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RESEARCH PAPER

Genomic selection for maize quality traits

Amit Adsul

Abstract: Genomic selection (GS) has emerged as an efficient breeding strategy for improving complex quantitative traits in maize (*Zea mays* L.). By utilizing genome-wide molecular marker information, GS enables the prediction of genomic estimated breeding values (GEBVs) and facilitates early selection of superior breeding materials. Maize quality traits, including protein, oil, starch, lysine, tryptophan, provitamin A carotenoids, micronutrients and kernel characteristics, exhibit diverse genetic architectures. While some nutritional quality traits are governed predominantly by major genes or major-effect loci and have been successfully improved through marker-assisted selection (MAS), including marker-assisted backcrossing and gene pyramiding, many other quality traits are polygenic and controlled by numerous loci with small effects. For such complex traits, GS offers an advantage by simultaneously capturing genome-wide genetic variation and estimating the cumulative effects of multiple loci. Prediction accuracy is influenced by training population size, genetic relatedness, marker density, trait heritability, phenotyping quality, population structure and genotype × environment (G×E) interaction. Various statistical approaches, including genomic best linear unbiased prediction (GBLUP), ridge regression BLUP (RR-BLUP), Bayesian models and machine-learning methods, have been evaluated for genomic prediction in maize. Recent studies have demonstrated the potential of GS for improving protein, oil, starch, kernel texture and other nutritional and processing-quality traits. Integration of GS with MAS, high-throughput phenotyping, genome-wide association studies, and multi-trait and multi-environment prediction can further enhance selection efficiency. Thus, GS should be viewed as a complementary approach to MAS, with particular value for accelerating the improvement of complex, polygenic maize quality traits and developing nutritionally superior and end-use-specific maize varieties.

Keywords: Genomic prediction • Genomic selection • Genotype × environment interaction • Grain quality • Maize • Marker-assisted selection • Nutritional quality • Polygenic traits

Introduction

Maize (*Zea mays* L.) is one of the world's most important cereal crops and is widely used as food, feed and industrial raw material. In recent years, increasing nutritional and industrial demands have intensified efforts to improve maize grain quality traits, including protein and oil content, starch composition, lysine and tryptophan concentration, provitamin A carotenoids and other nutritional attributes. These traits exhibit diverse genetic architectures. While some nutritional quality traits are governed predominantly by major genes or major-effect loci and can be effectively improved through marker-assisted selection (MAS), including marker-assisted backcrossing and gene pyramiding, many other quality traits are quantitative and controlled by numerous loci with small effects (Prasanna *et al.,* 2021; Ndlovu *et al.*, 2024). The latter traits are also strongly influenced by environmental conditions and genotype × environment (G×E) interactions, making their improvement through conventional phenotypic selection more challenging (Ndlovu *et al.,* 2024). For such complex

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polygenic traits, genomic selection (GS), which uses genome-wide marker information to predict the genetic merit of breeding candidates, provides an effective complementary approach by capturing the cumulative effects of numerous loci (Hao *et al.* 2019; Ndlovu *et al.,* 2024).

Maize is also a major staple crop in sub-Saharan Africa (SSA), where it contributes substantially to food and nutritional security. However, maize production in the region is constrained by climate variability, drought, pests and diseases, limited access to improved germplasm, and low productivity (Prasanna *et al.,* 2021). FAOSTAT (2024) identifies maize as one of the major cereal crops in Africa in terms of production and harvested area. These challenges highlight the need for breeding approaches that can simultaneously enhance productivity and grain quality in maize.

In 2025, India's maize cultivation area reached about 115 lakh hectares, showing nearly a 3% increase over the previous year. Maize is mainly grown during the Kharif season, accounting for around 85% of the total cultivated area. Indian maize breeding programmes focus on improving grain quality traits such as protein, starch, and oil content, along with enhanced lysine, tryptophan, iron, and zinc levels. Quality Protein Maize (QPM) hybrids are preferred for their better nutritional quality and digestibility (Amegbor *et al.,* 2022; Crossa *et al.,* 2014).

Molecular breeding methods such as marker-assisted selection (MAS) and genomic selection (GS) have greatly enhanced crop improvement programs. Among these approaches, genomic selection has emerged as a powerful breeding strategy for improving complex traits because it uses genome-wide molecular marker information to predict genomic estimated breeding values (GEBVs) of individuals (Meuwissen *et al.*, 2001). Unlike MAS, which mainly targets major genes or quantitative trait loci (QTLs), GS captures the effects of both major and minor genes distributed across the genome, thereby improving prediction accuracy for complex quantitative traits (Heffner *et al.,* 2009).

The concept of GS was first introduced by (Meuwissen *et al.,* 2001), who demonstrated that dense molecular markers covering the entire genome could effectively predict total genetic value. In maize breeding, GS offers several advantages, including shorter breeding cycles, reduced phenotyping costs, increased selection intensity, and higher genetic gain per unit time (Crossa *et al.,* 2014). Advances in high-throughput genotyping technologies and statistical prediction models such as GBLUP, RR-BLUP, and Bayesian approaches have further accelerated the adoption of GS in maize improvement programs.

Genomic selection has demonstrated considerable potential for improving complex maize grain-quality traits. By exploiting genome-wide genetic variation, GS can capture the cumulative effects of numerous loci and facilitate early selection of superior breeding materials. Evidence from maize studies supports its application to polygenic quality traits, particularly kernel oil, protein and starch, highlighting GS as a promising complementary approach to MAS for accelerating the development of nutritionally superior and end-use-specific maize varieties and hybrids (Hao *et al.,* 2019; Ndlovu *et al.,* 2024).

Genomic selection and prediction models used

Genomic selection (GS) is a genome-wide breeding approach that predicts the breeding values of individuals by simultaneously incorporating molecular marker information across the genome into a statistical model. Unlike marker-assisted selection (MAS), which generally relies on previously identified markers associated with QTLs or genes of interest, GS does not require prior identification of individual markers linked to specific QTLs. Instead, it uses information from a large number of markers distributed throughout the genome to estimate the cumulative effects of numerous loci, thereby capturing a substantial proportion of the genetic variation underlying complex quantitative traits. Consequently, GS can be implemented without requiring a complete understanding of the genetic architecture of the target trait (Bernardo *et al.,* 2007).

In GS, a training population (TP) is both genotyped using high-throughput genotyping platforms and phenotyped for target traits across relevant environments. The resulting genotypic and phenotypic data are then used to develop prediction models. These models are subsequently applied to a breeding population (BP) consisting of unphenotyped selection candidates to estimate their genomic estimated breeding values (GEBVs) based solely on marker information (Meuwissen *et al.,* 2001) (Figure 1).

The major advantage of GS over conventional phenotypic selection (PS) is its ability to accelerate genetic

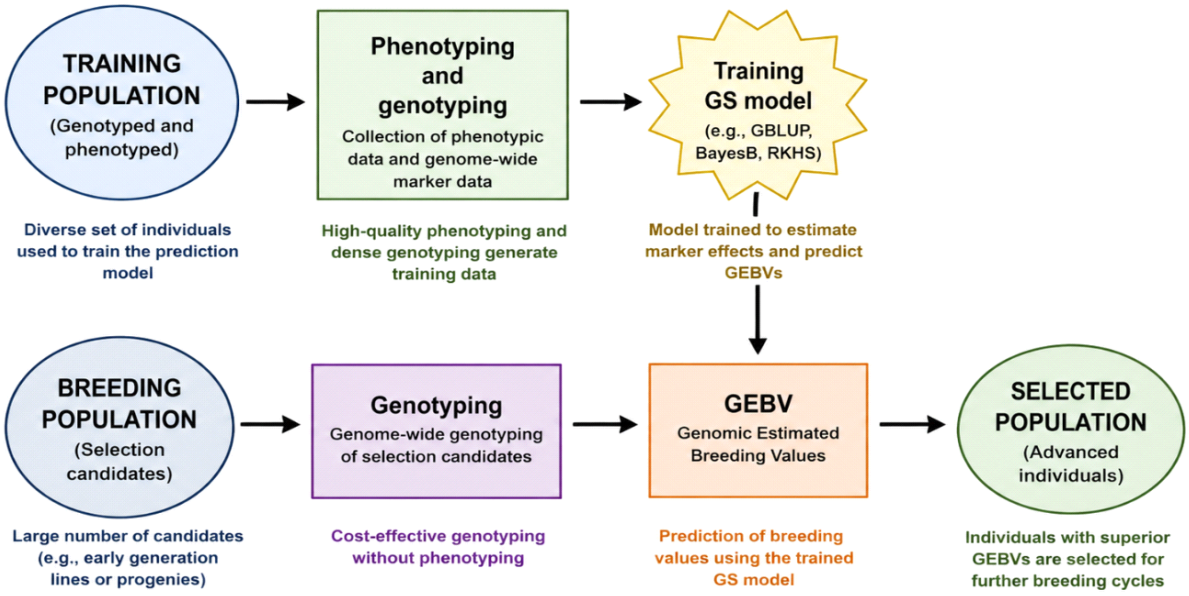


Figure 1. Flow diagram of a plant breeding program based on genomic selection (GS). The program involves genotyping the training population, developing a GS prediction model, genotyping the breeding population, predicting genomic estimated breeding values (GEBVs), and selecting superior individuals.
Source: Authors; illustration based on Meuwissen *et al.* (2001); Crossa *et al.* (2017).

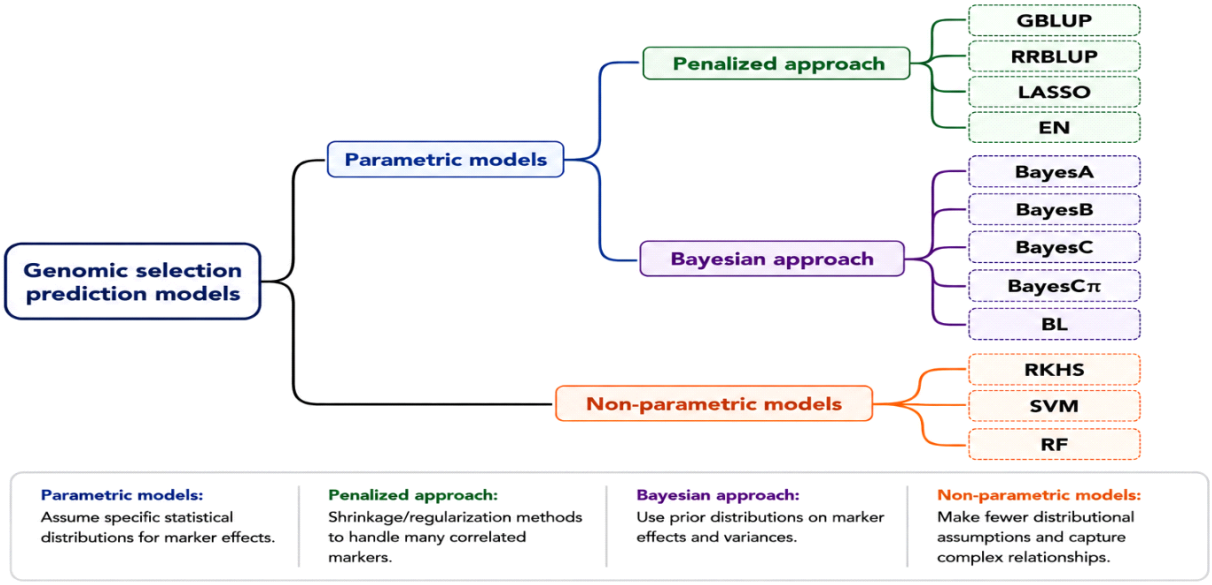
gain by significantly shortening the breeding cycle. This is achieved through reduced dependence on extensive phenotyping, enabling earlier and more efficient selection of superior genotypes (Sorrells, 2015; Voss-Fels *et al.,* 2019).

High-throughput genotyping generates large-scale genome-wide molecular marker datasets that form the basis of genomic selection (GS). In this approach, the number of marker-derived predictor variables is often substantially larger than the number of phenotypic observations, creating a high-dimensional estimation problem in which marker effects cannot be reliably estimated using conventional statistical approaches. To address this challenge, a range of parametric and non-parametric statistical models has been developed and applied for genomic prediction. These models differ in their assumptions regarding marker effects and genetic architecture and are designed to efficiently utilize genome-wide marker information while controlling overfitting and multicollinearity (Figure 2).

GS models mainly differ in their assumptions about marker-effect distributions and their contributions to genetic variance. Genomic best linear unbiased prediction (GBLUP) uses a genomic relationship matrix and assumes that marker effects follow a common distribution with equal variance (Meuwissen *et al.,* 2001). Ridge regression BLUP (RR-BLUP) assumes marker effects have a common variance and applies equal shrinkage toward zero, which may be less effective when traits are influenced by loci with relatively large effects (Heffner *et al.,* 2009). Bayesian models, including BayesA, BayesB, BayesC and BayesCπ, differ in their prior assumptions about marker effects and allow varying degrees of shrinkage, making them suitable for traits with different genetic architectures. LASSO performs variable selection through an L1 penalty, whereas Bayesian LASSO combines variable selection and shrinkage within a Bayesian framework. Bayesian ridge regression applies Gaussian priors and equal shrinkage to marker effects. Elastic Net combines L1 and L2 penalties and can be useful when predictors are highly correlated (Friedman *et al.,* 2010). Non-parametric approaches such as Random Forest and Support Vector Machine can model complex marker–trait relationships, whereas Reproducing Kernel Hilbert Space regression can accommodate nonlinear and non-additive genetic effects (Jannink *et al.,* 2010; Gianola *et al.,* 2008).

Factors affecting prediction accuracies of genomic selection in maize

The prediction accuracy of genomic selection (GS) is commonly evaluated through cross-validation, in which genotyped and phenotyped individuals are divided into a



GBLUP: genomic Best Linear Unbiased Prediction; RRBLUP: Ridge Regression BLUP; LASSO: Least Absolute Shrinkage and Selection Operator: EN: Elastic Net; BayesA/B/C/Ci: Bayesian models; BL: Bayesian LASSO; RKHS: Reproducing Kernel Hibert Space; SVM: Support Vector Machine; RF: Random Forest.

Figure 2. Classification of the most frequently used genomic selection prediction models.

training population (TP) and a validation population (VP). Marker effects estimated from the TP are used to predict genomic estimated breeding values (GEBVs) in the VP, and prediction accuracy is generally assessed as the correlation between predicted GEBVs and observed phenotypic values. Prediction accuracy is influenced by several genetic, population and methodological factors, including linkage disequilibrium (LD) between markers and causal loci, marker density and collinearity, allele-frequency differences, population structure, TP size and composition, and genetic relatedness between the TP and VP. Trait heritability and phenotypic variance also affect prediction accuracy, while the statistical model used for prediction can further influence the reliability of genomic predictions (Isidro *et al.,* 2015; Norman *et al.,* 2018; Brauner *et al.,* 2020; Robertsen *et al.,* 2019). In general, larger and more representative training populations tend to improve prediction accuracy, whereas higher marker density becomes particularly important when the TP and VP are genetically less related (Meuwissen *et al.,* 2001). These factors should be considered when designing GS programmes for maize quality traits and are summarized in Table 1.

Overview of genomic selection research for maize quality improvement

Genomic selection (GS) has emerged as an advanced breeding approach for improving complex quantitative traits in maize. Unlike marker-assisted selection (MAS), which targets a few major genes or QTLs, GS uses genome-wide molecular marker information to predict the breeding value of individuals. This enables breeders to select superior genotypes without extensive phenotypic evaluation, thereby accelerating genetic gain and shortening breeding cycles (Anilkumar *et al.,* 2022). Maize is one of the world's most important cereal crops and serves as food, feed and industrial raw material. Although maize breeding has traditionally focused on grain yield and stress resistance, increasing attention is now being directed toward grain quality traits such as protein content, starch composition, oil content, amino acid composition, kernel hardness and processing quality. These traits have diverse genetic architectures: some nutritional traits are influenced by major-effect loci, whereas others are quantitative and involve multiple loci with relatively small effects and substantial environmental influence (Fang *et al.,* 2020; Ndlovu *et al.,* 2024).

Research in genomic selection for maize quality improvement has expanded rapidly with advances in high-throughput genotyping technologies and statistical prediction models. GS integrates dense genome-wide markers with phenotypic data from a training population to estimate GEBVs. These predictions are then used to identify promising breeding lines at early stages, reducing the need for repeated field testing (Crossa *et al.,* 2017).

Table 1. Factors affecting prediction accuracies of genomic selection in maize

Factor affecting GS accuracy	Description	Effect on prediction accuracy	References
Training population size	Number of genotyped and phenotyped individuals used to train the prediction model	Larger and representative training populations generally improve estimation of marker effects and prediction accuracy	Meuwissen *et al.* (2001); Crossa *et al.* (2017)
Relationship between training and validation populations	Genetic relatedness between the training and validation populations	Greater genetic relatedness generally results in higher prediction accuracy	Crossa *et al.* (2017)
Marker density	Number and distribution of molecular markers across the genome	Adequate marker density improves genome coverage and the probability of capturing marker–QTL associations	Meuwissen *et al.* (2001); Poland *et al.* (2012)
Trait heritability	Proportion of phenotypic variance attributable to genetic effects	Higher heritability generally results in higher prediction accuracy	Lorenz *et al.* (2011)
Genetic architecture	Number and magnitude of loci contributing to trait variation	GS is particularly useful for complex traits controlled by numerous loci with small effects	Bernardo and Yu (2007)
Population structure	Genetic differentiation among subpopulations within the breeding population	Population structure can alter marker–trait relationships and may bias genomic predictions if not appropriately accounted for	Crossa *et al.* (2017)
Genetic diversity	Extent of genetic variation within the training and target populations	Adequate diversity improves the representativeness and applicability of prediction models	Crossa *et al.* (2017)
Genotype × environment interaction	Differential performance of genotypes across environments	Accounting for G×E can improve prediction across environments, particularly when environmental conditions differ	Burgueño *et al.* (2012)
Phenotypic data quality	Accuracy, replication and environmental representation of phenotypic measurements	High-quality phenotyping improves estimation of genetic effects and prediction accuracy	Heffner *et al.* (2009)
Linkage disequilibrium (LD)	Association between markers and causal loci or QTLs	Adequate LD between markers and causal loci improves genomic prediction	Meuwissen *et al.* (2001)
Statistical prediction model	Statistical model used to estimate marker effects and genomic breeding values	Prediction performance varies according to the genetic architecture of the trait and assumptions of the model	Gianola *et al.* (2009)
Cross-validation strategy	Method used to evaluate the predictive ability of the genomic prediction model	Appropriate validation schemes provide reliable estimates of prediction accuracy and reduce overly optimistic estimates	Crossa *et al.* (2017)
Environmental conditions	Environmental variation among testing environments	Differences between training and target environments can reduce prediction accuracy	Burgueño *et al.* (2012)
High-throughput phenotyping	Use of imaging and sensor-based technologies for phenotypic characterization	Improved phenotyping precision can strengthen genomic prediction for complex traits	Araus and Cairns (2014)

Several prediction models have been used in maize GS studies, including genomic best linear unbiased prediction (GBLUP), ridge regression BLUP (RR-BLUP), Bayesian models, random forest, and machine learning approaches. Among these, GBLUP and RR-BLUP are commonly used because they efficiently handle large marker datasets and assume that many loci contribute small effects to complex traits. Recent studies also emphasize integrating machine learning and deep learning approaches to improve prediction accuracy (Anilkumar *et al.,* 2022).

Prediction accuracy in GS depends on several factors, including training population size, marker density, genetic relationship between training and validation populations, trait heritability, and genotype × environment interactions. Studies in maize have shown moderate to high prediction accuracies for several grain quality traits, especially kernel weight, grain texture, and grain protein content. Doubled haploid populations and closely related training populations often provide better prediction efficiency (Ndlovu *et al.,* 2024). Recent research has also focused on integrating

GS with modern breeding technologies such as speed breeding, doubled haploid technology, genome editing, high-throughput phenotyping, and genome-wide association studies (GWAS). Such integration can further accelerate maize improvement by combining rapid generation advancement with precise genomic prediction (Anilkumar *et al.,* 2022).

Despite its potential, several challenges limit the large-scale implementation of GS in maize breeding programs. These include the high cost of genotyping and phenotyping, limited computational resources, environmental variability, and the need for optimized prediction models. In many developing countries, public breeding programs still face constraints in adopting GS technologies. However, decreasing sequencing costs, improved bioinformatics tools, and collaborative breeding networks are expected to increase GS adoption in the future (Gunundu *et al.,* 2023). Overall, genomic selection represents a powerful tool for maize quality improvement. By enabling early and accurate selection of superior genotypes for complex grain quality traits, GS can significantly enhance breeding efficiency, reduce breeding time, and contribute to the development of nutritionally improved maize varieties suited for future food and feed demands (Ndlovu *et al.,* 2024).

Figure 3 illustrates variation in genomic prediction accuracy among maize grain-quality traits and populations (Ndlovu *et al.,* 2024). Pop1 generally exhibited the highest median prediction accuracy across the evaluated traits, particularly for protein, oil, starch and kernel weight, whereas Pop4 generally showed lower and more variable predictions. Pop2 and Pop3 displayed intermediate performance, although their relative ranking varied among traits. These population-specific differences highlight the influence of population characteristics on the genomic predictability of maize grain-quality traits (Ndlovu *et al.,* 2024).

Among the evaluated traits, kernel weight and texture displayed relatively higher and more stable prediction accuracies, whereas protein, oil, and starch contents showed moderate variability across populations (Crossa *et al.,* 2017). Overall, the results suggest that genomic selection is effective for improving maize quality traits; however, its success depends strongly on population structure, genetic diversity, trait heritability, and the genetic architecture of the target traits (Meuwissen *et al.,* 2001).

Multi-trait genomic selection

Multi-trait genomic selection (MTGS) is an advanced breeding strategy that improves multiple correlated traits simultaneously using genome-wide molecular marker information. In maize, MTGS has gained importance for improving grain yield, nutritional quality, stress tolerance, and disease resistance together. By utilizing genetic correlations among traits, MTGS generally provides higher

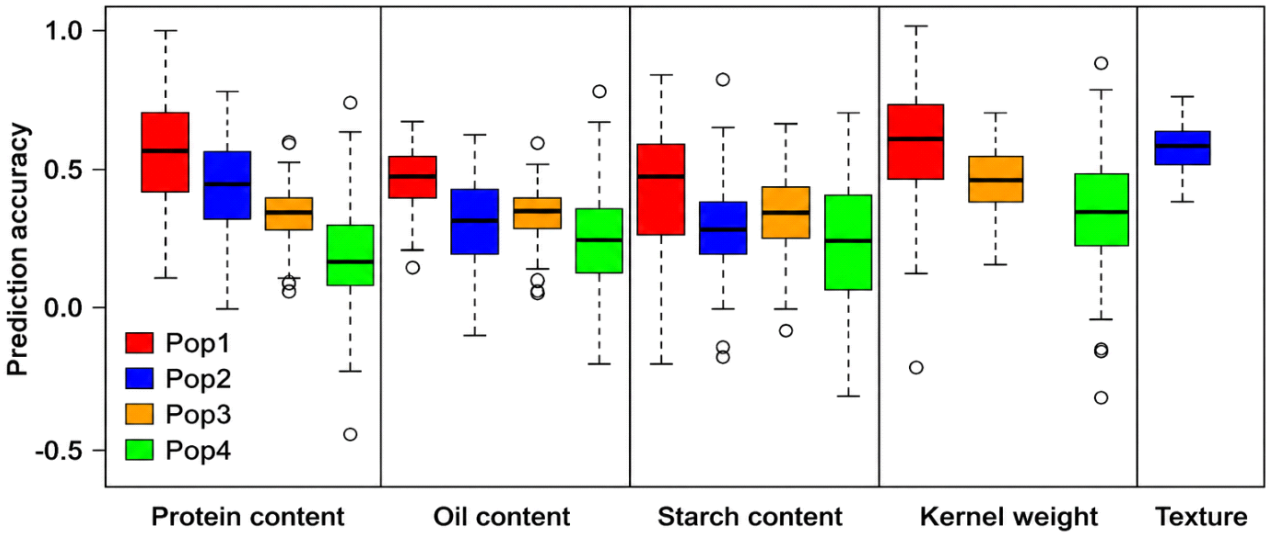


Figure 3. Genomic prediction accuracy for different maize quality traits across four populations (Pop1-Pop4).
Source: Adapted from Ndlovu, N., Kachapur, R. M., Beyene, Y., Das, B., Ogugo, V., Makumbi, D., Spillane, C., McKeown, P. C., Prasanna, B. M. & Gowda, M. (2024). Linkage mapping and genomic prediction of grain quality traits in tropical maize (*Zea mays* L.). *Frontiers in Genetics,* **15**: 1353289. https://doi.org/10.3389/fgene.2024-1353289

prediction accuracy than single-trait genomic selection, particularly for low-heritability traits (Budhlakoti *et al.,* 2019). Common MTGS models used in maize breeding include multi-trait genomic best linear unbiased prediction (MT-GBLUP), Bayesian multi-trait models, and machine/ deep learning approaches. These models integrate phenotypic and genotypic covariance among traits to estimate genomic estimated breeding values (GEBVs) more accurately (Saba Moeinizade *et al.,* 2020).

In maize, multi-trait genomic selection (MTGS) has emerged as a promising approach for the simultaneous improvement of multiple agronomic and grain-quality traits. Its application has been investigated for quality traits such as protein, oil and starch contents, as well as agronomic traits including grain yield and flowering time (Hu *et al.,* 2022; Ndlovu *et al.,* 2024; Mora-Poblete *et al.,* 2023). By exploiting genetic correlations among traits, multi-trait models can incorporate information from correlated secondary traits and thereby improve prediction over single-trait approaches (Budhlakoti *et al.,* 2019; Lozano *et al.,* 2023). The effectiveness of MTGS is influenced by training population size and composition, trait heritability, genetic architecture and the strength of genetic correlations among traits. Strong correlations between traits can enhance prediction accuracy and improve selection efficiency in maize breeding programmes (Budhlakoti *et al.,* 2019).

Conclusions

Genomic selection has emerged as a powerful and efficient breeding approach for improving complex maize quality traits governed by many genes with small effects. By utilizing genome-wide marker information, GS enables accurate prediction of breeding values, reduces dependence on extensive phenotyping, shortens breeding cycles, and accelerates genetic gain. The approach is particularly valuable for enhancing nutritional and end-use quality traits such as protein, oil, starch composition, provitamin A, and amino acid content. Although challenges such as high genotyping costs, environmental effects, and the need for large training populations remain, continuous advancements in genotyping technologies, high-throughput phenotyping, and computational tools are improving the effectiveness of GS. Integration of genomic selection with modern breeding technologies, including multi-trait prediction, speed breeding, and omics-assisted approaches, will play a crucial role in developing high-quality maize varieties to meet future food, feed, and nutritional demands.

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Author contributions

Amit Adsul drafted the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflicts of interest

The authors declare no conflict of interest.

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