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REVIEW ARTICLE

Review on genomic selection in plant breeding

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Abstract

Genomic selection has been considered as a novel methodology beyond traditional marker assisted selection methods (MAS). GS can be considered as a variant of MAS selecting favourable individuals largely based on estimated breeding values derived genomically. It involves genotyping markers and phenotyping individuals in reference population then predicting phenotypes of candidates forselection using statistical machine learning models. New candidate individuals get predictions performed on them post trained model output if genotypic information happens to be available somehow. Selection of training population proves highly crucial for testing purposes and ultimately determines accuracy in genomic selection processes. Genomic selection models frequently utilize involve stepwise regression, ridge regression, genomic best linear unbiased prediction, Ridge regression best linear unbiased Prediction, Bayes A, Bayes B, Bayes care Bayesian model and least absolute shrinkage selection operator. This review aims to present an overview of genomic selection as an advanced breeding strategy that integrates genome wide markers and statistical model to accelerate genetic improvement in plants. It highlights the principles, methods and applications of genomic selection in enhancing crop traits and breeding efficiency.

Keywords: genomic best linear unbiased prediction; genomic estimated breeding value; genomic selection; testing population; training population

Introduction

Genomic selection encompasses a variety of approaches, all of which are designed to predict breeding values for quantitative traits using whole-genome genotypic data by estimating marker effects simultaneously in a single step; it was first introduced by Meuwissen et al., 2001 (1) as wide genome selection, which enhances quantitative traits by utilizing genetic information across the entire genome (2). The first empirical validation of genomic selection was observed in dairy cattle (3) Selection in plant breeding has long been established based on breeding values estimated from mixed model based on pedigree (4-6) and in animal breeding it has been validated successfully across various species and population (7-9). Genomic selection involves developing a predictive model using a training population that possesses both genotypic and phenotypic data, which have only genotypic data that is applied to estimate the breeding values of individuals and the selection is based on the predictions. Subsequent studies have explored how factors such as, training population size, effective population size, marker density, trait heritability predict the impact accuracy of a breeding program (8-10). For over two decades, DNA engineering has been expected to revolutionize genetic improvement programs and enhance genetic gain through selection (11-12), yet marker aided selection has yet to deliver substantial improvements in polygenic traits (13). Its effectiveness is limited when numerous alleles with small effects are segregating, making it challenging to detect significant and consistent impacts (14). DNA-based molecular markers serve as essential tools for assessing genetic variation within germplasm collections and breeding lines. Over the past two decades, a range of molecular markers for principal crop species have been established to enable the creation of compact molecular genetics and physical maps and the markers have found widespread applications to detect genes or quantitative trait loci (QTLs) associated with economically important traits for MAS (15-16) divergent from MAS the genomic selection utilizes a reference population with both DNA sequence and trait data to create a model as predictive (17).

Genomic selection

Genomic selection relies on dense genetic markers spread across the complete set of genetic material to predict an individual reproduction value (1). The aim of genomic assessment is to determine the best prediction approach for precise estimation of the genetic values of candidates. Several genomic evaluation approaches have been suggested (18). The Finding implies that the accuracy of genomic estimated breeding values (GEBV) is much greater compared to that of estimated breeding values (EBV) using pedigree data (8). While polygenic breeding values and genomic data provide valuable insights, quantitative trait loci (QTL) that are not detected through marker effects may still be captured via progeny testing based on pedigree information (19). For multifactorial traits with many genes influencing them, the estimation of genetic lines' breeding values needs genetic markers throughout the whole genome, a procedure termed genomic selection (20) as well as, including meta-GWAS signals as fixed effect covariates within GS models was found to enhance prediction precision and minimize bias when predicting Jersey and Holstein bulls' stature (21). Here, the bar charts representing the accuracy the GEBV prediction using different genotypes under random mating and assortative mating selection method in Fig. 1.

Genomic estimated breeding value

In genomic prediction the total genetic variance is estimated by considering the effects of all markers in the dataset, without applying a significance threshold, based on the assumption that disequilibrium linkage is present in markers with quantitative trait loci (QTLs) and the result of these markers are determined using individuals with both trait and DNA data. The genomic estimated breeding value (GEBV) calculates the marker effects are then combined with an individual marker information as well as Improve a cross-validation approach is employed, where a testing population and a training population are used to assess predictive performance. The training population offers genotypic and phenotypic information for marker effect estimation, which is utilized to estimate GEBVs for individuals in the test population (21). The predictive accuracy of the model is evaluated by measuring the correlation between GEBVs and the actual phenotypes of the test population. Fig. 2 depicts the genomic selection using a training population to estimate marker effects to get a genomic estimated breeding value (GEBV) of lines in the test-population. Classification of genomic selection methods is given in Table 1

Prediction based genomic selection

Genomic prediction serves as the initial step in genomic selection (GS) within plant breeding programs (22-23). Traditional approaches, including regression-based techniques, have limited capacity to process high-dimensional datasets and to model complex, multivariate relationships between predictors and response variables.

Prediction in GS involves building statistical models that learn from a training set (genotyped and phenotyped individuals) to estimate the genetic merit of individuals in a testing set based solely on their genotypes. This predictive

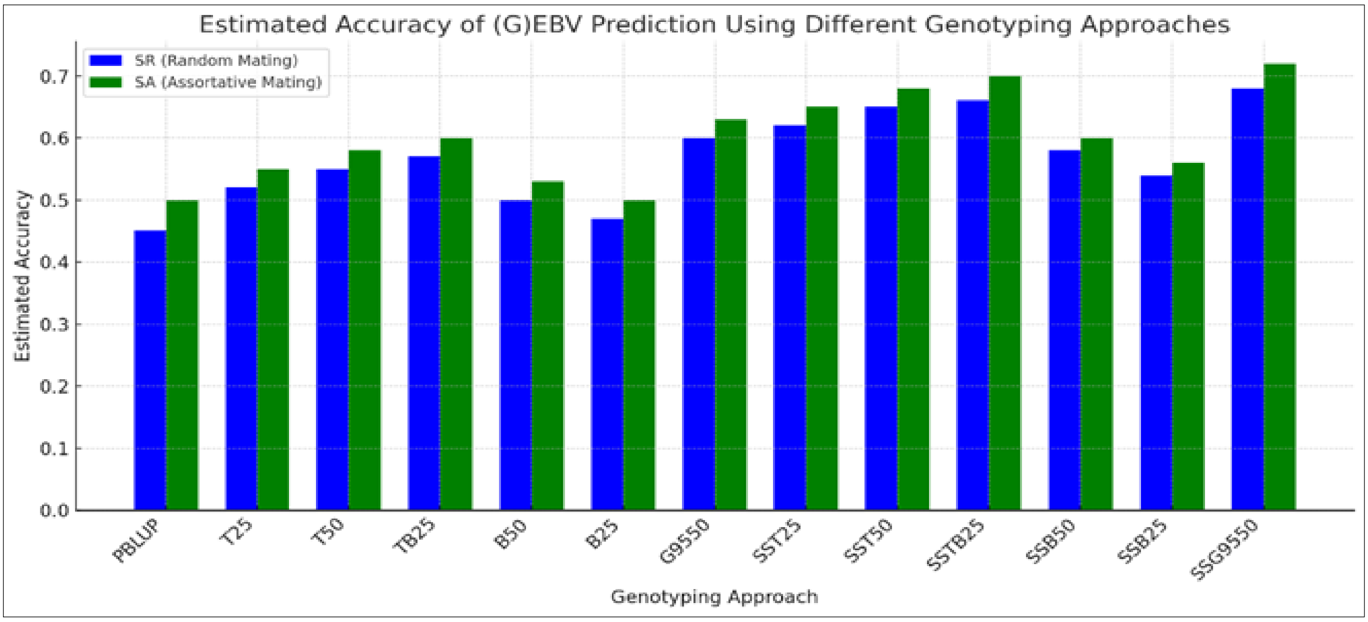

Fig. 1. The bar chart represents the accuracy of the GEBV prediction using different genotypes under random mating and assortative mating selection.

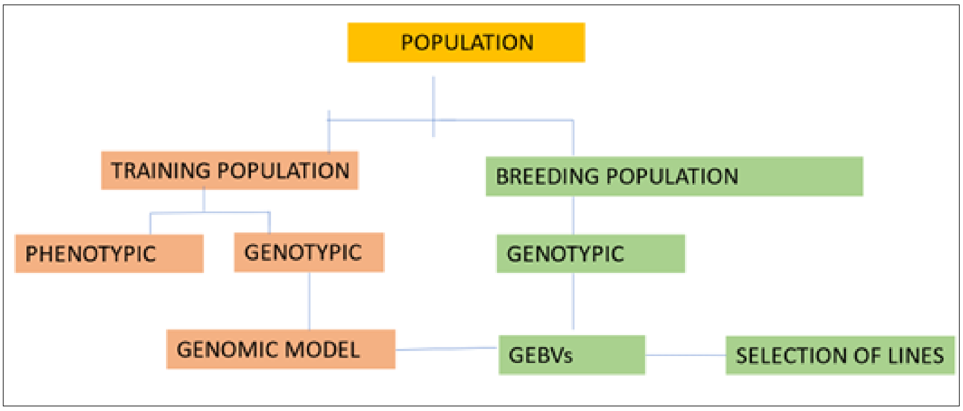

Fig. 2. Flow chart of population genomic selection (159).

Table 1. Comparison and integration of various models such as parametric, semi parametric and non-parametric statistical model

Features	Parametric	Nonparametric	Semi parametric
Definition	Models that describe data using a predefined set of parameters, with the model structure (such as linear or logistic) specified in advance.	Models that do not rely on a predetermined structure; instead, their form is inferred directly from the data.	Combine a parametric component (with a finite set of parameters) with a non-parametric component (infinite-dimensional structure).
Flexibility	Low	high	moderate
Data requirement	Low	high	moderate
Interpretability	high	Often low	moderate
Example	Linear Regression, Logistic Regression	K-Nearest Neighbours, Kernel density estimation	Cox Proportional Hazards Model, Generalized Additive Models (GAMs)
Advantages	Simple and interpretable. Requires less data to estimate parameters. Efficient if model assumptions are correct.	Highly flexible and adaptive. Better for discovering unknown relationships.	Flexible yet interpretable. Reduce the risk of model misspecification.
Disadvantage	Model misspecification risk (wrong functional form). Less flexible for complex patterns.	Require large datasets. Often computationally intensive. Harder to interpret.	Estimation can be more complex. Balance between bias and variance is delicate.
Reference	(152)	(153)	(65)

framework facilitates early selection and reduces the need for extensive phenotyping, especially in crops and animals with long reproductive cycles. Cross-validation is widely used to evaluate model performance and ensure the robustness of predictions (24). The selection of an appropriate method depends largely on the genetic architecture of the target trait. For instance, traits governed by a few major QTLs may benefit from sparse models like Bayes B, whereas highly polygenic traits often suit models like RR-BLUP or GBLUP (25). In genomic selection, cross-validation (CV) methods are essential for assessing the predictive accuracy of genomic prediction models is given in Table 2

Drawback of traditional breeding methods

Marker Assisted Selection

Conventional approaches, like regression-based methods, struggle to handle high-dimensional data and are often inadequate for capturing complex, multivariate relationships between predictor and response variables Integrating molecular marker technologies like MAS into breeding programs is becoming increasingly important for faster and more precise genetic gains (26). Although MAS shows promise for improving polygenic traits efficiently, its full potential is still unrealized (27). Simply mapping QTLs is not enough for trait improvement; MAS applies DNA markers at key selection points to boost effectiveness (28). Marker-assisted selection (MAS) combines molecular genetics with traditional phenotype-based selection. Selection indices are developed to optimize the improvement of quantitative traits by using both marker data and phenotypic information from individuals and their relatives (29). Genomic selection uses dense markers covering the whole genome so that markers exist in strong LD with all genes affecting the trait. This is also the strategy of genome wide association studies (e.g. Moffat et al. 2007). New breeding selection techniques, including the selection index, best linear unbiased prediction (BLUP) (30), marker-assisted selection (MAS), genome-wide association study (GWAS) and genomic selection (GS) (3), have been widely employed in both animal and plant breeding. GS is a type of MAS; whole genome markers are used to estimate breeding values; these estimations are called genomic estimated breeding values (GEBV). GEBV based on the genotypes of individuals have been remarkably accurate (31, 32). This accuracy has been verified in empirical studies in beef cattle, mice and chicken (33-35).

Marker aided selection has proven valuable for plant breeding, yet its effectiveness in improving complex traits has been limited, partly because it does not account for small-effect quantitative trait loci (36). The usable marker for Ppd-D1 has demonstrated its utility in marker-assisted selection by enabling the prediction of heading time variation. In European wheat breeding, the serviceable marker for Ppd-D1 serves as a key tool, describe genotypic variation is 30 % in heading time. Likewise, functional markers for Ppd-D1 (37) and Rht-B1 and Rht-D1 (38), are extensively utilised to enhance the breeding of wheat,

Table 2. Cross validation methods

Cross validation methods	Description	Purpose	Reference
Fivefold cross validation	The dataset is divided randomly into five equal segments. In each round, the model is trained on four of these segments, while the remaining one is used for validation.	To evaluate overall prediction accuracy across the entire population, without accounting for temporal or environmental factors.	(149)
Leave-One-Year-Out Validation (LOOV)	Data from one year is excluded at a time to be used as the validation set, while the model is trained on data from the remaining years.	Evaluates the model's capability to forecast upcoming years, simulating real-world breeding scenarios where predictions are required for seasons that haven't been tested.	(150)
Forward validation	The model is trained exclusively on data from past years and used to predict outcomes for future years.	Represents a realistic breeding context in which genomic selection models are built using historical data to predict newly untested generations.	(151)

contributing to about 40 % of the genotypic variation in plant height. Molecular markers have enabled breeders to decrease the necessity for large-scale phenotyping and conduct high-accuracy early-stage selection. MAS is exceptionally efficient for simple traits governed by a main gene (20). Diverse MAS, genomic selection employs genome-wide markers to predict the genetic potential of future individuals, bypassing the marker-detection step by incorporating all markers into genomic value prediction, when the number of markers exceeds the sample size, individual marker effects may not be uniquely estimated, yet the overall genomic value remains predictable. Consequently, genomic prediction focuses on the overall predictive power derived from the collective influence of all markers rather than on precise estimations of individual marker effects (39). Genomic selection (GS) estimates the effects of numerous genome-wide markers simultaneously to determine the genetic values, known as genomic estimated breeding values (GEBV), for untested populations, rather than relying on just a subset of markers for selection as done in marker-assisted selection (MAS) (40). Marker used in different crops of genomic selection is given in Table 3

Genomic wide associated selection

Marker-assisted selection (MAS) relies on the presence of genetic markers that are linked to the trait of interest. However, pinpointing the genetic regions connected to a specific phenotype is often challenging, as many traits are influenced by multiple genes, making their relationship with the phenotype more complex (41, 42). The common method for connecting genetic regions to specific traits, referred to as genetic mapping, involves two primary strategies: linkage mapping (LM), which uses biparental populations and association mapping (AM) (43). Association mapping (AM) has gained growing significance in genetic research thanks to the availability of cost-effective, high-throughput technologies for genotyping single nucleotide polymorphisms (SNPs), which allow for dense marker coverage (44). A specific approach within association mapping, known as genome-wide association studies (GWAS), has become a widely used method for exploring complex traits in plants overall, as well as in various crop species such as wheat (45). The main benefit of GWAS is its ability to examine thousands to millions of genetic variants (such as SNPs) across numerous individuals from diverse populations on a genome-wide level, enabling the identification of more complex genotype-phenotype relationships compared to linkage mapping (LM). However, conducting a genome-wide analysis relies heavily on having detailed knowledge and characterization of SNPs, which is made possible through whole-genome sequencing of the target organism. For wheat, its complete genome was successfully sequenced in 2018 (46). GWAS uses various statistical models, mainly linear and Bayesian approaches. Linear models apply equations to test each marker’s link to the phenotype separately, reducing computational complexity despite genetic data intricacies (47)

Limitations of GWAS

GWAS still face notable limitations in both their design and use (45). The number of apparent causal variants could be minimized by using data from genetically diverse populations, making it essential to ensure proper population representation to avoid potential biases (48). GWAS has become an essential tool for identifying loci linked to traits of interest. Among these traits, drought stands out as one of the most significant abiotic stress factors impacting wheat yield (49). Since many GWAS approaches rely on linear regression models, exploring non-linear models could help address the issue of missing heritability (50). Collinearity is another factor that can reduce the efficiency and statistical power of GWAS methods, highlighting the need for new strategies to overcome the challenge (51). Various AI techniques have been utilized to address the limitations and drawbacks of GWAS (52-53). Many traits targeted by GWAS are highly quantitative and complex. For example, grain yield and drought stress tolerance are influenced by interactions among various underlying component traits (54).

Statistical tools used in genomic selection

Ridge regression

One of the first techniques proposed for genomic selection was ridge regression, in the framework of mixed models, is equivalent to best linear unbiased prediction (BLUP) (55). It is represented as:

$$y = W\,Gu + \varepsilon,$$

u is the marker effects of vector,

G represents the matrix genotype and

W is the design matrix that connect lines to observations (y).

When applying genomic selection to develop lines for commercial varieties, the focus extends beyond just the additive value to encompass the entire genotypic value (56). A modified version of RR-BLUP, known as W-BLUP, was developed to incorporate specific weights is known functional markers. All statistical computations for genomic selection techniques were done (57). In maize and sorghum, from a GWAS conducted on training populations by

Table 3. Comparison genomic selection of marker used in different crop

Crop	Source	Trait analyzed	Marker used	Genotypes	Reference
Wheat	International wheat and maize improvement centre	Grain yield	234 DArT markers	94	25
Maize	Drought tolerance of maize for Africa	Northern corn leaf blight Greay leaf spot	1,152 SNP markers	300	25
Wheat	Cornell university	Yield and heading data	1158 DArT Markers	374	148
Wheat	CIMMYT	Yield	1279DArT	599	149
Maize	Lima grain Europe	Yield and moisture content	355SNP	332	148

incorporating peak-associated markers into an RR-BLUP model led to improvements out of 216 only 60 simulated genetic traits (58). Whereas RR-BLUP assumes an infinitesimal model, Bayes B has the premise that only a certain number of single-nucleotide polymorphisms (SNPs) affect the genotypic variation of a trait, but the Bayes B has been examined with experimental maize data and it observed only slight variations in accuracy between statistical models and no definitive relationship with genetic architecture (59).

Genomic Best Linear Unbiased Predicition

In genomic selection, various statistical methods estimate marker effects in the training population. These methods fall into two categories and one assumes all markers influence the trait equally, in RR-BLUP, follow different statistical distributions which allows marker effects (55), in plant breeding, animal and tree BLUP has been widely used for decades, with its predictive accuracy for individuals lacking phenotypic data relying on the structure of the random effect variance covariance matrix (60) it implement of recombinant inbred lines to estimate the genomic value and BLUP is also referred to as genomic BLUP (61). Current implementations of the random regression model (RRM) follow the infinitesimal model (62) and the method for estimating GEBVs using RRM is known as GBLUP (63). Quantitative trait loci mapping studies indicate that many quantitative traits are under the effect of a few significant genes (64). Statistical procedures used in the selection of key variables it is referred as 'variable selection methods,' include Bayes A and Bayes B (1).

Application of BLUP

Best linear unbiased prediction technology has been utilized to forecast hybrid corn performance by leveraging existing hybrids and their pedigree relationships with untested hybrids. Advances in genomic research have significantly expanded the availability of molecular markers that span the entire genome, enabling the calculation of relationship matrices. This advancement has led to the development of genomic best linear unbiased prediction (GBLUP) (65). Current genomic prediction methods include Bayes B, empirical Bayes (66) and the least absolute shrinkage selection operator (LASSO) (67). Extensive research has demonstrated that GBLUP often achieves breeding values as accurately or more accurately than traditional pedigree-based BLUP in livestock breeding programs (65). GBLUP is particularly advantageous when a trait is primarily influenced by polygenes, making it potentially more robust compared to selective shrinkage methods. These genomic selection techniques predominantly focus on additive genetic effects (68).

Bayes A

Bayes A method variances assume the marker effect vary across loci (69). While Bayes A functions similarly to BLUP at the data level, it differs in that chromosome segment variances are model using an inverted chi-square distribution (70). Compared to Bayes A, the GBLUP method requires less computational time (71). Colombani demonstrated that Bayes B outperforms a modified version of Bayes A, in terms of genomic estimates accuracy which incorporates a polygenic effect (72).

Bayes B

Bayes B is generally more precise if large QTL exist, but its precision becomes comparable to gBLUP when many QTL have small effects (73) and the use of best linear unbiased prediction (BLUP) has resulted in significant genetic improvements in most livestock breeding schemes. Certain nonlinear methods, such as Bayes A, Bayes B and Bayes C (74) have also been considered. But few differences in precision between gBLUP and nonlinear models like Bayes B and Bayes A (71).

Bayseian analysis

Bayesian methods estimate marker effects collectively to predict genomic values for quantitative traits without the need for marker selection (75). Bayesian analysis is increasing due to its broader assumptions compared to classical methods and its adaptability in addressing various biological challenges (76-77). In recent time, Bayesian model has been widely applied to overcome limitations of traditional statistical methods, expanding their use in animal and plant breeding data analysis (78). Bayesian inference integrates prior knowledge about a statistical system, represented as prior probability distributions, with new observed data. The formula of Bayesian is:

$$P(\theta|y)\ P(y|\theta)\ P(\theta)$$

where $P(\theta)$ represents the prior distribution,

$P(y|\theta)$ assesses how likely the observed data is given θ,

$P(\theta|y)$ α combines both prior knowledge and observed data for more precise inference.

Bayesian methods based on their predictive accuracy with other genomic selection techniques (70). Several Bayesian statistical models have been applied in genomic assessment with different assumptions regarding marker effect distributions. Bayesian methods assuming the prior distribution of SNPs (1), which have the potential to enhance the accuracy of breeding values beyond the conventional BLUP methodology (8-9). Studies have also reported increased accuracy using Bayesian models over BLUP (79)

In Bayesian Lasso models, hyperparameters are usually assumed to be random, but in Student's t-based models, they are usually set fixed, though there are exceptions (80). In traditional genomic analyses, breeding values are estimated when the components of variance are known, but in Bayesian approaches, variance components and genomic breeding values are simultaneously estimated (77). Bayesian methods employ marker-based genomic relationship matrices rather than pedigree-based numerator relationship matrices in a mixed-model setup (81). The Bayesian formulation of G-BLUP that estimates the variance components concurrently has shown marginally better accuracy than the frequentist one with known heritability (82).

Integration of omics data

The Greek-derived suffix “ome,” meaning “body,” signifies the complete set of a biological component. For example, the genome includes all genes, the transcriptome all transcripts, the proteome all proteins and the metabolome all metabolites of an organism (83). In recent years 2016, high-throughput omics (HTO) technologies including genomics, epigenomics, transcriptomics, proteomics and metabolomics have advanced significantly across various areas of biology. These developments have driven the rise of the systems biology era, with applications extending to animal production and health traits (84). Transcriptomic and phenomics datasets tailored to complex traits can help clarify how genetic variants such as single nucleotide polymorphisms (SNPs), insertions, deletions and copy number variations (CNVs) influence the traits (85). Combining genomic and transcriptomic data such as through the expression quantitative trait loci (eQTL) method helps identify genomic regions linked to gene expression levels (86) SNPs are chosen using a more rigorous genome-wide significance threshold than is usually applied in conventional GWAS. SNPs' epistatic interactions are then calculated. The association weight matrix (AWM), which combines findings from several GWAS by evaluating SNP interactions based on the size of their estimated additive effects, is another useful technique (87)

Transcriptomics

The concept of genetical genomics (GG), which involves genome-wide genetic analysis of gene expression data, was initially introduced by Jansen and Nap (2001) and Jansen (2003) and is also referred to as transcriptome mapping (88). Beyond stats, leveraging biological and functional data from layers like the epigenome, transcriptome, proteome and metabolome linking DNA to phenotype can offer key insights into genetic architecture. As these layers become more accessible across species, they enhance our understanding of complex traits (89). At the statistical level, omics data such as sequence polymorphisms and transcriptomics are likely to exhibit some degree of overlap or interdependence (90-91). Techniques such as genomics and transcriptomics offer a balance between cost and efficiency for modern researchers, helping to bypass the lengthy and labour-intensive traditional breeding processes in developing improved genotypes (92). Genomic and transcriptomic data aid in identifying genotypes with superior performance compared to neighbouring, related, or parental lines and in revealing phylogenetic and evolutionary relationships among genotypes (93). Genomics provides a new basis for crop breeding systems, especially when integrated with advanced automated phenotyping methods and functional genomics research (94). Genomics and transcriptomics techniques like DNA Sequence, RNA-Sequence, Methyl-Sequence, have significantly enhanced our understanding of gene expression and regulation in plants (95). As costs and complexity continue to drop, these preferred methods are being widely adopted, routinely producing millions of sequencing reads. Genomics and transcriptomics data, such as RNA-Sequence outputs, are inherently large and require high-performance computing systems for effective analysis (96). Genome and transcriptome-based analyses facilitate the identification of valuable alleles in both cultivated and wild relatives, while also revealing genomic regions where diversity may have been altered during the domestication process (97). Advanced genomics enables the identification of specific genome segments associated with a particular trait (98). A pantranscriptome combines multiple genomes or transcriptomes to represent variant effects and structural variations, aiding plant variation analysis alongside SNPs and CNVs and identifying variant presence or absence (99).

Proteomics

Genomic and proteomic sequence databases from various organisms, equipped with integrated bioinformatics tools, now provide an extensive and ever-growing resource for biologists and geneticists (100). In the past decade, omic technologies like genomics, proteomics and metabolomics have advanced significantly, allowing high-throughput analysis of molecular and biological processes methods are widely used to identify biomarkers, study complex systems and understand disease mechanisms by analyzing genes, mRNA, proteins and metabolites (101). protein abundance cannot be reliably predicted based on the corresponding mRNA levels on bacteria and yeast (102). In proteomics, proteins are digested into peptides, analysed by mass spectrometry and matched to genomic databases for identification. Modern proteomics relies on this sequence matching, with mass spectrometry becoming increasingly sensitive and high throughput, as seen in shotgun proteomics (103). Mass spectrometry is key for protein quantification, comparison and detecting post-translational modifications. Bioinformatics plays a crucial role in proteomics, just as in genomics and transcriptomics (104). Cancer progression is driven by genomic alterations and instability that result in a series of genomic changes including mutations, methylation, copy number aberrations or translocation (105). Proteomics differs from genomics and transcriptomics in two keyways: proteins can't be amplified like DNA or RNA, requiring prior purification and effective large-scale protein arrays are still lacking (106). Proteomics-based gene annotation has been successfully used in both model and non-model organisms. Proteogenomic annotation typically involves searching peptide mass spectra against a six-frame translation of a reference genome (107). The Proteogenomic Mapping Pipeline uses string search algorithms to map peptides to a genome translated in six reading frames. However, the tools are not designed for visualization, making their output files incompatible with genome browser tools (108).

Metabolomics

Metabolomics, the study of small molecules and metabolites, is widely used to explore interactions between gene/protein products and environmental factors (109). Metabolomics is widely used to investigate diseases like type 1 diabetes and cancer, aiming to identify biomarkers for early detection, prognosis and treatment monitoring (110). Due to technical limitations, researchers traditionally focused on a few key metabolic traits important for industrial or nutritional value, such as carotenoid content in tomatoes, protein content in maize and starch content in potatoes and rice (111). The majority of metabolomic studies on natural variation have been conducted in *Arabidopsis*, but crop species are increasingly becoming the focus of metabolomic research (112).

Multi-trait Genomic selection

Multi-trait genomic selection allows for the improvement of low-heritability traits by leveraging information from highly heritable traits. In humans, multivariate gBLUP has already been used to predict genetic risk for multiple diseases (113). Its first use in plants, the MT-GS statistical framework, has been widely implemented in different breeding schemes and human genetic research (114).

In plant breeding, MT-GS has been assessed using data from crops such as soybean (115), rye (116), cranberry (117) and for predicting hybrid wheat disease resistance. The effectiveness of MT-GS over single-trait genomic selection has been demonstrated through simulated data in animal breeding studies, particularly for genetically correlated traits (118). In addition, MT-GS models can be augmented to a multi-trait and multi-environment Bayesian system by utilizing the R package BMTME (Bayesian Multi-Trait and Multi -Environment) (119). Trait-assisted genomic selection was demonstrated to increase prediction precision more than 50 % greater compared to single-trait choice methodologies (120). Wide genome regression model explained in Fig. 3.

Phenotypic data analysis

The phenotypic data analysis was performed in two steps.The adjusted entry means for each location were first estimated (121). In the second step, the adjusted entry means were used to estimate the genetic variance components of hybrids and parents, as well as the variance due to genotype-by-location interactions, according to the procedure suggested by Möhring et al., 2009 (122). The general combining ability (GCA) can be assessed using a linear model following the g BLUP (genomic Best Linear Unbiased Prediction) approach. This method uses a genomic relationship matrix from whole-genome markers to make predictions of phenotypic values (20).

Genotypic data analysis

Genotyping was done with a 9K SNP array based on the Illumina Infinium assay (123). Because complex traits are under the control of many genes, the breeding values for genetic lines need to be estimated based on genetic markers placed throughout the entire genome, an approach called Genomic Selection. The genotype-photo-thermal time relationship was described as a genotype-specific reaction norm and gave a quantitative expression of genotype-by-environment (G×E) interactions' contribution to phenotypic variation (124). Flowering time can be predicted if information on the genotype of an inbred line and the photo-thermal time of various locations is available, thereby allowing the identification of the optimal environment for the inbred line and helping construct training populations (20). Genomic selection has the potential to realize genetic gains faster than classical selection approaches based on pedigree and phenotypic information. Genome-wide evaluation approaches employ statistical models that combine phenotypic data with dense marker data to forecast the genetic potential of individuals for complex traits (125).

Machine learning and deep learning

Genomic selection is a new agriculture technique that increases productivity by utilizing molecular genetic markers to formulate superior breeding programs and marker-based genetic assessment techniques for plants and animals (126). It entails building a prediction model with individuals that have known genotypic and phenotypic information. The model is subsequently employed to estimate genomic estimated breeding values (GEBVs) for specific traits, enabling the ranking of individuals with unobserved phenotypes for selection. The growing use of GS is primarily facilitated by the reducing cost of acquiring enormous numbers of DNA markers in plant and animal genomes, coupled with robust empirical evidence that proves this approach increases genetic gains per unit time. This, in turn, shortens breeding cycles and enables rapid selection of high-quality genotypes (127).

Machine learning applications

Machine learning software in genomic selection has been investigated (128) and the genomic BLUP can also be considered as a ML expert method. Current developments in ML for genomic prediction now also include multiple ML

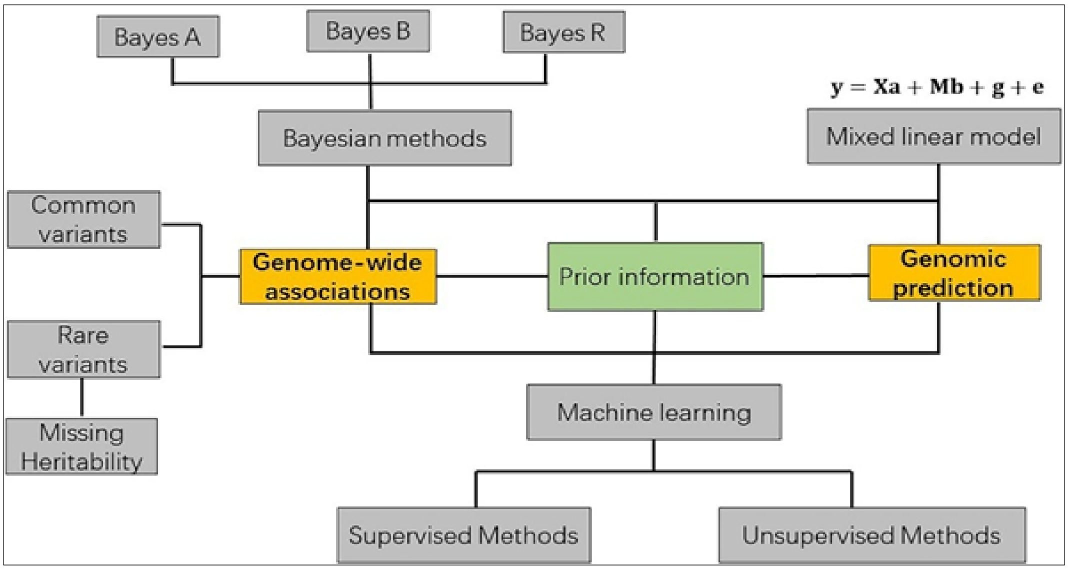

Fig. 3. Classification of whole genome regression models used in genomic selection.

areas, including deep learning, which has been contrasted to other ML methods in crops like wheat. ML techniques have been used with randomly assigned cross-validation methods to big populations for single phenotype prediction (129).

Unsupervised learning entails discovering patterns, associations, or clusters in input data without reference to an output response variable (130). Deep learning, a branch of ML, can be applied to both supervised and unsupervised learning and converts input data into progressively abstract representations by using multiple layers of neural networks. The main goal of deep learning is to learn the weights of neural networks using input data. Popular neural network structures are densely connected networks, convolutional neural networks (CNNs) and recurrent neural networks (119). Supervised learning-based ML algorithms are especially well suited for genomic prediction (131). GWAS is one important method, which applies genome-wide marker data for genomic prediction. This method determines the best number of markers for prediction using suitable statistical models combined with machine learning and deep learning techniques and then choosing the most effective model (132).

Integrated genomic selection

Breeding programs are planned with fewer replications in the early segregating generations and more replications, larger plot sizes and multi-location testing in subsequent generations (133). When incorporating genomic selection, breeders need to consider the tiered structure of the breeding program, as it affects genetic gain and implementation costs. Using GS in the initial generations can greatly reduce the breeding cycle by eliminating one or two selfing cycles (134). Using genomic selection (GS) in subsequent generations to assess the performance of lines will enhance selection accuracy but not reduce the breeding cycle. Although reduced genotyping costs make GS attractive in advanced generations, its benefits over phenotypic selection at this point are minimal (135). Effects of dominance were observed while predicting grain yield genomic estimated breeding values in maize single crosses employing the BLUP [N Cantelmo F] for additive and dominance model (136). In addition, epistasis has also been identified to be an influential element in expressing traits when addressing the genetics and improvement of intricate traits. It has been identified to reduce imperative contribution to characteristics like flowering time in rice (137). As well as oil, protein and starch levels of corn (24). Genomic selection is known as an effective tool for breeding qualitative traits, drastically reducing the duration of breeding cycles and facilitating its extensive and uniform use in routine crop breeding schemes (138).

Genomic selection implications in crop improvement

Genomic selection in cereals

Grains are an essential food source, contributing 50 % of the world's dietary energy intake. The four principal cereal crops such as wheat, rice, maize and barley these are grown on arable land globally and the total yield is 2817 million tonnes (139). Their growth, however, is confronted with enormous challenges, such as climate change-related disasters and the increased demand due to population growth (140). To solve these urgent problems, crop production should be efficient and sustainable with reduced environmental impact. This can be achieved through the design of high-yielding, resource saving crop varieties that can tolerate these conditions. However, breeding these variable and tolerant crops is a slow process because the major portion of crop productive traits lies under the influence of polygenic systems, in which there are many genes with small effects. Low heritability and complex gene interactions like epistasis further add to the complexity. Although the classical methods have contributed significantly, their genetic gains remained behind those realized through GS. However, classical methods can nonetheless speed up the breeding cycle (141). GS offers a distinct advantage by enabling the identification of individuals with the highest breeding values within early-generation populations, significantly reducing the need for extensive phenotyping. This approach has recently proven effective in cereal crops, particularly wheat, rice, maize and barley. The application of GS in these crops has led to the development of predictive models that accurately assess trait performance and identify the most valuable breeding material are given in Table 4

Genomic selection in oilseeds

Oilseeds are crucial for Asian and African smallholder farmers, but their potential yield remains underexploited owing to abiotic and biotic stresses (142). Genomic selection has been used for crops such as groundnut and Brassica, enhancing prediction precision for traits that include oil yield and quality (143). In sunflower, GS was superior to general combining ability (GCA) when parent lines were unknown (144). In soybean, NAM populations increased precision for yield and oil content whereas high genetic relatedness and training population size still improved the predictions. GS has also been applied to evaluate embryogenesis capacity with

Table 4. Genomic selection models used for cereal crops

Model	Application in cereal	Strength	Reference
GBLUP	Wheat, Rice, Maize, Barley	Simple, robust, good for polygenic traits	(1)
Bayesian models	Wheat, Rice, Maize, Barley	Good for traits with major genes (large QTL effects)	(1)
Random forests	Mainly Maize, Wheat	Captures non-linear gene interactions	(119)
Deep learning models	Maize, Wheat, Rice	Excellent for complex traits; high accuracy	(154)

great precision (145). Genomic model used and strength of sunflower, soybean, groundnut and Brassica are given in Table 5.

Genomic selection in pulses

The multi-trait Bayes B as the best GS approach for lentil using the STL-A11 marker, while single-trait GS (STGS) is better in the absence of major-effect QTLs. They also noted that multi-trait GS (MTGS) enhances prediction accuracy for low-heritability traits affected by genotype-by-environment (G×E) interactions. In *Phaseolus cumingii*, GS was applied to predict cooking time as a selection criterion for fast-cooking genotypes in different populations, including RILs, MAGIC populations and Andean and Mesoamerican breeding lines. Heritability of cooking time was high (0.64-0.89), with MAGIC populations being predicted with the highest accuracy (0.55) and Mesoamerican genotypes with reduced accuracy (0.22). Also, when genetic similarity between training and prediction populations is low, whole-genome re-sequencing (WGRS) markers increase accuracy of prediction (146) employing all the SNPs from whole-genome re-sequencing (WGRS) gave poor prediction accuracy for yield under drought (0.148-0.186) (124). Accuracy increased appreciably (0.56-0.61) when only yield-causal SNPs were considered. In addition, GS was utilized to resistance to root rot in *Phaseolus* with high prediction accuracies (0.7-0.8) for Pythium and Fusarium rots, signifying its viability for the promotion of quantitative resistance (147) Genomic model used for pulses are given in Table 6.

Conclusion

The future of genomic selection (GS) is headed toward deeper integration with real-time, high-throughput phenotyping and advanced big data analytics. With the progression of machine learning, GS models are expected to become more flexible, non-linear and better equipped to manage complex traits shaped by gene-environment interactions. Emerging technologies like deep learning and ensemble methods will work alongside traditional parametric and semi-parametric models to boost prediction accuracy. On the ground applications, such as real-time genomic selection in crops and precision breeding in livestock, will grow more common with the use of portable sequencing devices. Furthermore, cloud-based computing and AI driven platforms will enable faster, decentralized training and deployment of models. However, ethical considerations, data privacy concerns and computational hurdles will need to be carefully managed as GS becomes more widespread. In the long run, genomic selection is poised to be a key driver in promoting sustainable agriculture and advancing personalized medicine.

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Authors' contributions

NB and VSR developed the concept of this manuscript. NB carried out the literature review and wrote the initial draft. AP, NSK and JPS contributed initial feedback and revision. NB and SRV finalized the manuscript. All authors reviewed and approved the final version for submission.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

Table 5. Genomic selection models used for oilseed crops

Crop	GS model used	Strength	Reference
Sunflower	RKHS (Reproducing Kernel Hilbert Space regression), GBLUP,	RKHS was more effective in capturing non-additive effects such as general combining ability (GCA)	(155)
Soybean	Deep learning, Bayes B, Support Vector Machine (SVM), GBLUP,	Nested Association Mapping populations enhanced the accuracy of genomic selection, while deep learning models are increasingly being used for predicting yield and oil-related traits.	(156)
Brassica	Bayesian LASSO, GBLUP, BayesB,	Particularly useful for complex traits such as oil content, flowering time and resistance to diseases	(157)
Groundnut	Bayesian Ridge Regression (BRR), GBLUP,	drought tolerance, quality traits, Used for oil yield	(141)

Table 6. Genomic selection models used for pulse crops

Crop	GS model used	Strength	Reference
Lentil	Multi-trait Bayes B, Single-Trait GS (STGS)	Oil content, low-heritability traits under G×E interaction	(146)
Phaseolus cumingii (Common bean relative)	GBLUP, possibly Bayesian Ridge Regression (BRR)	Cooking time, yield under drought, disease resistance (root rots)	(147)
Common bean (*Phaseolus vulgaris)*	GBLUP, WGRS-based GS	Resistance to Pythium and Fusarium root rots	(158)

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