Precision agriculture involves the use of sensors, drones, and other technologies to monitor and manage crop production at a fine scale. By combining GS with precision agriculture, breeders can develop varieties that are optimized for specific environments and management practices, leading to increased productivity and sustainability [57]. The adoption of GS is expected to drive innovation and collaboration in plant breeding. The need for advanced genotyping, phenotyping, and computational resources will encourage breeding programs to collaborate and share data, tools, and expertise. This collaborative approach can accelerate the development of improved varieties and ensure that the benefits of GS are realized globally.

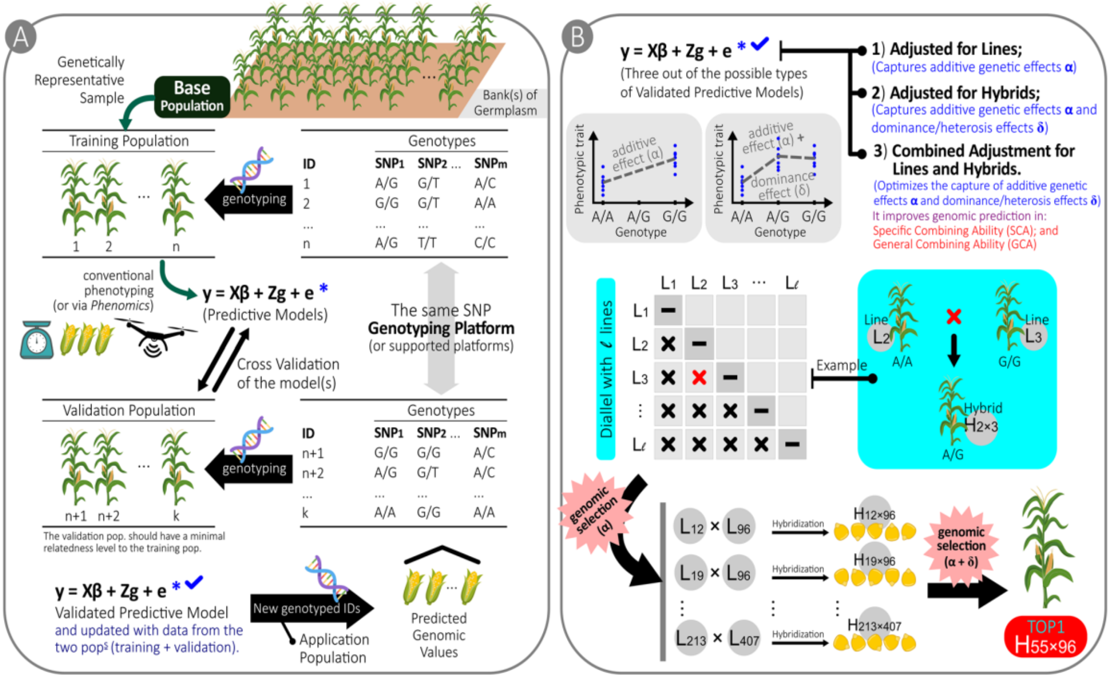

Fig. 1. Simplified diagram of a genomic selection (GS) process, using corn as an example
Part 'A' of the figure illustrates the process of fitting and validating predictive genomic models. Part 'B' of the figure depicts possible schemes for use, both for the prediction of inbred lines and for the prediction of hybrids based on the best inbred lines or validated models with hybrid information. Adapted from Vianello, Resende & Brondani [58]

8. CONCLUSION

Genomic selection (GS) has revolutionized allogamous plant breeding by providing a comprehensive and accurate method for predicting genetic potential, thereby accelerating genetic gains and enhancing breeding efficiency. Key points include the integration of high-density genotyping, advanced statistical models, and high-throughput phenotyping, which collectively improve prediction accuracy and selection precision. The implications for plant breeding are profound, offering faster breeding cycles, increased genetic diversity, and the development of climate-resilient crops. However, challenges such as high costs, resource constraints, and ethical considerations must be addressed. Future research should focus on optimizing resource allocation, integrating GS with conventional methods, and fostering collaborative efforts to share data and innovations. Advancements in AI, machine learning, genome editing, and multi-omics approaches will further enhance GS's impact.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of manuscripts.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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