Genomic Selection and Its Application in Pearl Millet Improvement

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Abstract

Pearl millet [*Pennisetum glaucum* (L.) R. Br] is a staple grain for about 90 million people in India, sub-Saharan Africa, and South Asia. Genomic selection is a new tool that helps to identify better lines among experimental cultivars in plant breeding programs. Genomic selection examines the phenotypes and high-density marker scores of lines in a population to predict breeding values. The integration of all marker information in the prediction model contributes to the effectiveness of genomic selection by eliminating biased marker effect estimations and collecting more of the variance associated with small-effect quantitative trait loci (QTL). The whole genome sequence of pearl millet has recently been sequenced, allowing genomic selection models to be used to improve the selection process in the pearl millet breeding program. Genomic selection, which employs genomic-estimated breeding values of individuals obtained from genome-wide markers to identify candidates for the next breeding cycle, is a powerful tool for enhancing quantitative traits. Models used for genomic selection frequently encounter problems when the number of markers

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exceeds the number of phenotypic data. To address this issue and enhance prediction accuracy, genomic selection models and algorithms such as Bayesian, Gaussian, and machine learning have been used. This chapter focuses extensively on the transition from conventional selection techniques used in plant breeding to the genomic selection, the underlying statistical models and methods used for this purpose, the current state of genomic selection research in pearl millet, and the prospects for its successful application in the development of climate resilient pearl millet varieties suitable for different end users.

6.1   Introduction

The primary objective of any crop improvement program is to develop varieties and cultivars with increased yield and biotic and abiotic stress tolerance. The process of developing varieties is continuous to meet the food demand of a growing global population. The current rate of genetic improvement in major agricultural crops is about 0.8–1.2%, which is insufficient to meet global food security in the future (Krishnappa et al. 2021). As the human population is expected to increase to 9.5 or 10 billion by 2050, the varietal improvement needs to be accelerated to 2.4% to feed the hungry stomach (Hickey et al. 2019; Ray et al. 2012, 2013).

In general, the development of high-yielding crop varieties has been achieved through forward genetics and/or conventional breeding approaches with difficulties. Because most of the yield and yield contributing traits are genetically complex and highly influenced by changing environmental conditions and climate change, the rate of genetic improvement is restricted (Bailey-Serres et al. 2019).

Over the decades, different molecular breeding approaches have been developed to speed up domestic and global breeding programs. After the discovery of molecular markers, marker-assisted selection/breeding (MAS/MAB) has been used to facilitate the development of crop varieties in different crop plants. MAS/MAB has been used successfully in crop improvement programs. This has led to the release of improved varieties of many crops, such as HHB67-Improved in pearl millet (Rai et al. 2008), C214 in chickpea (Varshney et al. 2014a), JL24 and TAG24 in groundnut (Varshney et al. 2014b), JTN5503 and DS880 in soybean (Arelli et al. 2006, 2009), HUW510 in wheat (Vasistha et al. 2017), Pusa Samba 1850 (Krishnan et al. 2019), Pusa Basmati 1728 (Singh et al. 2017a), Pusa Basmati 1637 (Singh et al. 2017b), Improved Pusa Basmati1 (Gopalakrishnan et al. 2008), Swarna-Sub1 (Neeraja et al. 2007), Improved Samba Mahsuri (Ratna Madhavi et al. 2016), and CR 1009 Sub 1(Robin et al. 2019) in rice. However, MAS/MAB is inefficient for improving traits like yield and biotic and abiotic stress tolerance because it is controlled by many genes or quantitative loci with small effects. The biggest

problems with MAS/MAB are (1) that it uses a low-density marker system, (2) that it doesn't have a good statistical method for improving traits that are controlled by many loci with small effects, and (3) that it uses a certain type of population. Hence, we need an appropriate approach for improving polygenic traits such as yield and biotic and abiotic stress tolerance.

A genomic selection (GS) approach was proposed by Meuwissen et al. (2001) for a breeding population to facilitate the selection of polygenic traits. The GS approach is used to predict the individual marker effect along with the sum of all the marker effects, which is used to calculate the genomic-estimated breeding values (GEBV) of the individual genotype.

Pearl millet (*Pennisetum glaucum* (L) R. Br., syn. *Cenchrus americanus* (L.) Morrone) is a drought-tolerant, open-pollinated, climate-resilient, C4 plant that grows primarily in resource-limited or marginal soil and environmental conditions such as low soil fertility, high temperatures, and limited water availability (Srivastava et al. 2020). As a C4 plant, it has great photosynthetic and high biomass-producing potential, which makes pearl millet an important staple food for those who are living in poverty or developing countries. It was considered an orphan/neglected crop and limited efforts have been made to improve its yield and quality. Later, much emphasis was given to the development of genetic and genomic resources to breed high-yielding and climate-resilient pearl millet varieties/hybrids for marginal farmers. The discovery of the pearl millet reference sequence in 2017 (Varshney et al. 2017) aided in the advancement of the pearl millet crop.

In this chapter, we present the current status and promising prospects of genomic selection methods, prediction models, and trait improvement concerning their application in pearl millet improvement.

6.2   Prediction Methods and Models

Several different series of models and algorithms for genetic prediction have been proposed by several researchers in GS. Initially, GS prediction approaches were mainly proposed and performed for animal genetic prediction. Later, the development of GS models provided a platform to utilize the models in plant breeding programs.

Compared to conventional plant breeding, genomic prediction models can accelerate crop improvement per unit of time by reducing labor costs and shortening the generation interval in a breeding cycle. A fundamental prerequisite for genomic prediction is the distribution of markers across the genome, with at least one marker being in linkage disequilibrium (LD) with each QTL. When estimating effects with a "training" population, all markers are employed concurrently. Genomic selection (GS) uses a "training population" of individuals that have been both phenotyped and genotyped to train a prediction model for calculating genomic estimated breeding values (GEBVs). Genomic prediction can foretell the GEBVs of individuals for selection based on the information from the training population. There are two steps involved in estimating the GEBVs with high prediction ability

1. Determining the size of the training population and the number of markers utilized in the suitable prediction model;
2. Testing and model validation to foresee the phenotype of those lines that were not included in the training models.

The genetic diversity and size of the training population, marker density, trait heritability, marker or gene effects, and the extent and distribution of LD between markers and QTL are a few variables that impact the accuracy of genomic prediction.

The basic process of any genomic selection process starts with the creation of a training population, i.e., individuals having both genotypic and phenotypic information and this information is used to build a model, where the phenotype is used as a response and the genotype as a predictor. In "training" populations, the effects of each marker are used simultaneously to create prediction models. Fixed regression methods utilizing ordinary least squares cannot be utilized to create prediction models since the number of predictors (markers) is typically more than the sample size ($P \gg n$). Prediction models are created using statistical techniques that see marker effects as random, such as ridge regression best linear unbiased prediction (RR-BLUP) and various Bayesian models. One can evaluate the accuracy of genomic selection, by comparing GEBVs to the breeding values predicted using conventional techniques that depend on phenotypic data. For the purpose of predicting phenotypes utilizing a large number of markers, several GS models have been created. The key area where these models diverge is in the proportion of variance that is attributable to marker effects.

6.3   Methods Used in Genomic Selection

6.3.1   M1: General Combining Ability (GCA) Model ($E + G_{P1} + G_{P2}$)

For characterizing the ith hybrid, this model utilizes genomic information obtained from the inbreds via the GCA of the parents; hence, modeling of male and female effects can be performed. This model is composed of two genetic scores, which are derived from the main effects of the markers of those inbreds acting as parent 1 or B-lines (g_{P1i}) and parent 2 or R-lines (g_{P2i}), respectively (Technow et al. 2014; Kadam et al. 2016). Collecting the aforementioned results and assumptions, the linear predictor for modeling the hybrid performance via the GCA of inbreds is obtained as follows

$$y_{ij} = m + E_j + g_{P1i} + g_{P2i} + e_{ij}$$

where y_{ij} is the yield performance of the ith ($i = 1, 2, \ldots, I$) hybrid in the jth ($j = 1, 2, \ldots, J$) environment, m is the common mean, E_j is the main effects of the jth environments, $g_{P1} = \{g_{P1i}\} \sim N(0, G_{P1}\sigma^2_{P1g})$ and $g_{P2} = \{g_{P2i}\} \sim N(0, G_{P2}\sigma^2_{P2g})$ with $G_{P1} = X_{P1}X^1_{P1}/p$, $G_{P2} = X_{P2}X^10_{P2}/p$, $\sigma^2_{P1g} = p \times \sigma^2_{bP1}$ and $\sigma^2_{P2g} = p \times \sigma^2_{bP2}$ as the corresponding variance components of the parental effects, and $e_{ij} \sim N(0, \sigma^2_e)$ and

$\sigma 2_E$ and $\sigma 2_e$ represent the associated variance components of environments and residual terms. One of the disadvantages of this model is that it does not take into consideration the specific effect of crossing parent 1 with parent 2, but rather the average effects between both parents. Moreover, it returns a common genetic effect for the same hybrid in different environments (Jarquin et al. 2020).

6.3.2 M2: General Plus-Specific Combining Ability Model $(E + G_{P1} + G_{P2} + G_{P1 \times P2})$

This model is an extension of model M1, and it not only accounts for the main effects of the genetic components of the inbreds but also includes the specific interaction effect of crossing inbred parent 1 and parent 2 (Acosta-Pech et al. 2017). The main effect is accounted for by the GCA component, and the interaction effect is accounted for by the SCA component. The SCA was modeled using the cell-by-cell product of the entries of the covariance structures from inbred parent 1 (G_{P1}) and inbred parent 2 (G_{P2}), such that $g_{P1xP2} = \{g_{P1ixP2i}\} \sim N(0, G_{P1xP2}\sigma^2_{P1gxP2g})$, where $G_{P1xP2} = (Z_{gP1}G_{P1}Z^1_{gP1})\cdot(Z_{gP2}G_{P2}Z^1_{gP2})$, $\sigma^2_{P1gxP2g}$ is the variance component associated with this interaction term, and Z_{gP1} and Z_{gP2} are the corresponding incidence matrices for parent 1 and parent 2 for the hybrids.

The model in which both the GCA and the SCA components are included can be written as.

$$y_{ij} = m + E_j + g_{P1i} + g_{P2i} + g_{P1ixP2i} + e_{ij}$$

Although this model considers the effects of crossing parent 1 with parent 2, it brings a common genetic effect across environments for the same hybrid in different environments similar to the previous model.

6.3.3 M3: General Plus-Specific Combining Ability in Interaction with Environments Model $(E + G_{P1} + G_{P2} + G_{P1 \times P2} + G_{P1} \times E + G_{P2} \times E + G_{P1 \times P2} \times E)$

This model is an extension of M2, in that it includes both the GCA and SCA components but also accounts for the interaction of the inbred markers with environments by including the interaction between GCA and SCA components and environments. The model can be written as

$$y_{ij} = m + E_j + g_{P1i} + g_{P2i} + g_{P1ixP2i} + gE_{P1i}j + gE_{P2ij} + gE_{P1ijxP2ij} + e_{ij}$$

where $gE_{P1} = \{gE_{P1ij}\} \sim N(0, (Zg_{P1}G_{P1}Z^1_{gP1})\cdot(Z_EZ^1_E)\sigma^2_{gEP1})$, $gE_{P2} = \{gE_{P2ij}\} \sim N(0, (Z_{gP2}G_{P2}Z^1_{gP2})\cdot(Z_EZ^1_E)\sigma^2_{gEP2})$ and $gE_{P1xP2} = \{gE_{P1ijxP2ij}\} \sim N(0, (I_4 \bigotimes ((Z_{gP1}G_{P1}Z^1_{gP1})\cdot(Z_{gP2} G_{P2}Z^1_{gP2})))\cdot(Z_EZ^1_E)\sigma 2_{gEP1xP2})$; σ^2_{gEP1}, σ^2_{gEP2}, and $\sigma^2_{gEP1xP2}$ are the corresponding variance components for interaction terms between

markers of inbred and environments for the GCA (parent 1 and parent 2) and SCA (P1 × P2) terms; Z_E is the corresponding incidence matrix for environments. The genetic effects of the genotypes derived from this model are particular to each environment.

6.4   Models Implied for Genomic Selection

The process of selecting suitable individuals in GS starts with a simple linear model also known as least-squares regression or ordinary least-squares regression (OLS):

$$Y = I_n \mu + X\beta + \varepsilon$$

where Y = n × 1 vectors of observations, μ is the mean, β = p × 1 vectors of marker effects, ε = n × 1 vectors of random residual effects, X = design matrix of order n × p (where each row represents the genotype/individuals/lines (n), and each column corresponds to the marker (p)), and $\varepsilon \sim N(0, \sigma^2_e)$.

One major limitation in linear models using several thousands of genome-wide markers is that the number of markers (p) exceeds the number of observations (n), i.e., genotypes/individuals/lines and this creates the problem of over-parameterization (large "p" and small "n" problem ($p \gg n$)). Using a subset of significant markers can be an alternative for dealing with the large "p" and small "n" problem. Meuwissen et al. (2001) modified the least-squares regression for GS and performed least-squares regression analysis on each marker separately with the following model.

$$Y = X_j \beta_j + \varepsilon$$

where X_j = jth column of the design matrix of the markers and β_j = genetic effect of the jth marker.

Markers with significant effects are selected using the log-likelihood of this model, and those are further used for estimating the breeding values. However, some key information may be lost by selection based on the subset of markers. Hence, an efficient solution for the over-parameterization problem in linear models is using ridge regression (RR), which is a penalized regression-based approach (Meuwissen et al. 2001). It also solves the problems of multicollinearity simultaneously (i.e., correlated predictors, e.g., SNP or markers). RR shrinks the coefficients of correlated predictors equally towards zero and solves the regression problem using $\ell 2$ penalized least squares. Here, the goal is to derive an estimator of parameter β with a smaller variance than the least-squares estimator. Similar to RR, the least absolute shrinkage and selection operator (LASSO) (Usai et al. 2009) is another variant of penalized regression, which uses the $\ell 1$ penalized least-squares criterion to obtain a sparse solution. However, sometimes LASSO may not work well with highly correlated predictors (e.g., SNPs in high linkage disequilibrium) (Ogutu et al. 2012). The elastic net (ENET) is an extension of the LASSO that is

robust to extreme correlations among the predictors (Friedman et al., 2010), and it is a compromise between $\ell 1$ penalty (LASSO) and $\ell 2$ penalty (RR) (Zou and Hastie 2005).

The RR model considers that each marker contributes to equal variance, which is not true for all traits. Therefore, the variance of the markers based on the trait's genetic architecture has to be modeled. For this purpose, several Bayesian models have been proposed where it is assumed that there is some prior distribution of marker effects (Budhlakoti et al. 2022). Furthermore, inferences about model parameters are obtained based on posterior distributions of marker effects. There are several variants of Bayesian models for genomic prediction such as Bayes A, Bayes B, Bayes Cπ, and Bayes Dπ (Meuwissen et al. 2001; Habier et al. 2011) and other derivatives, e.g., Bayesian LASSO and Bayesian ridge regression (BRR). Besides the marker-based models, the best linear unbiased prediction (BLUP) (Henderson et al. 1959) is one of the most commonly used genomic prediction methods. There are many variants of BLUP available for this purpose, e.g., genomic BLUP (GBLUP), single-step GBLUP (ssGBLUP), ridge regression BLUP (RRBLUP), and GBLUP with linear ridge kernel regression (rrGBLUP), of which GBLUP is very frequently used. The GBLUP uses the genomic relationships calculated using markers instead of the conventional BLUP which uses the pedigree relationships to obtain the GEBV of the lines or individuals (Meuwissen et al. 2001).

The genomic prediction models perform well for traits with additive genetic architecture, but their performance becomes very poor in the case of epistatic genetic architecture. Hence, Gianola et al. (2006) first used nonparametric and semiparametric methods for modeling the complex genetic architecture. Subsequently, several statistical methods were implemented to model both additive and epistatic effects for genomic selection (Xu 2007; Cai et al. 2011; Legarra and Reverter 2018). Several nonparametric methods have been studied in relation to genomic selection, e.g., NW (Nadaraya–Watson) estimator (Gianola et al. 2006), RKHS (reproductive kernel Hilbert space) (Gianola et al. 2006), SVM (support vector machine) (Maenhout et al. 2007; Long et al. 2011), ANN (artificial neural network) (Gianola et al. 2011), and RF (random forest) (Holliday et al. 2012), among which SVM, NN, and RF are based on the machine learning approach.

Methods discussed earlier are based on genomic information where information is available for a single trait, i.e., single-trait genomic selection (STGS). As the performance of STGS-based methods may be affected significantly in the case of pleiotropy, i.e., one gene linked to multiple traits, a mutation in a pleiotropic gene may have an effect on several traits simultaneously. It was observed that low heritability traits could borrow information from correlated traits and consequently achieve higher prediction accuracy. However, STGS-based methods consider the information of each trait independently.

Hence, crucial information may be lost which may ultimately result in poor genomic prediction accuracy. Nowadays, as we are receiving data on multiple traits, multi-trait genomic selection (MTGS)-based methods may provide more accurate GEBV and subsequently a higher prediction accuracy. Several MTGS-based methods have been studied in relation to GS, e.g., the multivariate mixed model
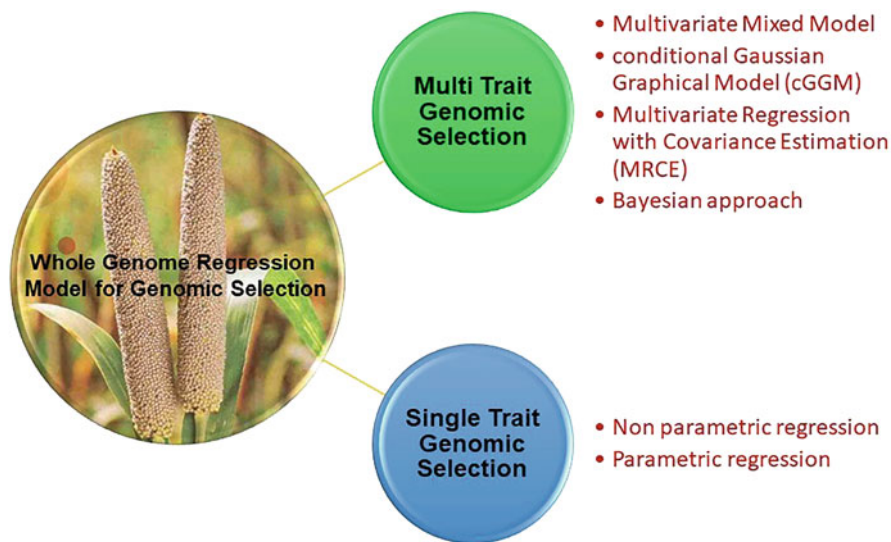
Fig. 6.1 Summary of models utilized in genomic selection

approach (Jia and Jannink 2012; Klápště et al. 2020), Bayesian multi-trait model (Jia and Jannink 2012; Cheng et al. 2018), MRCE (multivariate regression with covariance estimation) (Rothman et al. 2010), and cGGM (conditional Gaussian graphical model) (Chiquet et al. 2017). Jia and Jannink (2012) presented three multivariate linear models (i.e., GBLUP, Bayes A, and Bayes Cπ) and compared them to univariate models, and a detailed comparison of various STGS and MTGS-based methods has also been studied by Budhlakoti et al. (2019). A brief structure of different STGS- and MTGS-based methods used in GS studies is given in Fig. 6.1.

The architecture of the target traits may impact how well prediction models for complex traits function (Momen et al. 2018). At ICRISAT, India, whole genome resequencing (WGRS) along with phenotypic data for several important traits of PMiGAP lines was exploited for GWAS and GS. Different whole-genome prediction/genomic selection models were created and optimized based on the numerous target features identified by GWAS in pearl millet. Varshney et al. (2017) performed GS to predict grain yield for test crosses by ridge regression best linear unbiased prediction (RR-BLUP) at ICRISAT. GS strategy was also used to predict the performance of the hybrids derived from a CMS (Cytoplasmic male sterility) using both (RADseq and tGBS) techniques and four genomic prediction schemes (Liang et al. 2018). Pilot studies on the genomic selection with different prediction models in pearl millet are summarized in Table 6.1.

Table 6.1 Studies on genomic selection in pearl millet

Traits studied	Breeding material	Prediction model employed	References
Grain yield	170 hybrid combinations	RR-BLUP (ridge regression best linear unbiased prediction)	Varshney et al. (2017)
1000-grain weight, days to flowering, grain yield, and plant height	Two common control lines/hybrids and 13 experimental lines	RR-BLUP (ridge regression best linear unbiased prediction)	Liang et al. (2018)
Grain yield	320 pearl millet hybrids and 37 inbred parents	Bayesian generalized linear regression (BGLR)	Jarquin et al. (2020)

6.5 Trait Improvement

6.5.1 Yield

Modern breeding efforts have increased the productivity of almost all agricultural crops. Pearl millet productivity increased by almost four times from 1950 to 2019. This genetic improvement of pearl millet is divided into four phases (Yadav et al. 2019; Yadav and Rai 2013). Each phase of improvement and its emphasis are presented in Fig. 6.2. Pearl millet yielded 162% more after adopting high-yielding, pest and disease-resistant, and abiotic stress-tolerant standard agronomic management practices, while sorghum, wheat, rice, and maize yielded 26%, 59%, 69%, and 113%, respectively (Yadav et al. 2019; Yadav and Rai 2013).

The rate of genetic gain achieved in pearl millet and other cereals is the collective outcome of improved varieties and best crop management strategies. This quantum jump in the productivity of pearl millet was achieved in two different ways. First, almost 90% of pearl millet is grown under rainfed conditions; second, pearl millet has attracted fewer human resources and infrastructure than other crops (Yadav et al. 2019). In pearl millet association studies (Anuradha et al. 2017), Xibmsp11/AP6.1, a known SNP marker found on acetyl CoA carboxylase gene, was shown to be significantly linked with yield and yield components (grain harvest index and grain yield). Stay green and grain yield-related traits are closely linked to Xibmcp09/AP10.2 and Xibmcp09/AP10.1 InDels markers on chlorophyll a/b binding protein genes. (Anuradha et al. 2017).

6.5.2 Grain Quality

Since pearl millet is a particularly nutritious grain with higher quantities of protein and various minerals than other cereals, breeding has sought to focus on increasing the yield potential (Singh and Nainawatee 1999) along with other important traits (Fig. 6.3). Earlier studies revealed that the protein concentration of pearl millet was
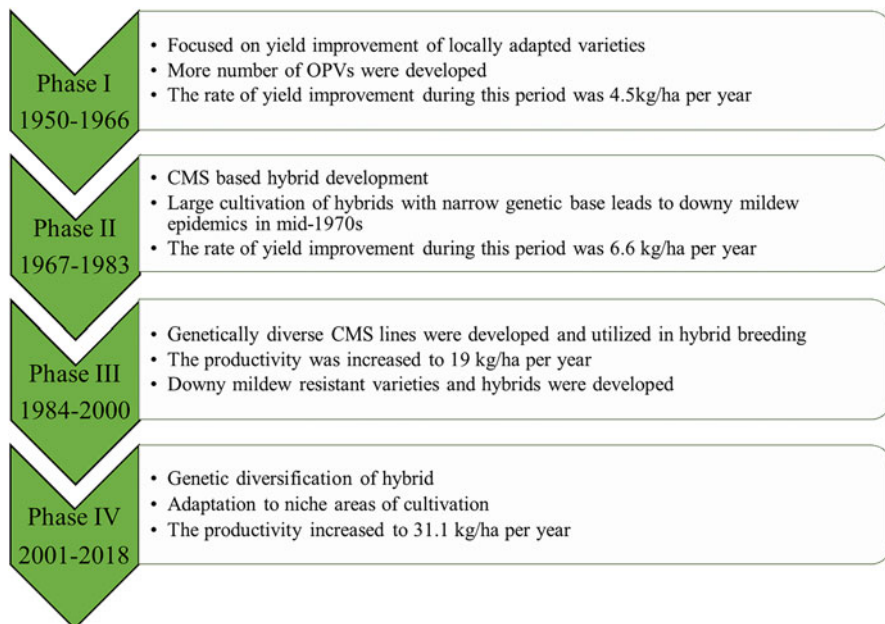
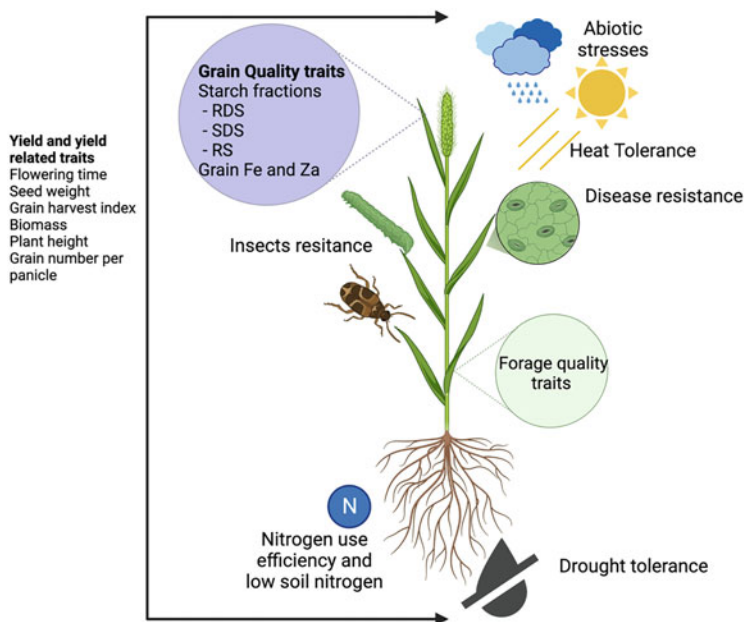**Fig. 6.2** Four phases of yield improvement in pearl millet

Fig. 6.3 Important traits improved in pearl millet

reported at up to 24.3% (Jambunathan and Subramanian 1988), with top breeding lines reaching 19.8% (Singh et al. 1987). However, due to the unfavorable associations between protein content and grain yield, no significant efforts to enhance it were made in most of the pear millet breeding programs (Singh and Nainawatee 1999). In light of the growing awareness of widespread iron (Fe) and zinc (Zn) deficiencies worldwide, improving grain nutritional characteristics has recently been included as a breeding target. The main areas focused on include the evaluation of genotype-environment interactions; correlations between grain minerals and agronomic features; genetic regulation of micronutrients; and assessment of the degree of genetic variation for grain Fe and Zn content.

There is a lot of variation in the amount of Fe and Zn in pearl millet germplasm and breeding lines. This suggests that these micronutrients could be improved through pre-breeding approaches. The mapping populations and germplasm accessions originating from the *Iniadi* landrace have the greatest levels of Fe and Zn, respectively (Velu et al. 2008; Govindaraj et al. 2016; Govindaraj et al. 2020a, b; Govindaraj et al. 2021). When more than 120 commercial Indian hybrids were tested, 46–56 ppm Fe and 37–44 ppm Zn were found (Rai et al. 2016). In 2018, the Indian national testing and cultivar release policy set 42 ppm Fe and 32 ppm Zn as a baseline for the mainstreaming of Fe and Zn in pearl millet (AICPMIP 2018). For Indian adults, the daily recommended amounts of Fe and Zn are 17–21 mg/d and 10–12 mg/day, respectively.

The presence of Fe and Zn in pearl millet is mostly determined by additive gene action, implying that both parental lines of hybrids would be required to enrich these minerals (Kanatti et al. 2014). Lower G × E influences interaction on Fe and Zn accumulation in pearl millet grains and also revealed the success of progeny selection in pedigree breeding to generate lines with higher grain Fe and Zn densities (Kanatti et al. 2014; Govindaraj et al. 2016). Between Fe and Zn, a significant and positive association has been found (Kanatti et al. 2014; Govindaraj et al. 2020a, b). Additionally, there was a significant positive correlation between these two micronutrients and grain size (Kanatti et al. 2014; Govindaraj et al. 2016). These relationships would help generate pearl millet cultivars rich in Fe and Zn without compromising their grain size, regardless of color, and also increase micronutrient content through crop improvement.

6.6 Biotic Stress Tolerance

6.6.1 Disease Resistance

The most important disease in pearl millet in India and Africa is Downy Mildew (DM), caused by *Sclerospora graminicola* (Sacc.) J. Schröt. DM in pearl millet causes significant yield loss in major growing countries, mainly in India and Africa (Yadav et al. 2021). Identifying various resistance sources through greenhouse and field screening of large panels of germplasm accessions and breeding lines has helped to advance the development of DM-resistant hybrids in pearl millet

significantly. This hybrid population of diverse genetic backgrounds has been an important factor in successfully managing widespread DM outbreaks in pearl millet (Singh et al. 1987, 1990).

The severity of smut (*Moesziomyces penicillariae* Bref. Vanky) and ergot (*Claviceps fusiformis* Lov.) significantly reduces the grain yield in pearl millet. Both infections are soil-borne and infect the host through the stigma during flowering (Thakur and Williams 1980). Pollen wash is the main reason for the severity of smut and ergot diseases during the rainy season. The development of field and greenhouse screening methods was aided by knowledge of the biology and epidemiology of these diseases. Numerous lines have been examined to determine their resistance to these diseases. The lack of incredibly high ergot resistance in germplasm accessions has driven the development of ergot-resistant lines by interbreeding less susceptible germplasm lines and selecting and rescreening resistant progeny for multiple generations under intense disease pressure. Resistance to Smut is a dominant trait that is easy to pass on to the next generation. But there have also been reports of quantitative resistance incorporating both additive and nonadditive gene effects (Thakur et al. 2011). Smut and DM resistance has been discovered in several lines (Thakur et al. 1992, 2011).

It is common knowledge that rust (*Puccinia substriata* var. *indica* Ramachar & Cumm) has little impact on grain (Pearl millet) crops, but in the fodder industry, it has a significant impact on yield and quality. A combination of field and greenhouse screening resulted in the discovery of stable sources of resistance. DArT and SSR-based linkage maps were created using a mapping population of 168 F7 RILs, which was also screened for rust resistance (Ambawat et al. 2016). Three QTLs on linkage groups 1, 4, and 7 were identified for pearl millet rust resistance, accounting for 58% of the phenotypic variation in rust reactivity. A newly discovered QTL for rust resistance, Linkage Group 1 (LG1), confers a long-lasting slow rusting phenotype (Ambawat et al. 2016).

The leaf spot or blast disease, caused by *Pyricularia grisea* Sacc. (syn. *Magnaporthe grisea*), has emerged as a major pearl millet disease (Rai et al. 2012). The identification of blast-resistant lines from pearl millet breeding and germplasm accessions allowed for the development of hybrids that are resistant to the disease (Sharma et al. 2013; Goud et al. 2016). In pearl millet, a single dominant gene is responsible for resistance to Indian strains of *Magnoporthe grisea* (Gupta et al. 2012; Singh et al. 2018). A total of six blast-resistant pearl millet genotypes (ICMB 97222, ICMB93333, ICMR 11003, IP 21187-P1, and ICMR 06222) were crossed with two susceptible genotypes (ICMB 89111 and ICMB 95444) to study the inheritance pattern. Their generations and backcrosses were screened for resistance against Pg53 and Pg45 (*Magnoporthe grisea* isolates). Molecular markers are also being used to identify QTLs for blast disease pathotypes. Using SSR markers, two significant QTLs for blast resistance have been identified in linkage groups 1 (LG1) and 6 (LG6) (Maganlal et al. 2018). A large panel of germplasm accessions of pearl millet was collected from 13 different countries and tested against *Magnoporthe grisea* isolates Pg45, Pg53, Pg56, Pg118, and Pg119. The accessions were then classified according to the amount of resistance. It was found that

182 different accessions of pearl millet exhibited resistance against different pathotypes. (Sharma et al. 2021).

6.6.2 Insect Resistance

Although there have been reports of more than 100 insect pests linked with cropping systems based on pearl millet, only a small number of these insects are considered to have the ability to cause considerable damage to the crop. These include the stem borers (*Chilo partellus* in India and *Coniesta ignefusalis* in western Africa), shoot flies (*Atherigona approximata*), and white grubs (*Holotrichia consanguinea*) in India. Additionally, ear head worms (*Helicoverpa armigera*), gray weevils (*Myllocerus species*), and leaf rollers (*Marasmia trapezalis*) are found (Raghvani et al. 2008). Pest control techniques have been created based on research into the pests' life cycles and the types of harm they cause. Each region has its own unique pattern of insect-pest dispersion and devastation. Long-term research has shown that no single approach to pest management is successful against any kind of pest. Cultural and chemical management is needed as part of an integrated pest management strategy (Sharma and Youm 1999). Insect pest incidence on commercial cultivation and experimental test genotypes is regularly monitored, and no breeding initiatives are pursuing insect resistance as a goal trait in pear millet.

6.7 Abiotic Stress Tolerance

6.7.1 Drought Tolerance

Crop plants suffer from impaired growth and development when drought conditions persist due to insufficient rainfall and its unpredictable distribution pattern. It has been discovered that QTL for drought tolerance contributes to differences in photosynthetic pigments and ROS scavenging enzymes in different accessions of pearl millet. The ascorbate peroxidase (APX) activity was found to be elevated in tolerant genotypes, although the superoxide dismutase (SOD) and catalase (CAT) activities remained unaltered, according to the QTL that was investigated. It was shown that the presence or lack of drought-related QTL had no effect on the molecules that make up photosynthetic pigments (Kholová et al. 2011).

The pearl millet grain filling stage is the most susceptible stage to drought stress, which results in a decrease in grain size and grain test weight (Fussell et al. 1991). A pearl millet germplasm association panel was recently constructed and is being used for drought tolerance trait association mapping. A significant association was observed between an SNP in the acetyl-CoA carboxylase genes and panicle yield, grain harvest index, and grain yield, whereas an InDel was shown to be significantly connected with grain yield and stay-green phenotype traits under drought conditions (Sehgal et al. 2015). Debieu et al. (2018) used genotyping by sequencing (GBS) to identify QTLs linked with agronomic parameters in 188 inbred lines under drought

conditions. Four marker-trait relationships for the stay-green trait were identified on chromosome 6, and two SNPs were shown to be significantly linked with biomass yield under early drought stress conditions. One of the two SNPs identified for biomass yield was mapped between two predicted genes, Pgl GLEAN 10037359 and Pgl GLEAN 10037360, while the other was mapped between two predicted genes, Pgl GLEAN 10036946 and Pgl GLEAN 10036945. Early drought stress in lines resulted in a decreased grain and biomass yield, although only minor changes were found in grain weight (Debieu et al. 2018). Shivhare et al. (2020) discovered 1129 DEGs on all seven pearl millet chromosomes except chromosome 4. Most genes were found on and mapped to chromosome 2 (196), followed by chromosome 3 (171), chromosome 5 (168), chromosome 6 (164), chromosome 7 (140), and chromosome 4 (108). Recent research on transcriptome analysis identified 2792 transcription factors, 1223 transcriptional regulators, 315 transcription factors, and 128 transcriptional regulators expressed under drought conditions. Using RNA-Pacibio sequencing, a total of 6484 genes for drought stress were identified (Sun et al. 2020). In recent research, Zhang et al. (2021) investigated the mechanism of drought resistance in pearl millet by comparing physiological and transcriptome data under drought and controlled conditions. It has been found that 12 genes were elevated under stress, some of which are connected with drought stress in other species, such as ADH1, FtsH, and CCCH. Also, the expression levels of genes like SnRK2 and PP2C involved in ABA signaling pathways were found to vary (Zhang et al. 2021).

6.7.2 Heat Tolerance

The ideal temperature for normal pearl millet development is 33–34 °C. The seedling and reproductive phases of pearl millet are equally susceptible to the effects of higher temperatures. By 2050, climate change models predict that sub-Saharan Africa (SSA) and South Asia (SA) pearl millet yields will fall by 6–17%. (Knox et al. 2011). High-temperature stress during the flowering stage of pearl millet produces sterility in the flowers, resulting in a drastic decrease in seed set and grain yield (Gupta et al. 2015; Djanaguiraman et al. 2018). Pearl millet has evolved as a very prolific and profitable crop throughout the hot and dry summer season in northern and western India during the last two decades. With increased air temperatures (typically >42 °C) coinciding with blooming during this season, the crop suffers from reproductive sterility, resulting in dramatic decreases in seed set and subsequently decreased grain production (Gupta et al. 2015; Djanaguiraman et al. 2018). During the reproductive stage, plants' ability to handle high temperatures has become an important trait in improving genetic gains.

Pearl millet roots have recently been studied to see how heat stress affects the plant's physiological and transcriptional systems. Trehalose concentration in the roots increased between 3 and 7 h of heat stress. Furthermore, peroxidase (POD) activity steadily increased from 3 to 7 h of heat stress. HSFs, bZIP, and bHLHs were the most frequently identified transcription factors expressed under heat stress. There

was a total of 16 bZIPs, 7 HSFs, and 18 bHLH genes that showed different expressions under heat stress (Sun et al. 2021).

The ability to withstand high temperatures during the reproductive phase has emerged as an essential genetic characteristic of pearl millet. Guidelines for flowering-period heat stress screening in controlled environments (greenhouses and growth chambers) and the field have been established (Gupta et al. 2015). There is a substantial amount of genetic heterogeneity between breeding lines and among open-pollinating populations. Multi-location field experiments were carried out to understand the sensitive plant reproductive parts highly susceptible to heat stress and found that stigma is more heat-sensitive than the pollen in pearl millet, thus helping researchers to pyramid heat tolerance in high-yielding hybrids and open-pollinated varieties (OPVs) (Gupta et al. 2016, 2019).

6.8   Genomic Selection (GS) in Pearl Millet

Genomic selection (GS) is a promising method that has tremendous potential to investigate and enhance the genetic gain per selection (in a set of timeframes) in a breeding scheme and, as a result, speed and efficiency in breeding programs. Genomic selection can also be called genome-wide selection (Spindel et al. 2015). In cereals and numerous other crops, including pearl millet, GS has been shown to be a cost-effective and feasible alternative to marker-assisted selection (MAS) and phenotype selection (PS) for quantitative traits and rapid crop development initiatives (Zhong et al. 2009; Heffner et al. 2009; Crossa et al. 2010; Poland et al. 2012; Ornella et al. 2012; Spindel et al. 2015; Muleta et al. 2019; Liang et al. 2018; Jarquin et al. 2020).

Pearl millet's genome was recently assembled and is available in the public domain (Varshney et al. 2017). Because a reference genome is now widely available, genomic selection can be used to predict the general combining ability (GCA) of newly inbred parents and the specific performance of individual pearl millet hybrids (Liang et al. 2018). It has been demonstrated that adding information about the parents into genetic prediction can be advantageous (Massman et al. 2013). Genotyping based on sequencing makes it possible to produce thousands of SNPs that are used for differentiating breeding lines within the population. As stated in the introduction of this chapter, genomic selection-assisted breeding programs that include high-throughput genotyping and estimated breeding values have the ability to overcome all three of the most significant bottlenecks in pearl millet breeding efforts. GS uses genome-wide high-density DNA markers in linkage disequilibrium (LD) with QTL to predict the genomic estimated breeding values (GEBV) of the testing population, which only has genotypic data. The predicted GEBVs are used for selection (Meuwissen et al. 2001). Making selection decisions during the off-season allows for increases in genetic gain each year, which is one of the main benefits of GS (Heffner et al. 2009). The development and use of GS in pearl millet breeding programs make it possible to use resources well and predict how well hybrids will perform.

In ICRISAT, efforts are being undertaken to take advantage of the pearl millet inbred germplasm association (PMiGAP) panel, along with whole-genome resequencing (WGRS) and phenotyping data for several characteristics for GS. The development and optimization of several whole-genome prediction/genomic selection models in pearl millet are based on the various target features using genome-wide association studies (GWAS). To predict grain yield for test crosses in different environments, ICRISAT applied WGRS data for genomic selection by ridge regression best linear unbiased prediction (RR-BLUP). In this prediction, high prediction accuracies were found for the performance of genotypes across different environments. Additionally, it was reported that the GS strategy (additive and dominance effects) was used to analyze grain yield data with 302,110 SNPs to predict hybrid performance. One hundred and seventy promising hybrid combinations were discovered. Among them, more than ten hybrid combinations are already being utilized in heterosis breeding. Liang et al. (2018) analyzed the effectiveness of genomic selection and prediction using two potential genotyping techniques, RAD-seq and tGBS, to characterize a series of ICRISAT-developed inbred pearl millet lines. Twenty random rounds of fivefold cross-validation were performed for a tested SNP set, utilizing the projected hybrids from both (RADseq and tGBS) methodologies and four genomic prediction systems in pearl millet and assessing for each trait. The genomic prediction technique (RR-BLUP) was found to produce median prediction ranges (in parenthesis) for various traits, including 1000-grain weight (0.73–0.74), days to flowering (0.87–0.89), grain yield (0.48–0.51), and plant height (0.72–0.73), respectively, using hybrid data. It was also predicted that adding inbred phenotypic data sets and hybrid trait values relative to the mean trait values of that population made hybrid GEBVs slightly better.

Recently, Jarquin et al. (2020) implemented and compared three GS models utilizing grain yield and high-density molecular marker information from two distinct genotyping platforms for pearl millet (C [conventional GBS RAD-seq] and T [tunable GBS tGBS]). The three GS models were evaluated using different cross-validation (CV) schemes that mimic the scenarios of breeders encountered during the varietal developmental processes in breeding projects. While CV1 forecasts the performance of untested hybrids and CV0 predicts the performance of hybrids in unobserved environmental conditions, CV2 is similar to an incomplete field trial. Through this study, Jarquin et al. (2020) discovered that the addition of phenotypic information of the parental inbreds, consideration of genotype-by-environment interaction, and use of molecular markers derived from tGBS improved the predictive ability and performance of the GS models.

6.9 Implications and Future Prospects

Pearl millet, as a poor man's crop, has received less attention despite its enormous potential. Pearl millet breeding has lagged behind that of other crops. With a growing population, the worldwide demand and diversification of feed, energy, and food are on the rise, urging the development of efficient methods for the development of

varieties for different end users. Pearl millet's genetic and genomic insights could be gained using genomics if the wide range of wild species and germplasm accessions were studied. On the other hand, heterozygosity, high outcrossing rates, inbreeding depression, and residual heterozygosity pose bottlenecks in inbred development programs, thus influencing the association mapping panels and parental line/cultivar development. Furthermore, populations for functional genomics, such as mapping populations, natural diversity panels, molecular modules, GWAS, and genetic engineering, could aid in dissecting the population's valuable variables. GS should be carried out based on different end users. Single-cross hybrids dominate the Indian market, whereas top-cross and three-way hybrids are prominent in Africa. Therefore, an appropriate GS model can be employed based on the type of populations and genotype x environment interactions.

Genome editing, a new method in the genomic era, is important for creating novel targeted mutations and identifying genes and their functions for crop improvement. However, limited efforts have been made in pearl millet breeding. The implementation of this approach is heavily reliant on transformation efficiency, which is still significantly lower in crops like pearl millet and sorghum than in other key crops. To enhance CRISPR/Cas9 use in pearl millet breeding, it is necessary to optimize the transformation system. Even though a lot of progress has been made in finding the genetic loci that control important agronomic and grain quality traits, epigenomes, pan-genomes, and other fields should be brought together for the dissection of genetic diversity and identification of superior alleles for the development of superior pearl millet varieties to achieve global food and nutritional security.

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