

Genome-Wide Prediction and Selection in Plant and Animal Breeding: A Systematic Review of Current Techniques

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Abstract With the advancement of genomics technology, whole genome prediction (GWP) and genome selection (GS) have become important tools in plant and animal breeding. Genomic selection utilizes whole genome marker information to select target traits through predictive models, improving breeding efficiency and accuracy. This study comprehensively reviews the application of whole genome prediction technology in plant and animal breeding, with a focus on exploring its role in improving breeding efficiency. Analyzing current genome selection models and methods, exploring the potential application of GS in improving important agronomic and economic traits, as well as its prospects in different fields. Research has shown that GS technology has greatly improved selection efficiency in multiple breeding projects, particularly in enhancing plant disease resistance and increasing crop yield. In animal breeding, genome selection has been widely applied to improve the reproductive traits, health, and productivity of livestock.

Keywords Genomic selection; Plant breeding; Animal breeding; Machine learning; Genotype-environment interaction

1 Introduction

Genome-wide prediction and selection (GWPS) have revolutionized the fields of plant and animal breeding by enabling the prediction of complex traits through the use of dense genomic markers. This approach involves the implementation of whole-genome regression (WGR) models, where phenotypes are regressed on thousands of markers concurrently, allowing for the accurate prediction of genetic values (Campos et al., 2013). The advent of high-throughput sequencing technologies has facilitated the capture of both additive and non-additive genetic effects, thereby enhancing the prediction of genetic gains from selection (He et al., 2023). Various statistical models, such as genomic best linear unbiased predictor (G-BLUP) and Bayesian least absolute shrinkage and selection operator (BLASSO), have been developed to address the high dimensionality and multicollinearity challenges inherent in GWPS (Lima et al., 2019a). Additionally, non-parametric methods like Delta-p have been proposed to further improve prediction accuracy (Lima et al., 2019b).

The integration of GWPS into modern breeding programs has significantly increased the efficiency and speed of genetic evaluations, leading to higher genetic gains per unit of time (Alkimim et al., 2020). This is particularly crucial for perennial species, where traditional breeding cycles are lengthy. By leveraging genomic estimated breeding values (GEBVs), breeders can identify superior genotypes early in the breeding cycle, thus accelerating the selection process (Lima et al., 2019a). The application of GWPS has shown promising results in various crops, including cassava, *Coffea canephora*, and Asian rice, demonstrating its potential to enhance breeding outcomes across diverse species (Lima et al., 2019a; Lima et al., 2019b; Alkimim et al., 2020). Moreover, the use of deep learning models in GWPS has further improved prediction accuracy for complex traits, making it a valuable tool in large-scale breeding programs (Sandhu et al., 2021).

This study provides a comprehensive overview of the current technologies and methods used in genome-wide prediction and selection (GWPS) in plant and animal breeding. It summarizes the various statistical models and methods employed in GWPS, including both parametric and non-parametric approaches, and evaluates their effectiveness and efficiency in different breeding programs and species. The study also discusses the challenges

and limitations associated with GWPS, such as high dimensionality, multicollinearity, and genotype-environment interactions. Additionally, it highlights recent advancements and future directions in the field, including the integration of deep learning models and digital breeding technologies.

2 Overview of Genome-Wide Prediction Techniques

2.1 Genomic selection (GS)

Genomic Selection (GS) has revolutionized the field of plant and animal breeding by enabling the rapid selection of superior genotypes and accelerating the breeding cycle. Unlike traditional marker-assisted selection, which focuses on identifying individual loci associated with traits, GS uses all marker data as predictors of performance, leading to more accurate predictions (Jannink et al., 2010; Crossa et al., 2017). This approach is particularly beneficial for complex traits controlled by many genes with small effects, which traditional methods struggle to address effectively (Meuwissen et al., 2016; Varshney et al., 2017). The integration of GS into breeding programs has shown tangible genetic gains, as evidenced by its application in maize breeding, where significant improvements have been observed (Crossa et al., 2017).

The success of GS hinges on its ability to incorporate all marker information into the prediction model, thereby avoiding biased marker effect estimates and capturing more of the variation due to small-effect quantitative trait loci (QTL). This comprehensive approach allows for the prediction of breeding values of lines in a population by analyzing their phenotypes and high-density marker scores. The accuracy of these predictions has been demonstrated in both simulation and empirical studies, with correlations between true breeding value and genomic estimated breeding value reaching levels as high as 0.85 for polygenic low heritability traits (Varshney et al., 2017). This level of accuracy is sufficient to consider selecting for agronomic performance using marker information alone, substantially accelerating the breeding cycle and enhancing gains per unit time.

2.2 Genomic prediction models

Genomic prediction models are central to the implementation of GS, as they estimate the effects of markers across the entire genome on the target population based on a prediction model developed in the training population. These models are designed to capture small QTL effects that are often ignored in traditional association analysis, thereby providing a more comprehensive understanding of the genetic architecture of complex traits (Desta and Ortiz, 2014). Various genomic prediction models have been proposed, each with its strengths and limitations. For instance, the Bayesian Lasso, weighted Bayesian shrinkage regression (wBSR), and random forest (RF) are among the models that have shown promise in terms of predictive accuracy and computational efficiency (Heslot et al., 2012).

The choice of genomic prediction model can significantly impact the accuracy of predictions and the genetic gain from selection. Comparative studies have shown that while many models achieve similar levels of accuracy, they differ in their susceptibility to overfitting, computation time, and the distribution of marker effect estimates (Heslot et al., 2012). Additionally, the integration of multi-trait and multi-environment models, high-throughput phenotyping, and deep learning approaches can further enhance the accuracy and efficiency of genomic predictions (Merrick et al., 2022). These advancements highlight the importance of continuous research and optimization of genomic prediction models to maximize their potential in breeding programs.

2.3 Machine learning and artificial intelligence applications

The application of machine learning (ML) and artificial intelligence (AI) in genomic prediction represents a significant advancement in the field of breeding. Machine learning methods, such as random forest and deep learning, have been shown to capture non-additive effects and improve the accuracy of genomic predictions. These methods can handle large datasets with complex interactions, making them well-suited for genomic prediction tasks. For example, random forest, a machine learning method, has been found to be effective in capturing non-additive effects, which are often missed by traditional linear models (Heslot et al., 2012).

The integration of ML and AI into genomic prediction models offers several advantages, including the ability to analyze large and complex datasets, improve prediction accuracy, and reduce computation time. High-throughput

phenotyping and deep learning approaches can leverage the large amount of genomic and phenotypic data collected across different growing seasons and environments to increase heritability estimates, selection intensity, and selection accuracy (Merrick et al., 2022).

3 Data Requirements and Management

3.1 High-throughput genotyping

High-throughput genotyping is a cornerstone of modern plant and animal breeding programs, enabling the identification and utilization of genetic variation on a genome-wide scale. Single Nucleotide Polymorphisms (SNPs) are the most commonly used markers due to their abundance and the development of high-throughput genotyping technologies such as SNP arrays and whole-genome sequencing (WGS). SNP arrays, like the TaBW280K developed for wheat, allow for efficient genotyping of large populations, providing valuable data for diversity analyses and breeding programs (Rimbert et al., 2018). Similarly, genotyping-by-sequencing (GBS) has emerged as a cost-effective alternative, combining marker discovery and genotyping in a single step, which is particularly useful for species with large genomes (He et al., 2014; Gorjanc et al., 2015).

The effectiveness of genomic selection (GS) is highly dependent on the density and coverage of genetic markers. High-density SNP arrays and WGS provide comprehensive coverage of the genome, capturing a wide range of genetic variation. For instance, the TaBW280K array for wheat includes 280,226 SNPs, covering both genic and intergenic regions, which enhances the resolution of genetic mapping and the accuracy of GS models (Rimbert et al., 2018). In livestock, GBS has been shown to provide comparable accuracy to SNP arrays when a sufficient number of markers and appropriate sequencing depth are used (Gorjanc et al., 2015). The choice between SNP arrays and WGS often depends on the specific requirements of the breeding program, including the species, genome size, and available resources (Bhat et al., 2016; Moraes et al., 2018).

Cost and efficiency are critical factors in the selection of genotyping methods. SNP arrays, while having a high initial development cost, offer a cost-effective solution for routine genotyping once established. For example, the development of species-specific SNP arrays can be expensive, but they provide high-throughput and reliable genotyping for large breeding populations (Grattapaglia et al., 2011; Moraes et al., 2018). On the other hand, GBS and other NGS-based methods offer flexibility and lower initial costs, making them suitable for species where SNP arrays are not available or economically feasible (He et al., 2014; Gorjanc et al., 2015). The continuous decline in sequencing costs is expected to further enhance the feasibility of WGS for GS in the near future (Bhat et al., 2016).

3.2 Phenotypic data collection

Accurate phenotypic data is essential for the success of GS. High-throughput phenotyping technologies are being developed to complement genotyping efforts, enabling the collection of large-scale, precise phenotypic data. These technologies include automated imaging systems, remote sensing, and various sensor-based methods that can capture complex traits in real-time. The integration of high-throughput phenotyping with genotyping data is crucial for improving the accuracy of genomic predictions and achieving significant genetic gains in breeding programs (Figure 1) (Bhat et al., 2016; Wang et al., 2016).

Bhat et al. (2016) found that combining high-throughput phenotyping (HTP) with genomic estimated breeding values (GEBV) enables precise prediction of an individual's breeding value, thereby accelerating the identification, testing, and promotion of superior genotypes. NGS and HTP technologies significantly enhance the efficiency and accuracy of genomic selection by increasing the coverage of genotype data and the precision of phenotype data collection, speeding up the breeding process for superior varieties. The application of these technologies reduces costs, optimizes breeding resources, and provides powerful tools for crop improvement.

3.3 Data integration and management

The integration and management of large-scale genotypic and phenotypic data pose significant challenges. Effective data management systems are required to handle the vast amounts of data generated by high-throughput genotyping and phenotyping technologies. These systems must support data storage, retrieval, and analysis,

facilitating the seamless integration of diverse data types. Bioinformatics pipelines are essential for processing and interpreting GBS datasets, enabling the identification of genetic markers and the development of GS models (Ganal et al., 2014; He et al., 2014). Additionally, databases that compile marker data from multiple genotyping experiments can streamline downstream data processing and enhance the utility of genotyping data for both scientific research and breeding applications (Ganal et al., 2014).

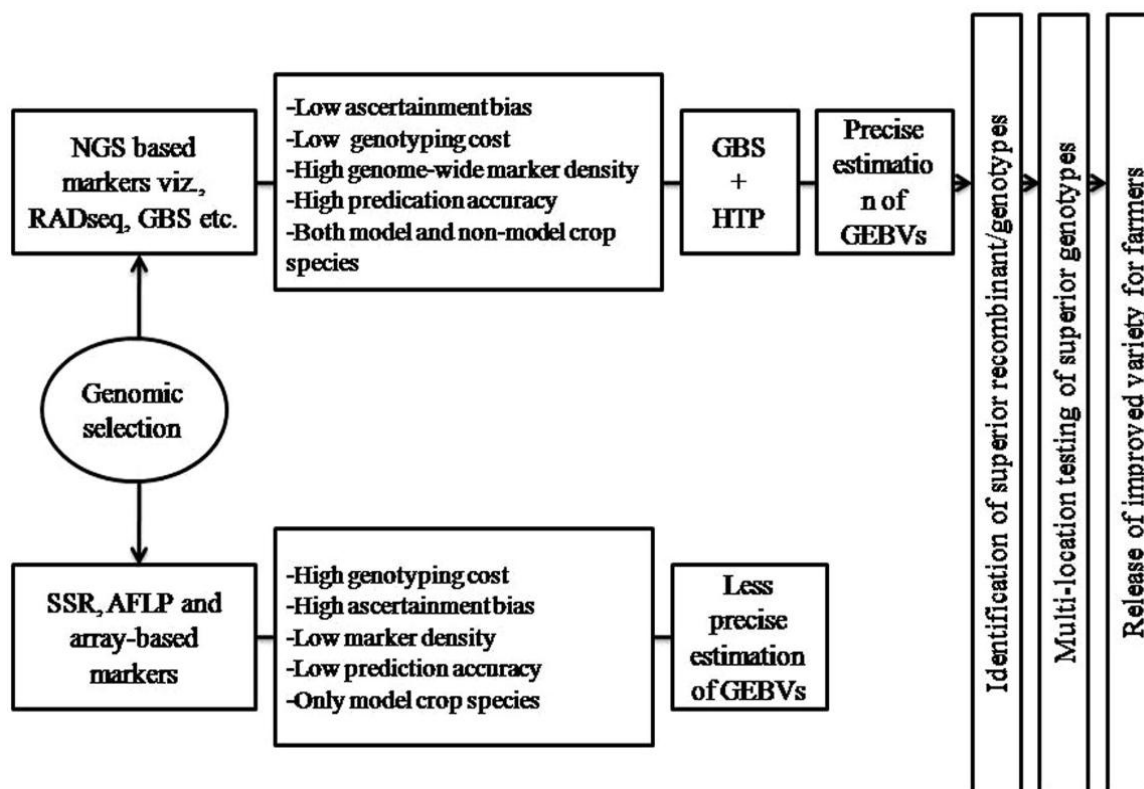


Figure 1 The role of NGS-Based marker technology and high-throughput phenotyping in genomic selection (Adopted from Bhat et al., 2016)

4 Statistical Methods and Models

4.1 Best linear unbiased prediction (BLUP)

Best Linear Unbiased Prediction (BLUP) is a widely used statistical method for estimating random effects in mixed models, particularly in the context of animal breeding. Originally developed for estimating breeding values, BLUP has been adapted for various applications, including plant breeding and variety testing. In plant breeding, BLUP has been employed to model and exploit genetic correlations among relatives using pedigree information, and to handle genotype-by-environment interactions through flexible variance-covariance structures. This method has demonstrated good predictive accuracy compared to other procedures, making it a valuable tool for genetic evaluation in both plants and animals (Piepho et al., 2008).

In animal breeding, BLUP has been adapted to address specific challenges such as the inclusion of dam effects in models for polytocous species like swine and poultry. This adaptation involves hierarchical models that account for sires, dams within sires, individuals within full-sib families, and records within individuals. The development of alternative computing algorithms has facilitated the timely genetic evaluation of large populations, ensuring that BLUP remains a robust and efficient method for genetic prediction. Additionally, the integration of genomic information into BLUP models, such as the use of trait-specific marker-derived relationship matrices, has further enhanced the accuracy of genomic breeding value predictions (Bauer et al., 2006; Muir, 2007; Zhang et al., 2010).

4.2 Bayesian methods

Bayesian methods have gained prominence in genomic prediction due to their flexibility and ability to incorporate prior information. These methods, such as BayesA, BayesB, and BayesC, allow for the estimation of marker

effects by treating them as random variables with specific prior distributions. This approach enables the modeling of complex genetic architectures and the incorporation of uncertainty in parameter estimates. Bayesian methods have shown superior performance in predicting breeding values, particularly for traits with low heritability, by effectively capturing the underlying genetic variance (Muir, 2007; Zhang et al., 2010).

One of the key advantages of Bayesian methods is their ability to handle large-scale genomic data and provide more accurate predictions compared to traditional methods. For instance, the BayesB method, which assigns a mixture of distributions to marker effects, has been shown to outperform other BLUP-based methods in terms of prediction accuracy. This is particularly evident in scenarios where the genetic architecture of the trait involves a few large-effect loci and many small-effect loci. The flexibility of Bayesian methods in accommodating different genetic architectures makes them a powerful tool for genomic selection in both plant and animal breeding (Muir, 2007; Zhang et al., 2010).

4.3 Machine learning algorithms

Machine learning algorithms have emerged as powerful tools for genomic prediction and selection, offering the ability to model complex, non-linear relationships between genotypes and phenotypes. Techniques such as random forests, support vector machines, and neural networks have been applied to genomic data to improve the accuracy of breeding value predictions. These algorithms can handle high-dimensional data and capture interactions among markers, making them suitable for predicting complex traits influenced by multiple genetic and environmental factors (Muir, 2007; Zhang et al., 2010)

The application of machine learning in genomic selection has shown promising results, particularly in enhancing prediction accuracy and selection response. For example, genomic best linear unbiased prediction (G-BLUP), a ridge-regression type method, has been effectively combined with machine learning techniques to improve the prediction of complex human traits. Studies have demonstrated that machine learning algorithms can outperform traditional BLUP methods, especially when dealing with large datasets and traits with low heritability. The integration of machine learning into genomic selection frameworks holds great potential for advancing breeding programs and achieving higher genetic gains (Muir, 2007; Zhang et al., 2010; Campos et al., 2013).

5 Applications in Plant Breeding

5.1 Genomic selection for crop improvement

Genomic selection (GS) has revolutionized crop improvement by enabling the prediction of breeding values using genome-wide markers. This method leverages high-density marker scores to predict the genetic potential of untested populations, thus accelerating the breeding cycle and enhancing genetic gains (Jannink et al., 2010; Desta and Ortiz, 2014; Varshney et al., 2017). Unlike traditional marker-assisted selection, which focuses on individual loci, GS incorporates all marker data, capturing the effects of small quantitative trait loci (QTL) and providing more accurate predictions (Desta and Ortiz, 2014; Varshney et al., 2017). Studies have shown that GS can achieve high correlation levels between true breeding values and genomic estimated breeding values, even for traits with low heritability, making it a powerful tool for selecting agronomic performance traits (Varshney et al., 2017). The integration of GS with advanced technologies such as high-throughput genotyping and phenotyping further enhances its efficiency and application in varietal development programs (Krishnappa et al., 2021).

5.2 Enhancing disease resistance

The application of GS in enhancing disease resistance in crops has shown significant promise. By using genome-wide markers, GS can predict the genetic potential for disease resistance traits more accurately than traditional methods (Crossa et al., 2011; Wang et al., 2018). For instance, in maize, GS has been used to improve resistance to diseases such as *Exserohilum turcicum* and *Cercospora zea-maydis*, demonstrating the method's effectiveness in real-world breeding programs (Crossa et al., 2011). The ability of GS to account for genotype \times environment interactions further enhances its utility in breeding for disease resistance, as it allows for the selection of genotypes that perform well across different environmental conditions (Crossa et al., 2011; Crossa et al., 2017). This holistic approach to selection ensures that disease-resistant traits are effectively incorporated into new crop varieties, contributing to sustainable agricultural practices.

5.3 Yield and quality traits

Improving yield and quality traits in crops is a primary goal of plant breeding, and GS has proven to be a valuable tool in this regard. By utilizing genome-wide markers, GS can predict complex traits influenced by multiple genes, such as yield and quality, with greater accuracy (Jannink et al., 2010; Wang et al., 2018). The method's ability to capture the effects of small QTL and incorporate them into prediction models allows for more comprehensive selection decisions (Desta and Ortiz, 2014; Wang et al., 2018). Empirical studies have shown that GS can lead to significant genetic gains in yield and quality traits, making it a critical component of modern breeding programs (Jannink et al., 2010; Crossa et al., 2017). Additionally, the integration of multi-trait genomic selection methods, which optimize selection decisions across multiple traits, further enhances the effectiveness of GS in improving yield and quality (Figure 2) (Moeinizade et al., 2020). This multi-objective optimization approach ensures that breeding programs can achieve balanced improvements in various economically important traits, ultimately leading to the development of superior crop varieties.

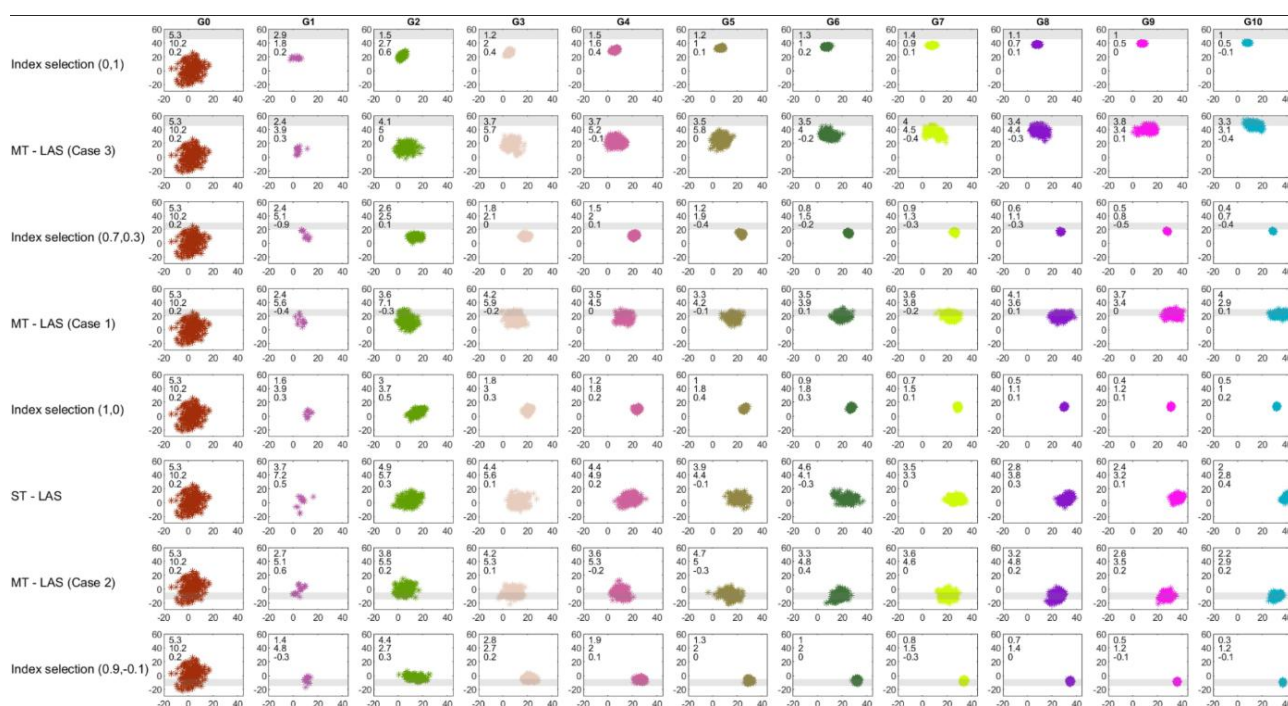


Figure 2 Comparison of multi-trait linear weighted selection (MT-LAS), single-trait linear weighted selection (ST-LAS), and Index selection methods (Adopted from Moeinizade et al., 2020)

Image Caption: This figure illustrates the performance of MT-LAS, ST-LAS, and different index selection methods over 10 generations in a simulation; Each small box represents the distribution of genetic estimated breeding values (GEBVs) for two traits across each generation, with the gray bars indicating the constraint boundaries; The three numbers in each box represent the standard deviations (SD) of trait 1 and trait 2, followed by the correlation between the two traits (Adopted from Moeinizade et al., 2020)

Moeinizade et al. (2020) studied the genetic performance and correlations of traits in multi-trait selection (MT-LAS) and single-trait selection (ST-LAS). Under genomic selection (GS), selecting multiple traits simultaneously (such as yield and quality) allows for better balancing of improvement goals and more effective selection of target traits. Index selection, on the other hand, influences the direction of selection through different weighting coefficients. Overall, MT-LAS performed excellently in balancing improvements across multiple traits, demonstrating significant potential for applications in improving crop yield and quality.

6 Applications in Animal Breeding

6.1. Genetic improvement of livestock

Genomic selection (GS) has revolutionized the genetic improvement of livestock by enabling more accurate predictions of breeding values. Traditional marker-assisted selection (MAS) was limited by the complexity of traits in livestock, which are influenced by thousands of genes with small effects. GS overcomes this by

considering all markers linked to genes affecting the trait, thus improving the accuracy of selection. The development of high-throughput genotyping technologies and the discovery of numerous single nucleotide polymorphisms (SNPs) have facilitated the widespread adoption of GS in livestock breeding programs (Meuwissen et al., 2016). This approach has been particularly impactful in dairy and beef cattle, pigs, and poultry, where it has significantly enhanced genetic gain by reducing the generation interval and increasing selection accuracy (Ibtisham et al., 2017).

6.2 Selection for reproductive traits

Reproductive traits are crucial for the efficiency and profitability of livestock production. Genomic selection has shown promise in improving these traits by enabling early and accurate prediction of breeding values. By using genetic markers spread across the entire genome, GS can capture the effects of multiple quantitative trait loci (QTL) associated with reproductive performance (Ibtisham et al., 2017). This allows for the selection of animals with superior reproductive traits at a younger age, thereby accelerating genetic progress. The integration of GS with other breeding tools and platforms can further enhance the selection process, making it more efficient and cost-effective (Xu et al., 2019).

6.3 Health and productivity enhancements

Improving the health and productivity of livestock is a primary goal of breeding programs. Genomic selection has been instrumental in achieving these objectives by providing a more precise estimation of genetic merit for health and productivity traits. Studies have shown that GS can significantly enhance the genetic gain for traits such as disease resistance, growth rate, and milk production (Ibtisham et al., 2017). The use of whole-genome regression models, which regress phenotypes on thousands of markers simultaneously, has been particularly effective in predicting complex traits (Campos et al., 2013). Additionally, the detection of selection signatures in livestock genomes has provided insights into the domestication and evolutionary processes, helping identify candidate genes associated with economically important traits (Saravanan et al., 2020). This knowledge can be leveraged to develop breeding strategies that improve the overall health and productivity of livestock populations.

7 Challenges and Limitations

7.1 Genotype-environment interactions

Genotype-environment ($G \times E$) interactions present a significant challenge in genomic selection for both plant and animal breeding. These interactions can complicate the prediction of phenotypic traits because the performance of genotypes can vary across different environments. Several studies have highlighted the importance of incorporating $G \times E$ interactions into genomic prediction models to improve accuracy. For instance, models that account for $G \times E$ interactions have shown superior predictive ability compared to single-environment models (Malosetti et al., 2016; Cuevas et al., 2016; Oakey et al., 2016). Additionally, the use of environmental covariables has been found to be beneficial in predicting phenotypes in untested environments, further emphasizing the need to consider $G \times E$ interactions in genomic selection (Malosetti et al., 2016). However, the complexity of these models and the computational resources required to implement them can be substantial, posing a significant limitation (Granato et al., 2018; Jighly et al., 2021).

7.2 Computational and resource constraints

The implementation of genomic selection models, especially those incorporating $G \times E$ interactions, often requires significant computational resources. The scale of multi-environment trials is increasing, which in turn increases the computational challenges associated with genomic selection (Granato et al., 2018). For example, Bayesian models that account for $G \times E$ interactions can be computationally intensive, although recent advancements have led to more efficient algorithms and software packages that reduce computational time (Cuevas et al., 2016; Granato et al., 2018). Despite these advancements, the need for high computational power and extensive data storage remains a barrier, particularly for smaller breeding programs with limited resources (Lado et al., 2016; Jighly et al., 2021). Additionally, the integration of high-throughput sequencing data and the need to process large datasets further exacerbate these computational challenges (He et al., 2023).

7.3 Ethical and regulatory issues

Ethical and regulatory issues also pose challenges in the application of genomic selection in breeding programs. The use of genomic data raises concerns about data privacy and the potential misuse of genetic information. Regulatory frameworks governing the use of genomic data in breeding programs vary across regions, which can complicate international collaborations and the sharing of genetic resources (Crossa et al., 2017). Moreover, the ethical implications of manipulating genetic material, particularly in animal breeding, require careful consideration to ensure that breeding practices are conducted responsibly and sustainably (He et al., 2023). The development of clear guidelines and regulations is essential to address these ethical and regulatory challenges and to ensure the responsible use of genomic selection technologies in breeding programs.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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