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## Relevance of genomic selection for development of crops with climate change resilience

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### Abstract

Global warming and climate change are one of the most important aspects hampering the global production scenario significantly. With the development in the molecular breeding technology due to the advents like next generation sequencing it has become possible to encompass the multidisciplinary approaches while formulate any breeding programme. Genomic selection is one of the promising tools for improving plants for the complex traits like biotic and abiotic stress resilience and sustainable production.

**Keywords:** QTLs, genomic estimated breeding values, Heritability, climate change resilience, prediction accuracy

### Introduction

The ever-increasing global population along with the serious threats of global warming and climate change are imposing a great challenge in maintenance of sustainable food production worldwide. The emergence of new diseases and insect pests, climatic fluctuations and temperature and moisture stress can lead to serious concern in the overall production and economic output of the crop plants. Major breeding technologies developed earlier were primarily focused on improving productivity levels of the crops without putting any serious concern for overall crop genetic diversity. Consequently, there has been great reduction in the genetic base of the crops which made them highly homogeneous and genetically vulnerable to new diseases and pests. Therefore, it has become very important to consider the crop genetic diversity while formulating any breeding programme to maintain the sustainability of crop production.

Therefore, it now requires serious attention from breeders to put attention on developing crops with sustainability in production along with the singular increase in the productivity levels. It requires a multidisciplinary approach in tackling such serious challenges of near future. Recent advancements in field of functional genomics with development of advents like next generation sequencing there is a ray of hope to incorporate crop plants with the resilience against such adverse natural vicissitudes. Genomic assisted breeding and technologies can help in mitigating adverse effects of climate change and developing climate ready crops for greater and sustainable yield levels along with better resilience.

In the recent past, there has been so many developments in the field of functional genomics which led to the identification and introgression of various novel QTLs responsible several important traits in different crops like rice, wheat, maize, soybean etc. Marker assisted selection is an indirect method of selecting plants based on markers linked to various genes controlling the trait of interest. There has been significant exploitation of MAS in selecting plants efficiently for various traits of agronomic importance. In case of cereals, Improved Pusa Basmati1, Improved samba mahsuri, Swarna sub1 and Improved Pusa RH 10 in rice, HUW510 in wheat (Vasistha *et al.*, 2017) <sup>[1]</sup> and HHB67-Improved in pearl millet (Rai *et al.*, 2008) <sup>[2]</sup> etc. provide excellent examples of utilization of marker assisted breeding for developing improved versions of excellent crop varieties. However, the constraint associated with MAS is that it is useful only when the trait is governed by one to few major genes, whereas, majority of the agronomically important traits are governed by poly genes involving hundreds of minor genes. In case of such polygenically inherited trait MAS is quite inefficient and not feasible practically in improving the crop plants. To address this issue and overcome the challenge a new selection means is developed which utilizes densely distributed markers covering the entire genome to estimate the net genetic worth of an individual, this selection

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technique is known as genomic selection which is an excellent tool for development of crops for traits with very low heritability. Here, individual marker effect is estimated and sum of all marker effect at all the loci are calculated for the estimation of genomic estimated breeding values of an individual. Therefore, GS can be regarded as a promising tool for developing crop plants for such complex traits related to various responses against abiotic and biotic stresses and improving crop plants under complex agricultural production environments. One of the chief advantages of utilizing GS as a selection tool is that it leads to a significant reduction in the overall duration of breeding cycle in comparison with conventional breeding along with reducing the expense associated with the extensive phenotyping with accelerating genetic gains for ensuring global food and nutritional security.

### Statistical models of genomic selection

Meuwissen *et al.* (2009) <sup>[37]</sup> provided a modified mathematical model for least-squares regression in GS. Here individual markers undergone least square regression as following statistical model.

$$Y = \sum x_j b_j + e$$

$x_j$  = genotype of the individuals for the marker  $j$

$b_j$  =  $j^{th}$  marker effect

$e$  = error associated.

Post regression markers with significant effects are selected which are further evaluated for the estimation of the breeding values. However, there is a possibility of some data may go missing as a smaller set of markers are utilized for the evaluation of the breeding values.

The problem of over parameterization and counter missing data can be solved utilizing models of ridge regression-based approach which also corrects for multi collinearity. It eliminates coefficients of correlated parameters and corrects the regression with 12 least squares. An estimator of the parameter  $b$  is derived which is smaller compared to the least square estimate. However, this model assumes equal contribution of each marker for every trait which is not correct for many of the traits. Therefore, it is necessary to module the marker variance based on the particular trait's genetic construction.

The genomic prediction models described earlier are mostly parametric which are superior for genetic architecture of additive nature but these are inefficient with the genetic construction of epistatic nature. Hence, it was necessary to develop semi-parametric and non-parametric models to model the traits with such complex architecture. Currently, there are several different statistical models which can be used for such complex genetic architecture and can be utilized for modelling of traits with both additive and epistatic nature.

Most of the genomic prediction models provides genomic information based on a single trait i.e. single trait genomic selection or STGS. But in several cases, such as pleiotropy it has been observed that a single gene may hamper the phenotypic expression of several traits simultaneously which significantly hampers the performance of the STGS models. Although traits with lower values of heritability where utilization of correlated traits may lead to the achievement much higher efficiency in estimation of genomic prediction values. However, such single trait-based methods may lead to

the loss of many crucial information which will ultimately result into poor accuracy of genomic values. Hence, the development of multi trait based genomic selection methods gaining popularity very rapidly. These methods provide much more accurate estimation of GEBV values and hence lead to the higher prediction accuracy of GS model.

### Statistical tools for evaluating genomic prediction values

#### RRBLUP

RRBLUP is one of the most widely employed packages among all statistical tools for evaluation of genotypes in terms of genomic prediction estimates. This tool is a spin-off of the package Best Linear Unbiased Prediction or BLUP which is a platform or model based on mixed linear framework (Endelman, 2011) <sup>[4]</sup>. This model approximates training population associated marker effects and utilized it in the final evaluation of GEBV estimates. A mixed linear model-based function is formed which approximates associated marker effects to predict GEBVs is most commonly utilized under this model. Further, a relationship matrix is formed of additive nature from the available genotypic data of the individuals can be estimated which is further utilizable for the prediction of genomic estimated breeding values.

#### GenSel

This statistical package employs Bayesian models for the estimation associated marker effects in the background of the training population and thereby approximates the genomic estimated breeding values for the selection of individuals from breeding population. GenSel produces the result files in the zipped format (\*.tgz) available for download and further study (Mukhopadhyay *et al.*, 2009) <sup>[9]</sup>. It utilizes an interface which is based on command line such as linux or mac. This system was initially programmed and executed through Bioinformatics to implement Genomic Selection Project or BIGS (Fernando and Garrick, 2009) <sup>[6]</sup>.

#### MTGS

There are several instances when it is necessary to select for multiple traits instead of a single trait where there is a requirement of selection index or a similar matrix in those cases MTGS is always superior in performance over STGS. This package first estimates associated marker effects and then utilizes this estimated marker effects to calculate genotypic worth of an individual. It also calculates correlation effects among various traits which indicates the information which is carried by one trait over the other. MTGS can be seen as all-inclusive tool which can provide single step resolution for multi trait genomic selection (Budhlakoti *et al.*, 2019) <sup>[7]</sup>.

#### STGS

In contrast to MTGS, STGS is a package based on R which evaluates genotypic worth of an individual based on single trait data. This model first calculates associated marker effects for various single traits. Then, these marker effects are utilized to evaluate individuals for their genotypic worth i.e. genomic estimated breeding values. Genomic selection may be built on single trait as well as multi trait data as this package utilizes single trait data for estimation of breeding values hence the name single trait genomic selection or STGS. This package provides an all-inclusive single step solution for single trait genomic selection.

### GM Stool

GM Stool is a package based on genome wide association study which utilizes various statistical and deep learning methods to search for the optimum number of markers and further presenting the best prediction model with that optimum set of markers. One of the most important factors contributing to the high prediction efficiency of any GS model is number of markers utilized for the model. In case of GM Stool it chooses optimum number of markers by choosing SNPS having minimal p-values. Therefore, it is highly beneficial in developing a model where only the highly pertinent markers are employed in the final prediction model (Jeong *et al.* 2020) <sup>[8]</sup>.

### solGS

solGS is based on RRBLUP model (Endelman *et al.*, 2011) <sup>[4]</sup> for prediction of genomic estimated breeding values of the individuals which works on linux based operating system model. It provides a highly instinctual web interface to evaluate and selection of individuals for modelling of training set which is selected and estimation of genomic estimated breeding values of those select individuals. It calculates total correlation along with heritability and there by develops selection indices for various traits. Here model data and results can be visualized interactively and it also provides the opportunity of downloading the data for later study (Teclé *et al.*, 2014) <sup>[9]</sup>.

### G selection

This is an R based package which utilizes an integrated model for estimation of genomic estimated breeding values. This model selects relevant set of markers to predict the performance of an individual on the basis of available data on the training set by utilizing an integrated model framework (Guha *et al.*, 2019). The integrated model framework which is used to prediction of the GEBVs is formed by the combination of an additive with one non-additive model thus it can include individuals with diverse genetic constructions.

### BWGS

BWGS or Bread Wheat Genomic Selection is a R based package which provides estimation of GEBVs comparatively easier than other models and is freely available in the sources. It helps in estimation of GEBVs by three processes firstly, it imputes for the any missing data present in the model. Secondly, it helps in selection of markers and training sets with reduction in dimensions which incorporates fewer markers which can reduce the complexity over a large data set and finally, it estimates genomic associated breeding values utilizing 15 different methods which may be parametric or semi-parametric (Charmet *et al.*, 2020) <sup>[11]</sup>. This model can be utilized for computation of GEBVs from a broader range of genetic architectures.

### lme4GS

This model is an extension of lme4R and RRBLUP package. The utilization of earlier model lme4R for computation of genomic predictions is restricted as it does not allow the correlations among different individuals or various groups of individuals to be defined. It is an R based package and also freely available utilized for fitting of mixed linear based models. Further, this model provides the flexibility to the user for fitting of models with a defined bandwidth, selection of covariate structures and finally estimates GEBVs (Caamal-Pat *et al.*, 2021) <sup>[12]</sup>.

### BGLR

BGLR is another R based package which permits integration of different parametric and semi parametric procedures to develop a large assembly of Bayesian models for computation of genomic prediction values. This model is particularly helpful while encountering a data with large number of parameters which may exceed the sample numbers. These large parameter-based datasets pose huge challenges while computational functions or statistical analysis is carried out. Hence, the model provides the necessary flexibility while deciding the marker density distribution and eases out the computational challenges encountered with such kind of datasets (Pérez *et al.*, 2014) <sup>[13]</sup>.

**Table 1:** List of different software packages utilized for estimation of GEBVs

Sl. No.	Statistical Package	Remarks	Reference
1.	GBLUP	Utilizes genomic relationships for estimation of GEBVs.	Clark <i>et al.</i> , 2013 <sup>[14]</sup>
2.	RRBLUP	Most widely utilized statistical package for estimation of GEBVs.	Endelman <i>et al.</i> , 2011 <sup>[4]</sup>
3.	ssGBLUP	Mostly used for animal breeding.	Alvarenga <i>et al.</i> , 2020 <sup>[15]</sup>
4.	GenSel	Provides a range of different analysis for genomic selection.	Mukhopadhyay <i>et al.</i> , 2009 <sup>[9]</sup>
5.	LASSO	Selection of feature and estimation of various parameters is done simultaneously.	Usai <i>et al.</i> , 2009 <sup>[16]</sup>
6.	BRR	Helps in case of data poorly distributed or insufficient.	Gianola <i>et al.</i> , 2003 <sup>[17]</sup>
7.	Bayesian LASSO	It tries to obtain data from full posterior distribution under a laplace prior.	Kiiveri, H.T. 2003 <sup>[18]</sup>
8.	Bayes A	Marker variance follows a inverted chi square distribution where basic statistics of the distribution is same as the marker.	Meuwissen <i>et al.</i> , 2003 <sup>[19]</sup>
9.	Bayes B	Number of markers are taken as non-effective and other markers are taken with large effects.	Meuwissen <i>et al.</i> , 2001
10.	Bayes C	Helps in the computation of additive genetic worth of the sample where variable is unknown and to be calculated.	Habier <i>et al.</i> , 2011 <sup>[20]</sup>
11.	Bayes C $\pi$	Helps in the computation of additive genetic worth of the sample where variable is known and value is reserved fixed.	Habier <i>et al.</i> , 2011 <sup>[20]</sup>
12.	RKHS	Captures associated effects which are non-additive of nature either parametrically or non-parametrically.	De Los Campos <i>et al.</i> , 2010 <sup>[21]</sup>
13.	Random Forest	Utilized for very high dimensionality and hypercomplex data; providing a flexible and easy to use solution.	Holliday <i>et al.</i> , 2012 <sup>[22]</sup>
14.	Support Vector Machine regression	Powerful in identifying understated patterns for a complex set of data.	Long <i>et al.</i> , 2011 <sup>[23]</sup>

15.	Adaptive LASSO	It possesses oracle properties which is computationally striking.	Zou <i>et al.</i> , 2006 <sup>[24]</sup>
16.	Elastic NET	An extension of LASSO utilized for high dimensional and complex datasets.	Ogutu <i>et al.</i> , 2012
17.	ADAENET	It combines properties of adaptive LASSO and ENET to enhance solidity.	Ogutu <i>et al.</i> , 2012

## GS in various crop improvement programmes

### Role of GS in improvement of yield and related traits

With the ever-increasing rise of global population there is an urgent requirement for substantial increment in the productive potential of crops as high as 70% from the present production standards. Genomic prediction accuracy ranged for a very complex trait like individual grain weight distribution in rice (Yabe *et al.*, 2018) <sup>[25]</sup> 0.28 to 0.81 for grain yield in soybean (Brown *et al.* 2019) <sup>[26]</sup>. Prediction accuracy for the traits like grain yield highly depends on the developed training population, the relation between training and breeding populations along with the model which was utilized to develop the training population as different set of models for the development of training population led to different prediction accuracy (Fristche-Neto *et al.*, 2018) <sup>[27]</sup>. The accuracy of a particular GS model is also highly influenced by the size of the training population and the affiliation of training population with the validation population (Lozada *et al.*, 2019) <sup>[43]</sup>. Biparental populations like RILs and doubled haploids provided better predictive performance as compared unrelated natural populations so such populations can be better utilized as training populations for the development of GS model (Liu *et al.*, 2018) <sup>[33]</sup>. GS can be utilized for germplasm enhancement in pre-breeding programmes to fasten the gene flow for unique traits from germplasm banks to elite lines. GS can also be greatly helpful while providing information prediction of hybrid performance (Crossa *et al.* 2017) <sup>[29]</sup>. NGS technologies based on genotyping by sequencing and genome wide SNP mapping have greatly facilitated GS owing to the unique advantages these technologies offer (Poland *et al.*, 2012) <sup>[42]</sup>. With the availability of genome wide distributed markers with hugely dense coverage can eventually lead to bring the cost comparable to those of phenotypic evaluation. (Jannink *et al.* 2010).

### Various factors governing the prediction accuracy of GS

#### Marker density

In majority of the GS models viz., RRBLUP, LASSO, machine learning based models like SVM etc. enhanced level of marker coverage leads to increased prediction efficiency but at the same time there is slow conjunction in case of methods like Bayes A, Bayes B, Bayes C $\pi$  etc. (Zhang *et al.*, 2017) <sup>[31]</sup>. Although, in many instances lower marker coverage like thousands in number with lower expense can lead to the production of similar results (if there is presence of significant LD among the markers) which are achieved at the higher marker density thus reducing the total cost of the GS and making it more accessible. In most of the breeding programmes it becomes very difficult to have very high coverage of markers in the genome as it will lead to significant increase in the total cost which is an immense constrain in most of the breeding programmes as like any breeding programmes here also economy is an important aspect for the improvement in any character. Therefore, there is a serious dichotomy to decide the optimum number of markers to keep a balance between the economic aspect of the programme and maintaining the efficiency of the model. Hence, it is suggested to have a moderate coverage with keeping a minimum of 2000 SNPs such that prediction

efficiency is not affected greatly (Abed *et al.*, 2018) <sup>[32]</sup>.

#### Population size

Population size is one of the important factors governing the success of any breeding programme be it traditional breeding, conventional MAS or models like genomic selection. In case of genomic selection deciding the effective size of training population is very crucial as a smaller size of this will lead to reduced accuracy of prediction values since there will be an inefficient estimation of the marker effects which will cause the reduced prediction accuracy. It has been observed in many studies that higher size of training population led to higher prediction accuracy, it was indicated that for a better GS model with good genomic predictions size of the training population should be at least three to five times higher than the validation population (Liu *et al.*, 2018) <sup>[33]</sup>. However, it has also been observed that if training population and breeding populations are related then better prediction accuracies can be achieved without resorting to larger size of training population. As in case of most of the programmes training and breeding sets are related, thus a higher prediction accuracy is achievable without increasing the size of the training population and hence maintaining the cost of the GS to be economical and accessible (Meuwissen, 2009) <sup>[37]</sup>.

#### Heritability of the trait

Heritability of the trait in question also a responsible factor governing prediction accuracy in a GS model (Hayes *et al.*, 2009) <sup>[34]</sup>. Heritability as a definition signifies the portion of total variance which is under genetic control (Lush, 1945). Several studies suggested that improvement under genomic selection for a trait is highly influenced by the heritability of that particular character. In majority of the occasions, it has been observed that trait with higher values of heritability provides better prediction accuracy as compared to traits with lower heritability and vice-versa. Usually, characters which are significant agronomically exhibits heritability values of moderate magnitude. It was also observed that as compared to simply inherited traits, in case of traits with complex interaction with the external environment heritability played the crucial role where increase in heritability led to better prediction accuracies for the traits (Zhang *et al.*, 2017) <sup>[31]</sup>. When heritability measures are less then and traits exhibit complex inheritance pattern, the performance of Bayesian methods and BLUP spinoffs provided much better performance in terms of selection accuracy as compared to other methods (Poland *et al.*, 2012; Lozada *et al.*, 2019) <sup>[42, 43]</sup>. However, several novel techniques are helpful for simultaneously tackle the challenges of low heritability and missing observations. Approaches like multi-trait selection can be very useful for employing EBVs from models like BLUP and its spinoffs which can result into higher prediction values and can be used for improvement of traits which possess low heritability (Slater *et al.*, 2016) <sup>[44]</sup>.

#### Minor allele frequency

Frequency of minor allele also plays an important role in the improvement of a trait under GS. Even with large marker coverage in the genome there are instances of decrease in the prediction accuracy after a point, it is due to the frequency of

minor allele in the population being to less. Studies are conducted with varying marker coverage with lower and higher frequency of alleles with smaller effects. Results suggested that utilizing a lower coverage of SNP chips with selection of less frequent markers which have large effects can be very useful and provide much better results in terms of prediction accuracy as compared to highly dense marker coverage with lesser number of minor alleles (Zhu *et al.*, 2017) <sup>[45]</sup>. Therefore, it is always advisable to utilize high quality of SNP genotyping data which possess minor allele frequency at least more than 0.1 to attain better estimates of genomic prediction values (Hickey *et al.*, 2012) <sup>[46]</sup>.

#### Role of GS in improvement for biotic stress tolerance

Climate change and intensive agriculture led to the danger of development of biotypes and pathotypes of different insect pests and diseases (Fones *et al.* 2020) <sup>[47]</sup>. Against so many diseases there are several reports of evolution of virulent pathotypes leading to breakdown of available resistance (Kumar *et al.* 2021) <sup>[48]</sup>. Therefore, it requires urgent attention from breeders in terms of identification of new and reliable sources of resistance and their incorporation in the available elite lines. Marker assisted backcross breeding is one of the widely employed method for introgressing different resistance genes from enriched germplasm sources to agronomically improved cultivars at least for the traits which are qualitatively controlled. Although, these methods have quite difficulty while development of lines with improved horizontal resistance which is controlled by many genes each with very little effect on the disease resistance. GS can be very useful for improvement of crops for disease resistance where resistance is polygenically controlled and shows quantitative inheritance. The genomic prediction accuracies for various important diseases of wheat were observed to be ranging from 0.1-0.8 in several studies reported earlier (Mirdita *et al.* 2015, Juliana *et al.* 2017) <sup>[49, 50]</sup>. Various studies utilizing GS for development of resistance against important diseases in agronomically valuable crops reported, such instances include stem rust of wheat (Rutkoski *et al.*, 2011) <sup>[51]</sup>; fusarium head blight resistance (Arruda *et al.*, 2015) <sup>[52]</sup>; blast and bacterial blight of rice (Balimponya, 2015) <sup>[53]</sup>; northern corn leaf blight (Technow *et al.*, 2013) <sup>[54]</sup>; phytophthora resistance in soybean (Rolling *et al.*, 2020) <sup>[55]</sup> etc. In many cases such as resistance against fusarium head blight resistance in barley quite high prediction accuracy of 0.72 was achieved.

#### Role of GS in improvement of quality of various crops

Inheritance of quality traits being complex varies greatly few of those are controlled by very few genes while others are controlled by polygenes with large influence of environment on the expression of the traits (Laidig *et al.*, 2017) <sup>[56]</sup>. Genomic selection applied for traits like end use quality in wheat which resulted a high prediction accuracy of 0.62 for mixing time (Battenfield *et al.*, 2016) <sup>[57]</sup>. It was also revealed that GS may become far more efficient than conventional MAS in terms of prediction accuracy for various traits in soft wheat dictating it to be far more rewarding in breeding applications (Heffner *et al.*, 2011) <sup>[58]</sup>. Quality traits like protein and oil content are popular to be negatively associated with productivity hence breeding for such traits always lead to some amount of compromise for yielding ability of the crops (Lam *et al.*, 1996) <sup>[59]</sup>. Genomic

selection involving multi-trait for such traits like protein content, dough making quality and grain yield have been observed to be efficient to breed for better quality without compromising for yield levels (Michel *et al.* 2019) <sup>[17]</sup>. In crops like cotton genomic prediction has been employed for various quality traits like fibre length, fibre strength and the yield of lint which resulted in very high prediction accuracies when genomic and pedigree information combined to build a model (Li *et al.*, 2022) <sup>[61]</sup>. There are various different factors which influence prediction accuracy of GS model while utilizing it for improvement of a quality trait. These include statistical model which is employed such as GBLUP or RRBLUP, frequency of the minor allele, genetic construction and heritability of the particular trait (Zhang *et al.*, 2019) <sup>[62]</sup>. Traits like protein content and ergosterol content have been utilized for genomic selection which showed encouraging results with virtuous prediction accuracies ranging from 0.4-0.8 (Nielsen *et al.*, 2016) <sup>[63]</sup>. Various such studies indicated that employment of GS for evaluation of large number of lines and cultivars has tremendous potential which will help to overcome the requirement of expensive and labour-intensive phenotypic assessment (Schmidt *et al.* 2016) <sup>[64]</sup>.

#### Implication of GS in breeding for climate resilience crops

Intensive agricultural practices along with the breeding activities to develop superior high yielding cultivars without taking factors like trait and genotypic diversity into consideration while preparing a breeding programme especially in the post green revolution era led to the event of genetic erosion leading to bottleneck and genetic vulnerability (Pingali, 2012) <sup>[65]</sup>. Breeding under such high resource intensive environments had resulted in loss of certain valuable alleles which helped in adaptation and tolerance to various stress situations (Brown, 2003) <sup>[66]</sup>, making the crops highly vulnerable and severely under prepared for threats like climate change and emergence of new diseases and pests. QTLs for several drought stress adaptive traits have been identified and transferred such traits include ABA accumulation (Rahman *et al.*, 2011) <sup>[67]</sup>, accumulation of sugars in the cell and their storage and distribution in various plant organs (Salem *et al.*, 2021) <sup>[68]</sup>, crop canopy temperature (Lopes *et al.*, 2014) <sup>[69]</sup>, delaying senescence (Borrell *et al.*, 2014) <sup>[70]</sup> and physiology and architecture of rhizospheric regions (Christopher *et al.*, 2013) <sup>[71]</sup>. These QTLs are being cloned utilizing various high-throughput technologies which can deliver innovative prospects for incorporation of resistance against such abiotic stresses and precise identification important genomic regions which confer such resistance in different crops (Salvi *et al.*, 2007) <sup>[72]</sup>. Recent advancements in the advents of genomics and sequencing technologies like NGS and TGS will be greatly useful for dissecting effect of climate change on crop phenotype which will further assist in development of resilience against severe climatic changes occurring throughout the globe and making our crops future ready (Kole *et al.*, 2015) <sup>[73]</sup>.

#### Utilization of genomic selection in horticultural improvement

Horticultural crops including various fruits and vegetables are important fractions of our entire dietary system which helps in ensuring overall nutritional security of a human being. There are several obstacles are encountered while breeding for fruits which include the span of vegetative phase and higher levels

of heterozygosity, in such circumstances GS with an efficient model can emerge out as a superior selection strategy in terms of accuracy and overall efficiency for prediction of such traits imbibed into a complex genetic system (Budhlakoti *et al.*, 2022) [73]. Jung *et al.* (2022) [75] attempted to evaluate genomic prediction of large no. of apple accession for 30 different quantitative traits and observed a varying prediction accuracy ranging from 0.18-0.82 for various traits under different environmental conditions revealing a significant potential of GS for improvement of those traits. In case of winter squash predictive ability for various fruit quality traits were evaluated which found to be low to moderate in terms of efficiency (Hernandez *et al.*, 2020) [76]. It has been observed that among various models available for GS ssGBLUP expressed higher prediction accuracy even better than GBLUP for different

traits associated with fruit quality parameters in citrus (Imai *et al.*, 2019) [77]. Kumar *et al.* (2019) [78] evaluated a population of 550 F1s of pear for several fruit traits, prediction efficiency for the different traits ranged from 0.32-0.6 with the average hovering around 0.42 indicating usefulness of GS in evaluation of fruit related traits. Breeding for horticultural crops is quite complex and the produce quality is associated with so many parameters such as shelf life, sugar metabolism, fruit formation and ripening process and the physiology associated with it etc. Though, omics-based approaches like GS can be very useful in breeding for improvement of such traits specially when the nature and pattern of the trait expression is such complicated (Mathiazhagan *et al.*, 2021) [79].

## Genomic selection

### Genomic selection for various important traits in different crops

Crop	Trait	Population	Model	Prediction accuracy	Reference
Rice	Grain filling traits	128 Japanese rice cultivars	GBLUP and PLS	Percent filled grains, variance of filled grain weight and filled grain avg. weight predicted with 0.30, 0.53 and 0.28 accuracy.	Yabe <i>et al.</i> 2018 [25]
	Various agronomic traits	A panel of 115 rice varieties	GBLUP, LASSO, PLS, NN, SVM and RKHS	Genomic prediction would lead to 35.5% increase in grain yield, 30.21% in panicle number and 23.3% in 1000 kernel weight.	Xu <i>et al.</i> 2018 [81]
	Grain yield and yield attributes	A panel of 3000 rice varieties	GBLUP	Very high prediction accuracy achieved ranging from 0.35-0.92.	Cui <i>et al.</i> 2020
	Grain yield, tiller number, 1000 kernel weight and kernel number	210 RILs (F9)	2D-BLUP	Metabolomic secondary traits can be utilized to increase in the prediction accuracy of traditional traits.	Wang <i>et al.</i> 2020 [83]
Wheat	Grain yield	Six different populations of size 52, 38, 31, 20, 13 and 242	RRBLUP, PLSR, RKHS, ELNET and RF	Moderately accurate predictive ability of the GS model.	Dunckel <i>et al.</i> 2017 [84]
	Baking quality	840 genotypes of winter wheat	RR-BLUP and WBLUP	Prediction accuracy for different characters ranged 0.38-0.63.	Michel <i>et al.</i> 2018
	Grain yield and quality traits	A population of 170 cultivars and 154 DH lines	RR-BLUP, G-BLUP, BayesA, BayesB, Bayesian LASSO and RKHS	Prediction accuracy for grain yield was 0.5-0.8.	Haile <i>et al.</i> 2018 [86]
	Grain yield and quality	A population 57 fixed lines of bread wheat	RR-BLUP, Bayes A, Bayes B, Bayes ridge regression and Bayes LASSO	Construction of a selection index based on yield, maximum resistance with extensibility can be useful for improvement of both traits.	Yao <i>et al.</i> 2018 [87]
	Grain yield	3 different populations with a total of 3282 genotypes	Mixed model BLUPs	Incorporation of data on secondary traits led to 146% increase in terms of predictions for grain yield by three cycles.	Sun <i>et al.</i> 2019 [88]
	Grain quality and yield	666 soft winter-wheat genotypes	RRBLUP, Bayes B, Bayes A, Bayes Lasso and Bayes C	Prediction accuracy for different characters ranged from 0.52-0.81 with 9 varying GS models.	Sandhu <i>et al.</i> 2021 [89]
	Fusarium head blight resistance	One panel of 237 lines and another of 367 breeding lines	ST-GBLUP and MT-GBLUP	MT-GBLUP models could lead to increase in prediction accuracy by two times during the early stages.	Gaire <i>et al.</i> 2022 [90]
Maize	Drought tolerance	240 lines	RR, LASSO, EN, Bayes A, Bayes B, RF and RKHS	SNPs for drought tolerance were identified to be used for resilience breeding.	Shikha <i>et al.</i> 2017 [91]
	Grain yield and yield attributes	212 RILS and 304 F <sub>2:3</sub> lines	GBLUP and RBLUP	Inclusion of non-additive effects led to increased predictive ability.	Liu <i>et al.</i> 2019 [92]
	Haploid induction rate	159 inducer lines	GBLUP	Average prediction accuracy ranged from 0.7 with overall ranging from 0.45-0.89.	Almeida <i>et al.</i> 2020 [93]
Sorghum	Biomass yield	453 diverse lines	GBLUP	Multi trait incorporated GS increased the prediction accuracy by 50% over single trait.	Fernandes <i>et al.</i> 2018 [94]
	High biomass for	200 genotypes of sorghum	BayesA, BayesB,	Prediction accuracy for various traits	Oliveira <i>et al.</i>

	bioenergy production		BayesC $\pi$ , BayesLasso, BRR and RRBLUP	ranged from 0.35-0.78.	2018 <sup>[95]</sup>
	Grain antioxidants	95 sorghum lines with 19 RILs	GBLUP, BRR, Bayesian LASSO and BayesB	Prediction accuracy for different traits ranged from 0.49-0.58.	Habyarimana <i>et al.</i> 2019 <sup>[96]</sup>
	Physiological characters	869 sorghum lines	BN, PBN, DBN, MTr-GBLUP and MTi-GBLUP	Prediction accuracies ranged from 0.46-0.75 for various traits.	Santos <i>et al.</i> 2020 <sup>[97]</sup>
Soybean	Soybean cyst nematode resistance	A panel of 282 genotypes	RRBLUP, BLR, BCP, SVM and RF	Prediction accuracy in various models for the trait ranged from 0.48-0.75 with a mean of 0.62.	Bao <i>et al.</i> 2014 <sup>[98]</sup>
	Yield and seed protein	1284 F6 lines	GBLUP	Average prediction accuracy for traits varied from 0.46-0.62.	Duhnen <i>et al.</i> 2017 <sup>[99]</sup>
	Yield and seed traits	483 lines of soybean	RRBLUP	Prediction accuracy for various traits observed to be ranging 0.26-0.81.	Brown <i>et al.</i> 2019 <sup>[26]</sup>
	Chlorophyll content	172 lines	RRBLUP, GBLUP, RF, BLR and SVM	Prediction accuracy observed for the trait 0.31(RRBLUP)-0.74(LASSO).	Ravelombola <i>et al.</i> 2019 <sup>[101]</sup>
	Yield and yield attributes	A panel of 250 soybean lines	RRBLUP	High prediction accuracy of 0.64 for various traits indicating traits can be selected through molecular breeding.	Ravelombola <i>et al.</i> 2021 <sup>[102]</sup>
Canola	Yield and yield attributes	A panel of 475 diverse lines	RRBLUP	For different traits prediction accuracy varied from 0.39-0.61.	Jan <i>et al.</i> 2016 <sup>[103]</sup>
	Seed traits, maturity traits and lodging resistance	950 F1 hybrids	RRBLUP	Prediction accuracy ranged from 0.29-0.81; highest for seed oil content and lowest for germination.	Jan <i>et al.</i> 2016 <sup>[103]</sup>
	Vigour, flowering, resistance to black leg and yield	400 genetically diverse lines	GBLUP	Prediction accuracy ranged from 0.37-0.8 for most of the traits.	Raman <i>et al.</i> 2018 <sup>[104]</sup>
	Black leg resistance and seed quality	202 genotypically diverse lines	GBLUP	Prediction accuracy varied from 0.29-0.69 for different characters.	Fikere <i>et al.</i> 2020 <sup>[105]</sup>
	Sclerotinia stem rot	187 genetically diverse lines	RRBLUP, Bayes C and BRR	Prediction accuracy for four different traits ranged 0.4-0.64.	Roy <i>et al.</i> 2022
	Seed yield and other agronomic traits	950 hybrids	GBLUP and RKHS	Prediction accuracy ranged from 0.247-0.717 for different traits.	Knoch <i>et al.</i> 2021 <sup>[107]</sup>
Tomato	Agronomic traits under high temperature stress	A population of F4 lines	RRBLUP	Prediction accuracy for yield was 0.729 and for soluble solid content was 0.715.	Cappetta <i>et al.</i> 2021
Pepper	fruit length, shape, width, weight, and pericarp thickness	351 genotypes	GBLUP, RRBLUP, BL, BayesB, Bayes C, EBL, RKHS and RF	Prediction accuracies for various traits ranged from 0.32 (fruit length)-0.48 (fruit weight).	Hong <i>et al.</i> 2020 <sup>[109]</sup>
Apple	Fruit quality	1120 F1s	RRBLUP and Bayesian LASSO	Very high average prediction accuracy of 0.7-0.9 for different traits.	Kumar <i>et al.</i> 2012 <sup>[110]</sup>
	Fruit texture	537 diverse genotypes	RRBLUP	Prediction accuracy ranged from 0.01-0.81 in different populations.	Roth <i>et al.</i> 2020 <sup>[111]</sup>
	Yield and yield related traits	269 diverse genotypes	RF, Bayes C, RKHS, GBLUP and MTM.UN	Average prediction efficiency varied from 0.18-0.88.	Jung <i>et al.</i> 2022 <sup>[75]</sup>
Peach	Fruit weight and quality traits	1147 F1s	GBLUP	A high prediction efficiency of 0.6-0.72 was achieved.	Biscarini <i>et al.</i> 2017 <sup>[113]</sup>
Arabidopsis	Growth under different environments	67 genetically distinct accessions	RRBLUP	Prediction accuracy for growth under different environments varied from 0.33-0.51.	Tong <i>et al.</i> 2020 <sup>[114]</sup>
Cassava	Yield traits	888 genetically diverse genotypes	GBLUP, RRBLUP, LASSO, BLASSO, IBLASSO and RKHS	Prediction accuracy varied from 0.457-0.57 for different traits under different models.	Andrade <i>et al.</i> 2019 <sup>[115]</sup>
Potato	Late blight and common scab resistance	273 and 370 genetically diverse genotypes for late blight and scab respectively	BRR and Bayes B	Prediction accuracy varied from 0.4-0.76 for two traits under different models.	Rodriguez <i>et al.</i> 2018 <sup>[116]</sup>
	Carotenoid content and other traits	632 clonal lines	GBLUP and RRBLUP	Prediction accuracy varied from 0.12-0.52 for different under different models.	Esuma <i>et al.</i> 2021 <sup>[117]</sup>

## Conclusion

Genomic selection has revealed humungous potential in terms of increasing genetic gains in crop plants recently. Along with the arrivals of technologies like next generation sequencing it has become very feasible to sequence the entire genome of various crop plants at a relatively lower expense. Advancements in the development of highly dense marker technologies can further strengthen the accuracy of such GS

models. Although, there is a great scope for further refinements in terms of successful implementation of the models. The principal barrier in this regard is the accessibility for implementing such technology and the overall expense associated with that. Improvements in terms of developing training populations under highly managed and well controlled conditions can greatly increase the prediction efficiency leading to higher genetic gains from a breeding

programme. There is an urgent need for development of an efficiently designed programme utilizing currently available technologies in arena of genomic assisted breeding. The various technologies linked with the genomics and genomics assisted breeding are evolving at such a pace that it can become much more accessible and cost effective to be successfully employed in due course of time.

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