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RESEARCH ARTICLE

Identification of superior parental lines based on BLUP breeding values in potato (*Solanum tuberosum* L.)

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Abstract

Identification of superior parental lines require phenotypic or genotypic characterization of the germplasm, which is time consuming and laborious. The advanced potato breeding clones including control varieties were evaluated under field conditions to identify the suitable parental lines for tuber yield, late blight and specific gravity based on estimated breeding values using historical data as training population during 2008-09 to 2019-20. Pedigree of all the clones was searched to a depth of 5-6 generations. The mixed model fitting using REML was true. The minimum and maximum values for total tuber yield, late blight area under disease progress curve (AUDPC) and specific gravity were 28.33-732.2, 0-1846.25, 1.043-1.087, respectively. Pedigree had 161 founders out of total 759 individuals and the pedigree matrix showed relationship in 1,09,057 pairs. Heritability estimate was highest for specific gravity (0.77) followed by late blight AUDPC (0.49) and total tuber yield (0.24). The estimate of the BLUP breeding values (EBVs) for total tuber yield were highest for Kufri Mohan, Kufri Pukhraj, Kufri Khyati, SM/14-342 and Kufri Pushkar while SM/10-05, SM/09-99, Kufri Girdhari, SM/11-120 and Kufri Karan for late blight resistance, and Kufri Chipsona-1, SM/14-225, SM/14-229, SM/10-220 and SM/09-153 for specific gravity were the best genotypes. The prediction accuracy measured as correlation between EBV and observed phenotype score for specific gravity (0.97) was near perfect, very high for late blight AUDPC (0.75), and high for total tuber yield (0.55). The prediction bias measured as regression coefficient and scatter plots of observed phenotype values on EBVs was nil to low for specific gravity andlate blight AUDPC, while underestimation was observed for total tuber yield. Overall, the prediction accuracies for all the three traits were very good and selection of parental lines using Best Linear Unbiased Prediction breeding values could result in enhanced genetic gain in potato breeding.

Keywords: Estimated breeding values, late blight, pedigree BLUP, specific gravity, tuber yield

Introduction

Potato is the third most important global food crop and is consumed both as fresh food as well as processed products. The crop was domesticated around 10000 years ago in Andean region of Peru, from where it spread throughout the globe including India. Cultivated tetraploid potato (*Solanum tuberosum* L.) was improved through introgression of genes for key traits from many wild *Solanum* spp. Introgression of genes drove the early improvement of potato as well as adaptation of both upland (*S. tuberosum* group Andigena) and lowland (*S. tuberosum* groups Chilotanum and Tuberosum) groups (Bethke et al. 2019; Ortiz 2020).

Development of new cultivars is a continuous process in breeding and more than 4000 potato cultivars have been developed globally (Sood et al. 2017). Genetic variation is important for selection and development of new recombinants for better genetic gain. However, the close parental selection in potato breeding has resulted in narrow genetic base of cultivated genepool (Li et al. 2018). Many of the genes in modern bred potato cultivars trace to few important cultivars of 19th and early 20th century (Ortiz 2020). In potato breeding programmes, the phenotypic recurrent selection is a commonly employed breeding strategy. In order to reduce the number of breeding clones, visual selection is practiced in early clonal generations to reduce

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the number of clones for their through assessment for tuber yield and quality traits (Jansky 2009; Slater et al. 2014).The practice of intense visual selection in potato have been found to be ineffective due to strong environmental influence on most visual traits. This leads to the elimination of several superior clones along with inferior clones (Bradshaw and Mackay 1994; Slater et al. 2014).

The Best Linear Unbiased Prediction (BLUP) procedure has been widely used in the prediction of genetic merit of animals (Henderson 1984) and has been extended to plant improvement but with limited enthusiasm (Bernardo 2002; Piepho et al. 2008; Slater et al. 2014; Vineeth et al. 2022). The parental lines selection can be improved by the estimation of breeding values using BLUP (Bauer et al. 2006). In contrast to the standard BLUP procedure, the estimated breeding values/predicted BLUP values are characterized by including pedigree information in the mixed model equations (Bauer and Leon 2008). BLUP is an advanced biometrical technique which can handle large, unbalanced data sets where information from different trials can be merged to estimate BLUP breeding values. Year and environment information can be fitted as fixed effects in the BLUP model (Piepho et al. 2008). There are very few reports of use of BLUP breeding values for prediction of genetic merit of breeding lines in potato breeding (Slater et al. 2014; Slater et al. 2016; Endelman et al. 2018; Sood et al. 2020a; Sood et al. 2020b). Thus, the study was carried out to assess the feasibility of BLUP breeding values based selection of parental lines in potato breeding in India for the first time.

Materials and methods

Advanced tetraploid potato breeding clones including varieties were evaluated for different agronomic parameters in preliminary yield trials in randomized complete block design at Central Potato Research Institute, Regional Station, Modipuram, Uttar Pradesh, India during 2008-2020. The data on tuber yield and specific gravity was compiled for different year trials of F_1C_6 and F_1C_7 clones. The late blight data was considered from F_1C_4 to F_1C_7 trials conducted at Central Potato Research Institute, Regional Station, Kufri, Shimla for late blight resistance breeding.The trials were conducted in randomized complete block design with 4 rows of 3m length and a spacing of 60×20cm. Modipuram is located at an altitude of 300 m amsl and caters potato research requirements of Central Indo-Gangetic Plains of India. The data on total tuber yield was recorded for all the advanced breeding clones, while specific gravity data was recorded on selected clones only. Total tuber yield data was recorded on plot basis and converted in quintals per hectare. Specific gravity was recorded as weight of tubers in air compared with their weight in water. Around 2.5kg tubers of each clone were used for assessing the specific gravity. The late blight resistance was recorded as Area Under Disease Progress Curve (AUDPC) based on 4 readings during the season at Kufri (Forbes et al. 2014). The observations were recorded on weekly intervals after first appearance of symptoms till 100% disease observed in susceptible control variety. Kufri is a hot spot for late blight screening and is located at an altitude of 2500 m amsl. For total tuber yield (TTY), the phenotypic data of 416 entries was used, while the number was 198 and 83 for late blight resistance and specific gravity. The data was merged in a single excel file for all the three traits along with year information.

The parentage of all the breeding clones as well as control varieties were searched in the local pedigree registers, potato pedigree database (van Berloo et al. 2007) andPotato Journal (Indian Potato Association). Efforts were made to get information on parents, grandparents and great grandparentsof each breeding line and varieties for more connections in the pedigree relationship matrix.There were total 579 individuals including 161 founders i.e. individuals with no parental information in the pedigree.

A linear mixed model, pedigree BLUP was fitted for each trait separately to estimate the BLUP breeding values (EBVs) as described earlier by Slater et al. (2014) and Sood et al. (2020b).

Since potato is an autotetraploid, the pedigree relationship matrix was worked out considering 10 per cent double reduction (Slater et al. 2014).

REML was used to estimate variance components and predict estimated breeding values (EBV's) for each advanced breeding clone for each trait. The heritability was calculated using pedigree relationship matrix as h^2 = [genetic variance/ (genetic variance + environmental variance)].

For prediction accuracy, 50 breeding lines for tuber yield and late blight and 25 breeding lines for specific gravity were sampled for cross validation for 50 replicates. Rest of the breeding lines were used as training population in each case. Year information was fitted as fixed effect in the model. The prediction accuracy was assessed as Pearson's correlation between the observed phenotypes and EBVs. Prediction bias was also calculated as the slope of regression of observed phenotypes on EBVs as well as scatter plots of observed phenotypes vs EBVs.

The mixed model analysis was carried out in R programming language (R Core Team 2018) using "Sommer" package (Covarrubias-Pazaran 2016). The package "AGHmatrix" (Amadeu et al. 2016) was used for construction of A matrix.The BLUP breeding values and heritability were estimated using mmer functionin "Sommer". Prediction bias was estimated using ggplot2 library and lm function, and heatmap of A matrix was made using package "superheat" (Barter and Yu, 2018).

Results and discussion

Potato is an auto-tetraploid clonally propagated crop. The breeding cycle in potato is longer than usual and takes around 12-15 years for the release of a new cultivar (Sood et al. 2020c). Therefore, it is pertinent to choose the right parents for hybridization and select the right progenies in different clonal generations without losing important genotypes. It is well known that the selections are based on visual observations in early clonal generations *i.e.,* F_1C_1 to F_1C_3 in potato breeding, making it categorical to lose some important clones in order to reduce the number of clones for advanced generations testing (Jansky 2009; Bradshaw et al. 2009). Use of pedigree or genomic BLUP could be a wise choice for selection of clones with best additive genetic values for enhanced genetic gain over time in potato breeding. Besides, it is difficult to generate phenotypic data on most traits in potato breeding lines compared to other major crops due to maintenance problems, low rate of multiplication and fast degeneration of tubers (Habyarimana et al. 2017). Thus, the use of historical phenotype data on major yield, biotic stresses and quality traits could be best utilized in pedigree or genomic BLUP or in combined pedigree genomic models for prediction of genetic merit of breeding lines without their actual phenotyping for complex traitswith low heritability. The study was thus carried out to assess the BLUP based predictions of breeding values and their accuracy with observed phenotypes for three important traits i.e. total tuber yield, late blight resistance and specific gravity in potato breeding.

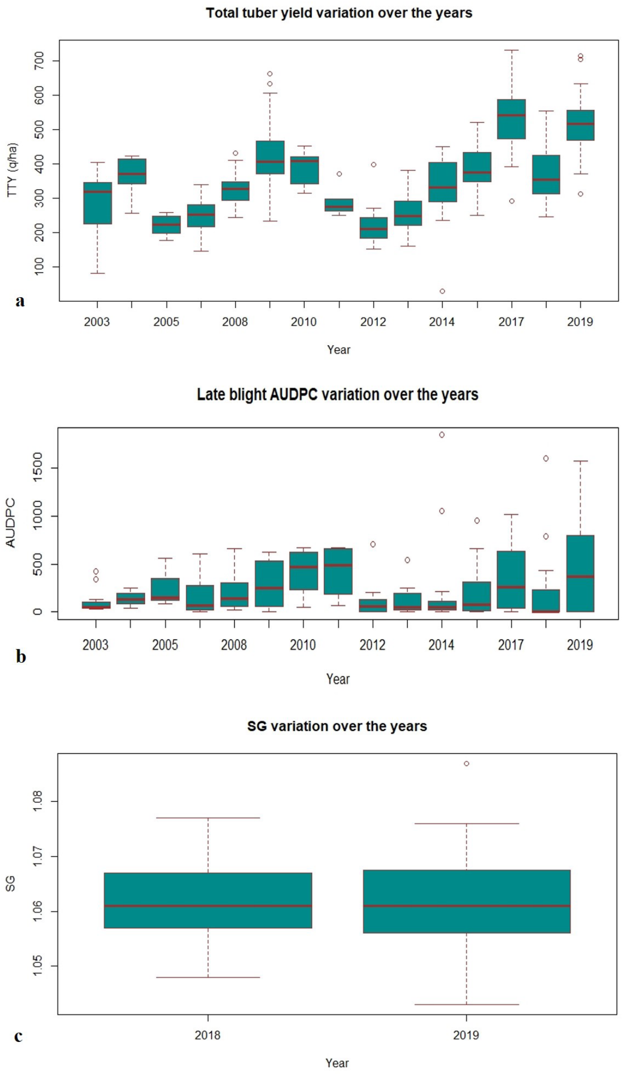

Fig. 1. **Variation in total tuber yield, late blight AUDPC score and specific gravity over the years, a) Total tuber yield (q/ha), b) Late blight AUDPC score and c) Specific gravity**

The linear mixed model fit by REML statistics are presented in Table 1. The model fit was good and convergence was true for all the three traits under study. The observed phenotype for total tuber yield, late blight AUDPC andspecific gravity showed wide variation among the advanced breeding clones (Fig. 1). The minimum, maximum and average values for total tuber yield were 28.3q/ha,732.2q/ha and 385.37q/ha, respectively (Table 2). The AUDPC for late blight varied from 0 to 1846.25 with an average of 244.41. The range of variation for specific gravity of advanced breeding clones and control varieties was 1.043-1.087 with an average of 1.061 (Table 2). The breeding lines showed wide variation as is evident from standard deviation for all the three traits under study (Table 2). The variation for tuber yield and late blight AUDPC score was high while specific gravity observed low variation due to more major emphasis on yield and late blight resistance rather

Table 1. Linear Mixed Model fit by REML

	logLik	AIC	BIC	Method	Converge
Total Tuber yield	-116.30	236.61	244.67	MNR	TRUE
Late blight AUDPC score	-26.18	56.36	62.93	MNR	TRUE
Specific gravity	-25.36	54.72	59.56	MNR	TRUE

logLik = Loglikelihood; AIC =The Akaike information criterion; BIC =The Bayesian information criterion

Table 2. Basic statistics of potato breeding lines evaluated in Modipuram, Uttar Pradesh from 2008-2020

Trait	Min.	Max.	Mean	SD
Total Tuber yield (q/ha)	28.33	732.2	385.37	118.88
Late blight resistance (AUDPC)	0	1846.25	244.41	323.92
Specific gravity	1.043	1.087	1.061	0.008

Min.= Minimum value; Max. = Maximum value; SD = Standard deviation than dry matter in the breeding programme. The recent introduction of a threshold limit of minimum 18% dry matter for evaluation of advanced potato clones in multi-location trials in India shifted focus on selecting clones with high dry matter along with optimum yield and late blight resistance.

The genetic variance was high for specific gravity followed by late blight AUDPC score and total tuber yield in comparison to their respective environmental variances (Table 3)indicating that genetic factors have major role in the inheritance of specific gravity and late blight whereas total tuber yield is most affected by environmental factors. Accordingly, high heritability was recorded for specific gravity (0.77 ± 0.09), while moderate and low heritability were observed for late blight AUDPC score (0.49 ± 0.09) and total tuber yield (0.24 ± 0.06) (Table 3). High heritability for specific gravity and late blight corroborates with earlier findings of Slater et al. (2014), Enciso-Rodriguez et al. (2018), and Sood et al. (2020b). Yield is a complex trait and is a function of many component traits and is universally reported as a low heritable trait in many studies (Ticona-Benavente and da Silva Filho 2015; Sood et al. 2020b), but few studies also reported moderate to high heritability (Slater et al. 2014; Aliche et al. 2019; Ortiz et al. 2021). Low heritability for tuber yield in our study indicates that there is low geneticvariability for further gains in selectively breeding fortuber yield. Varying heritability estimates for total tuber yield in different studies could be attributed to evaluation sites and the materials used in the study (Ortiz et al. 2021).

Availability of precise pedigree information allows assessing relatedness among breeding clones, thus facilitating increasing the power of association genetics analysis. Deep pedigree information results in finding co-ancestry in pedigree analysis to quantify relatedness among breeding clones.The pair wise relationship among individuals was computed using pedigree relationship andis presented in the form of heatmap (Fig. 2). The heatmap of the pedigree relationship matrix showed good connection among most individuals (Fig. 2). It indicates that most breeding clones and varieties are related in ancestry.More connectedness in pedigree relationship matrix will result in

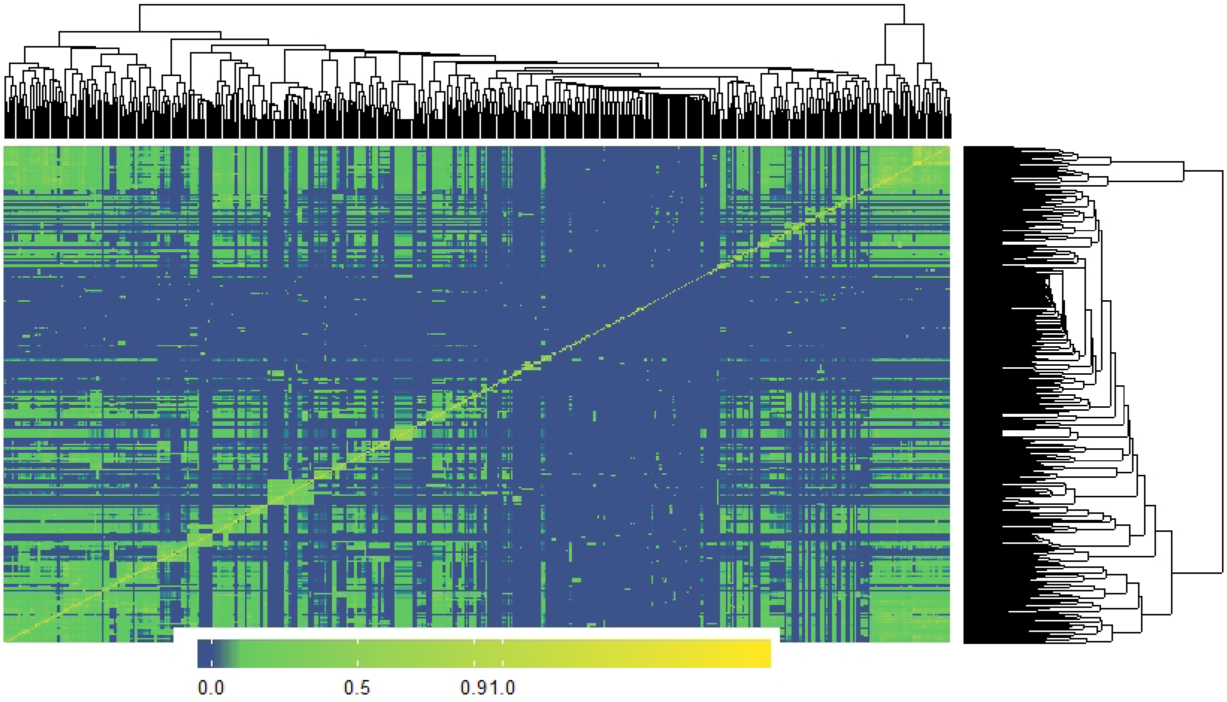

Fig. 2. Relationship among breeding clones depicted as heatmap of pedigree relationship matrix

Table 3. Variance components and heritability estimates of different traits (± s.e.)

Trait	σ_g^2	σ_e^2	h^2
Total Tuber yield	2395 ± 723.6	7635 ± 611.5	0.24 ± 0.06
Late blight AUDPC score	35116 ± 10403	36059 ± 4243	0.49 ± 0.09
Specific gravity	4.707e-05 ± 1.182e-05	1.450e-05 ± 4.574e-06	0.77 ± 0.09

σ_g^2–genetic variance;σ_e^2- environmental variance; h^2-Heritability better estimation of breeding values of advanced clones (Yu et al. 2017). Non-availability of deep pedigree information for more connections in the pedigree matrix, easy direct observations, a limited number of genotype and complexity of mixed model analysis are some of the reasons for limited use of pedigree based BLUP approach in crop breeding in comparison to animal breeding programmes (Piepho et al. 2008).

The selection based on BLUP breeding values have been shown to be superior to phenotypic selection (Aleta et al. 2004; Piepho and Möhring 2006; Piepho et al. 2007; Slater et al. 2014; Sood et al. 2020b). The size of training population however, affects the estimation of breeding values and prediction accuracy (Sverrisdóttir et al. 2018). The training population size was 366 for total tuber yield, 148 for late blight AUDPC score and 58 for specific gravity and rest were test/prediction candidates (Table 4). Since, the total number of advanced breeding clones were variable for each trait, the training population size too was variable (Table 4). The correlation between BLUP breeding values/ estimated breeding values of test/ prediction candidates and their observed phenotype values showed the prediction accuracy.The prediction accuracy varied from 0.55-0.97, high for all the three traits (Table 4). The prediction accuracy was highest for specific gravity (0.97 ± 0.003), followed by late blight AUDPC score (0.75 ± 0.01) and total tuber yield (0.55 ± 0.01) (Table 4).The results corroborates with earlier studies where high prediction accuracies were observed for specific gravity and late blight (Slater et al. 2014; Endelman et al. 2018; Sverrisdóttir et al. 2018;Sood et al. 2020b). High prediction accuracy for specific gravity and late blight could be attributed to high heritability of these traits coupled with robust phenotype data on all the breeding lines. Even though the heritability was low for tuber yield, the prediction accuracy was reasonable better for selection based on EBVs. Similar prediction accuracy for total tuber yield was reported earlier by Endelman et al. (2018) and Stich and Van Inghelandt (2018), however, low prediction accuracy was observed by us in our previous studies (Sood et al. 2020a; Sood et al. 2020b). Nearly perfect correlation of EBVs and observed phenotypes for specific gravity indicate that EBVs can be directly employed for selection of best breeding clones for specific gravity. However, the training population size was too small in the case of specific gravity and need further validation with more datapoints in the training population.

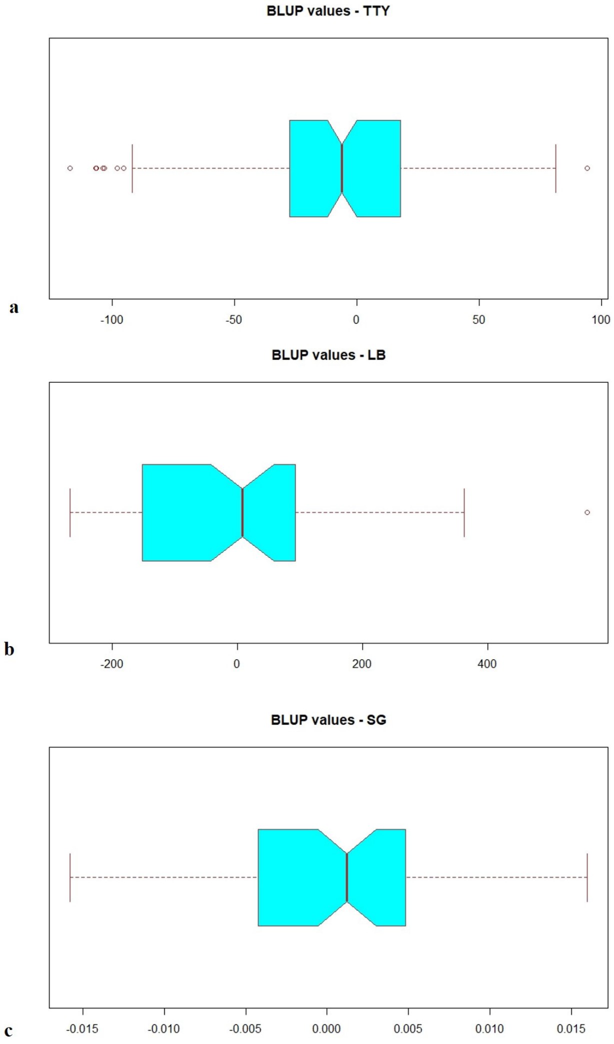

Fig. 3. Variation in BLUP values of breeding lines for total tuber yield, late blight AUDPC score and specific gravity

The selection of parental lines for high genetic gain in breeding require selection of breeding lines based on their BLUP breeding values/ EBVs. The advanced breeding lines along with control varieties were arranged in descending

Table 4. Training population size and Pedigree BLUP prediction accuracies for different traits

Traits	Pedigree BLUP Prediction Accuracy		
	Total data records	Training population size	$r_{ebv:opv}$*
Total tuber yield	416	366	0.55 ± 0.01
Late blight AUDPC score	198	148	0.75 ± 0.01
Specific gravity	83	58	0.97 ± 0.003

*values are mean ± s.e. for 50 individuals using 50 replicates for total tuber yield and late blight AUDPC score while 25 individuals using 50 replicates for specific gravity.

ebv-estimated breeding value; opv-observed phenotype value

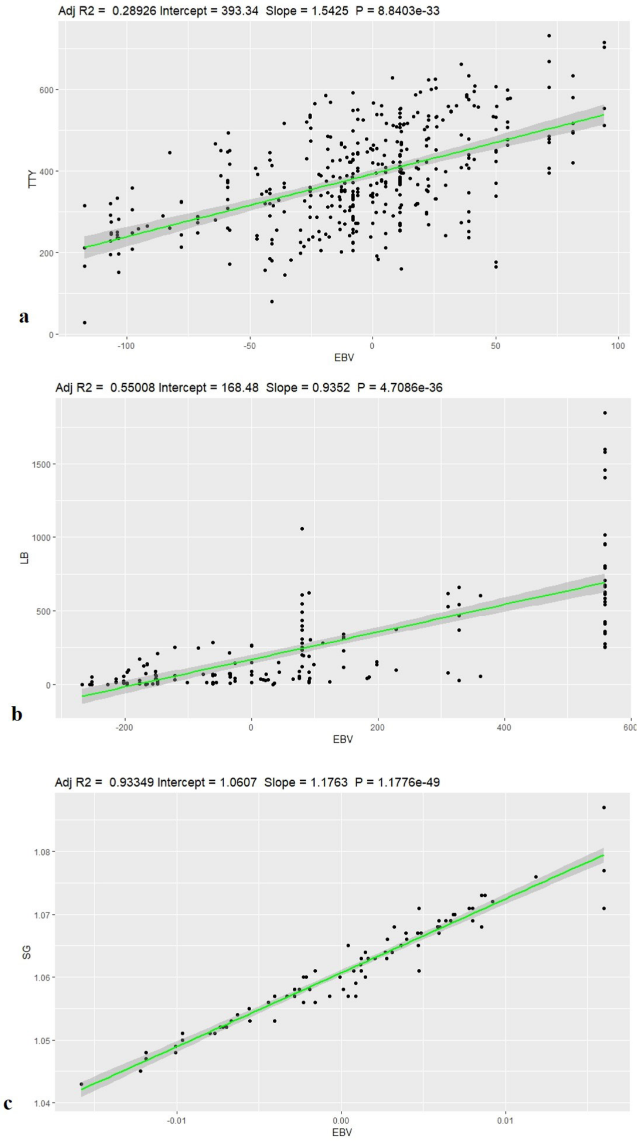

Fig. 4. Regression plots of observed phenotype value on estimated breeding value, a) Total tuber yield, b) Late blight AUDPC score and c) Specific gravity

order for total tuber yield and specific gravity and ascending order for late blight AUDPC score to select the best EBV lines. The top five lines for total tuber yield were Kufri Mohan, Kufri Pukhraj, Kufri Khyati, SM/14-342 and Kufri Pushkar. Based on EBVs of late blight AUDPC score, SM/10-05, SM/09-99, Kufri Girdhari, SM/11-120 and Kufri Karan were the best lines. Similarly, Kufri Chipsona-1, SM/14-225, SM/14-229, SM/10-220 and SM/09-153 were found promising for specific gravity (Supplementary Table S1 and Fig. 3). Four out of five top breeding lines for tuber yield and two out of five for late blight resistance were released cultivars. Similarly, the top most line for specific gravity was Kufri Chipsona-1, which is a released cultivar in the processing segment in India. However, none of the top most breeding lines were common across the traits.

In prediction bias, the deviation from 1 shows the over estimation or underestimation of EBV values in comparison to observed phenotypes. In order to check the bias in prediction, regression slope of observed phenotypes on EBVs was measured and goodness of fit was observed through scatter plots. The slope of regression values were close to 1 for late blight AUDPC scores (0.94 ± 0.06) and specific gravity (1.18 ± 0.04), while deviation was more for total tuber yield (1.54 ± 0.12) (Table 5). The scatter plots of observed phenotypes vs EBVs for all the three traits also depicted similar picture with specific gravity showing better goodness of fit *i.e.,* adjusted R^2 value (0.93), followed by late blight AUDPC score (0.55) and total tuber yield (0.29) (Fig. 4). The differences between observed phenotype values and EBVs were low for specific gravity and late blight in comparison to tuber yield in the scatter plots.

Table 5. Slope of regression/regression coefficients of observed phenotype values on EBVs

Traits	Regression coefficient*
Total tuber yield	1.54 ± 0.12
Late blight AUDPC score	0.94 ± 0.06
Specific gravity	1.18 ± 0.04

The success of BLUP based predictions in animal breeding could be replicated in crop breeding but it is important to train the model and test its accuracy first before its implementation in crop breeding programmes (Stich and Van Inghelandt 2018). The superior breeding lines can be selected as new clones for release as cultivars or parental lines in recombination breeding. The results of using pedigree BLUP in our study are encouraging for extension of BLUP based selections in potato breeding programme for high genetic gain in short time. We observed high prediction accuracy for specific gravity and late blight and reasonably good accuracy for tuber yield. Top breeding clones based on EBVs matched with observed phenotype data for respective traits indicating better selections based on BLUP breeding values for all the three traits. However, the combined selection for all the three traits together require a selection index based on EBVs of individual across multiple traits (Xu et al. 2012). Recently, the pedigree matrix has been replaced with genomic relationship matrix (GRM) in most studies due to reduced genotyping costs (Rodríguez-Ramilo et al. 2015; Endelman et al. 2018). The GRM provides more connectedness among the individuals in the matrix in comparison to pedigree relationship matrix, resulting better predictions (Sood et al., 2020a). Nevertheless, accurate and deep pedigree based EBVs too could be an effective strategy for parental selection in potato breeding until the marker information is generated on the breeding lines.

Authors' contribution

Conceptualization of research (SS); Designing of the experiments (SS, VB, SKK, D); Contribution of experimental materials (VB, SS, SKK, D); Execution of field/lab experiments and data collection (SS, VB, SKK, D, SSh, ML, MK); Analysis of data and interpretation (SS); Preparation of the manuscript (SS).

Supplementary materials

Supplementary Table S1 is provided.

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References

Aleta N., Ninot A. and Voltas J. 2004. Retrospective evaluation of parental selection in nursery tests of Juglans regia L. using a mixed model analysis. Silvae Genet., **53**: 26-33.

Aliche E.B., Oortwijn M., Theeuwen T.P.J.M. et al. 2019. Genetic mapping of tuber size distribution and marketable tuber yield under drought stress in potatoes. Euphytica, **215**: 186. https://doi.org/10.1007/s10681-019-2508-0.

Amadeu R.R., Cellon C., Olmstead J.W., Garcia A.A.F., Resende M.F.R. and Muñoz P.R. 2016. AGH matrix: R package to construct relationship matrices for autotetraploid and diploid species: A blueberry example. Plant Genome, **9**: 1-10. doi:10.3835/plantgenome2016.01.0009.

Barter R.L. and Yu B. 2018. Superheat: An R package for creating beautiful and extendable heatmaps for visualizing complex data. J.Comput. Graph Stat., **27**(4): 910-922.

Bernardo R. 2002. Breeding for Quantitative Traits in Plants. Stemma Press, Woodbury: 359.

Bauer A.M., Reetz T.C. and Leon J. 2006. Estimation of breeding values of inbred lines using best linear unbiased prediction (BLUP) and genetic similarities. Crop Sci., **46**: 2685-2691.

Bauer A.M. and Leon J. 2008. Multiple-trait breeding values for parental selection in self-pollinating crops. Theor. Appl. Genet., **116**: 235-242.

Bethke P.C., Halterman D.A. and Jansky S.H. 2019. Potato Germplasm Enhancement Enters the Genomics Era. Agronomy, **9**: 575. doi:10.3390/agronomy9100575

Bradshaw J.E., Dale M.F.B. and Mackay G.R. 2009. Improving the yield, processing quality and disease and pest resistance of potatoes by genotypic recurrent selection. Euphytica, **170**(1): 215-227. doi:10.1007/s10681-009-9925-4

Bradshaw J.E. and Mackay G.R. 1994. Breeding strategies for clonally propagated potatoes. In: Bradshaw JE, Mackay GR, editors. Potato Genetics. Cab International, Wallingford: 467-497.

Covarrubias-Pazaran G. 2016. Genome-assisted prediction of quantitative traits using the R package sommer. PLoS One, **11**: e0156744. doi:10.1371/journal.pone.0156744.

Enciso-Rodriguez F., Douches D., Lopez-Cruz M., Coombs J. and de los Campos G. 2018. Genomic selection for late blight and common scab resistance in tetraploid potato (*Solanum tuberosum*). G3, **8**: 2471-2481. doi:10.1534/g3.118.200273.

Endelman J. B., Schmitz Carley C. A., Bethke P. C., Coombs J. J. Clough M. E., da SilvaW. L., Yencho G.C. 2018. Genetic variance partitioning and genome-wide prediction with allele dosage information in autotetraploid potato. Genetics, **209:** 77-87. https://doi.org/10.1534/genetics.118.300685

Forbes G., Pérez W. and Andrade Piedra J. 2014. Field assessment of resistance in potato to Phytophthora infestans. Lima (Peru), International Potato Center (CIP): 35.

Habyarimana E., Parisi B. and Mandolino G. 2017. Genomic prediction for yields, processing and nutritional quality traits in cultivated potato (*Solanum tuberosum* L.). Plant Breeding, **136**(2): 245-252.

Henderson C.R. 1984. Applications of linear models in animal breeding. University of Guelph, Guelph.

Jansky S. 2009. Breeding, genetics and cultivar development. In: Advances in potato chemistry and technology (ed. J. Singh andL. Kaur) Academic Press, New York: 27-62.

Li X., Xu J., Duan S., Bian C., Hu J., Shen H., Li G. and Jin L. 2018. Pedigree-Based Deciphering of Genome-Wide Conserved Patterns in an Elite Potato Parental Line. Front. Plant Sci., **9**: 690. doi: 10.3389/fpls.2018.00690

Ortiz R. 2020. Genomic-Led Potato Breeding for Increasing Genetic Gains: Achievements and Outlook. Crop Breed Genet Genom., **2**(2): e200010. https://doi.org/10.20900/cbgg20200010

Ortiz R., Reslow F., Crossa J. and Cuevas J. 2021. Heritable Variation, Genetic and Phenotypic Correlations for Tuber Traits and Host Plant Resistance to Late Blight for Potato Breeding in Scandinavian Testing Sites. Agriculture, **11**(12): 1287. https://doi.org/10.3390/agriculture11121287.

Piepho H.P. and Mohring J. 2006. Selection in cultivar trials—is it ignorable? Crop Sci., **146**: 193-202.

Piepho H., Möhring J., Melchinger A. andBüchse A. 2008. BLUP for phenotypic selection in plant breeding and variety testing. Euphytica, **161**: 209-228.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rodríguez-Ramilo S.T., García-Cortés L.A. and de Cara M.Á.R. 2015. Artificial selection with traditional or genomic relationships: consequences in coancestry and genetic diversity. Front. Genet., **6**: 127. doi: 10.3389/fgene.2015.00127

Slater A.T., Cogan N.O.I., Forster J.W., Hayes B.J. and Daetwyler H.D. 2016. Improving genetic gain with genomic selection in autotetraploid potato. The Plant Genome, **9**(3): https://doi.org/10.3835/plantgenome2016.02.002

Slater A.T., Wilson G.M., Cogan N.O., Forster J.W. and Hayes B.J. 2014. Improving the analysis of low heritability complex traits for enhanced genetic gain in potato. Theor. Appl. Genet., **127**: 809-820.

Sood S., Bhardwaj V., Pandey S. K. and Chakrabarti S. K. 2017. History of potato breeding: Improvement, diversification, and diversity. In: The Potato Genome(ed. S.K. Chakrabarti, C. Xie and J.K. Tiwari), Springer, India: 31-72.

Sood S., Lin Z., Caruana B., Slater A.T. and Daetwyler H.D. 2020a. Making the most of all data: combining non-genotyped and genotyped potato individuals with HBLUP. The Plant Genome, **13**(3): e20056.doi: 10.1002/tpg2.20056.

Sood S., Bhardwaj V., Kaushik S.K. and Sharma S. 2020b. Prediction based on estimated breeding values using genealogy for tuber yield and late blight resistance in auto-tetraploid potato (*Solanum tuberosum* L.). Heliyon, **6**: e05624.

Sood S., Bhardwaj V. and Sundaresha S. 2020c. Major Paradigm Shifts in Potato Breeding. In: Accelerated Plant Breeding, Volume II, (ed. S. S. Gosal and S. H. Wani), Springer: 1-16.

Stich B. and Van Inghelandt D. 2018. Prospects and Potential Uses of Genomic Prediction of Key Performance Traits in Tetraploid Potato. Front. Plant Sci., **9**: 159. doi: 10.3389/fpls.2018.00159.

Sverrisdóttir E., Sundmark E.H.R., Johnsen H.Ø., Kirk H.G., Asp T., Janss L., Bryan G. and Nielsen K.L. 2018. The Value of Expanding the Training Population to Improve Genomic Selection Models in Tetraploid Potato. Front. Plant Sci., **9**: 1118. doi: 10.3389/fpls.2018.01118

Ticona-Benavente C.A. and da Silva Filho D.F. 2015. Comparison of BLUE and BLUP/REML in the selection of clones and families of potato (*Solanum tuberosum*). Genet. Mol. Res., **14**(4): 18421-18430. http://dx.doi.org/10.4238/2015.

van Berloo R., Hutten R., van Eck H. and Visser R. 2007. An online potato pedigree database resource. Potato Res., **50**: 45-57.

Vineeth T.V., Prasad I. , Chinchmalatpure A.R., Lokeshkumar B. M., Kumar S., Ravikiran K. T. and Sharma P.C. 2022. Weighted average absolute scores of BLUPs (WAASB) based selection of stable Asiatic cotton genotypes for the salt affected Vertisols of India. Indian J. Genet. Plant Breed., **82**(1): 104-108. doi: 10.31742/IJGPB.82.1.15

Xu Y., Lu Y., Xie C., Gao S., Wan J. and Prasanna B. 2012. Whole-genome strategies for marker-assisted plant breeding. Mol. Breed., **29**: 833-854.

Yu H., Spangler M.L., Lewis R.M. and Morota G. 2017. Genomic Relatedness Strengthens Genetic Connectedness Across Management Units. G3, **7**(10): 3543-3556. doi: 10.1534/g3.117.300151.

Supplimentary Table S1. BLUP/EBV of potato breeding clones for total tuber yield (TTY), late blight (LB) AUDPC and specific gravity (SG)

Genotype	TTY	Genotype	LB	Genotype	SG
Kufri Mohan	94.14	Sm/10-05	-267.56	Kufri Chipsona-1	0.01599
Kufri Pukhraj	81.32	Sm/09-99	-255.57	Sm/14-225	0.01183
Kufri Khyati	71.78	Kufri Girdhari	-251.67	Sm/14-229	0.00923
Sm/14-342	55.77	Sm/11-120	-227.47	Sm/10-220	0.00874
Kufri Pushkar	54.89	Sm/00-42	-213.31	Sm/09-153	0.00855
Sm/15-103	50.38	Sm/03-32	-201.86	Sm/10-253	0.00798
Sm/92-338	50	Sm/03-23	-196.16	Sm/14-182	0.00778
Sm/14-335	49.01	Sm/09-153	-194.05	Sm/10-75	0.00692
Sm/15-719	42.93	Sm/03-13	-177.07	Sm/14-111	0.00685
Sm/15-574	41.39	Sm/03-45	-170.65	Sm/09-02	0.00666
Sm/13-150	41.13	Sm/05-75	-167.32	Sm/15-739	0.00638
Kufri Sadabahar	38.97	Sm/09-161	-166.28	Sm/14-202	0.00599
Sm/13-122	38.09	Sm/03-16	-165.1	Sm/13-165	0.00595
Hr 2-5	36.01	Sm/09-14	-156.4	Kufri Surya	0.00594
Sm/13-152	34.05	Sm/01-07	-151.72	Vmt 12-7	0.00586
Sm/13-154	31.84	Sm/00-120	-150.12	Sm/15-472	0.00484
Sm/13-155	31.68	Sm/02-01	-148.09	Sm/12-02	0.00475
Sm/15-472	30.65	Sm/02-08	-121.38	Sm/14-216	0.00468
Sm/91-1515	29.45	Sm/00-43	-101.21	Sm/13-154	0.00465
Sm/13-170	28.57	Sm/04-20	-83.38	Sm/13-170	0.004
Sm/13-149	26.05	Sm/10-103	-75.61	Sm/14-347	0.00395
Sm/14-213	25.92	Sm/00-72	-70.41	Sm/14-19	0.00367
Vmt 3-1	25.66	Vmt 5-1	-60.32	Sm/15-18	0.00322
Sm/13-158	25.35	Sm/98-239	-57.6	Sm/09-13	0.00312
Sm/14-347	23.76	Sm/00-191	-55.64	Sm/15-719	0.00282
Sm/13-163	22.62	Sm/05-170	-34.17	Sm/09-14	0.00276
Hr 9-4	22.61	Lby-24	-33.67	Sm/13-152	0.0027
Sm/87-151	22.31	Lby-2	-26.32	Sm/13-155	0.0027
Sm/14-216	22.11	Vmt 2-5	0.37	Sm/10-174	0.00208
Lby-17	21.91	Sm/95-43	15.02	Sm/00-42	0.00163
Sm/14-229	20.94	Hb/82-372	18.78	Sm/13-163	0.00148
Sm/10-174	19.24	Vmt 2-4	21.8	Sm/11-120	0.00123
Sm/87-55	18.61	Lby-26	23.67	Sm/15-574	0.00117
Lby-2	18.35	Sm/88-343	26.57	Kufri Girdhari	0.00088
Sm/15-122	18.31	Lby-11	34.59	Sm/13-149	0.00076
Sm/88-991	18.02	Lby-14	36.54	Sm/10-05	0.00042
Sm/00-191	17.71	Hr 2-5	43.25	Sm/14-213	0.00012
Sm/11-93	17.51	Sm/88-991	43.95	Sm/13-150	-0.00009
Sm/15-36	16.56	Sm/91-1515	66.11	Sm/09-99	-0.00071
Sm/87-185	15.25	Kufri Giriraj	75.43	Sm/13-122	-0.00159
Sm/15-04	14.1	Kufri Himalini	79.91	Sm/09-161	-0.00192
Sm/14-225	13.74	Ks/96-725	82.86	Sm/15-28	-0.00213
Sm/15-739	12.83	Lby-18	90.94	Kufri Bahar	-0.00228

Cont...

Genotype	TTY	Genotype	LB	Genotype	SG
Sm/00-72	12.51	Lby-16	91.96	Kufri Himalini	-0.00254
Sm/15-75	12.31	Kufri Bahar	93.04	Kufri Jyoti	-0.00284
Sm/14-202	11.68	Sm/90-45	98.36	Vmt 3-1	-0.0033
Vmt 5-1	11.6	Kufri Sadabahar	112.93	Sm/13-172	-0.00403
Sm/15-19	11.2	Sm/96-127	123.82	Sm/15-75	-0.00442
Kufri Bahar	11.06	Lby-15	145.43	Sm/13-129	-0.00554
Sm/10-103	9.92	Sm/87-185	182.64	Sm/15-103	-0.00558
Sm/13-172	9.52	Sm/87-55	185.07	Sm/14-342	-0.0063
Hr 7-5	8.37	Sm/87-151	186.07	Sm/15-19	-0.00668
Sm/12-67	7.94	Kufri Shailja	198.07	Sm/15-04	-0.00699
Sm/15-22	5.55	Hr 9-3	228.48	Kufri Pushkar	-0.00716
Kufri Giriraj	5.3	Lby-19	311.24	Sm/15-27	-0.00733
Sm/00-120	5.25	Lby-17	327.86	Sm/14-333	-0.00768
Sm/13-165	5.08	Hr 5-2	361.95	Sm/15-22	-0.00798
Vmt 5-3	4.78	Kufri Jyoti	559.23	Kufri Pukhraj	-0.00965
Hr 5-1	3.83			Sm/15-36	-0.01005
Sm/10-05	3.63			Sm/14-335	-0.01008
Kufri Shailja	2.08			Kufri Khyati	-0.01185
Hr 5-2	1.72			Sm/15-122	-0.01221
Sm/15-18	1.69			Kufri Mohan	-0.01579
Lby-26	1.39				
Sm/14-333	0.32				
Sm/09-09	0.19				
Lby-15	0.03				
Hr 9-3	-0.82				
Sm/00-43	-2.13				
Vmt 6-3	-2.41				
Sm/14-111	-3.96				
Kufri Himalini	-6.11				
Hr 7-1	-6.69				
Vmt 2-10	-6.92				
Kufri Jyoti	-8.15				
Vmt 14-7	-8.37				
Sm/15-28	-8.93				
Sm/88-343	-9.18				
Lby-18	-9.51				
Vmt 11-7	-10.58				
Vmt 4-10	-10.58				
Lby-24	-11.31				
Vmt 2-3	-11.52				
Vmt 2-5	-12.83				
Lby-16	-13.3				

Cont...

Genotype	TTY	Genotype	LB	Genotype	SG
Sm/14-182	-13.42				
Lby-19	-13.64				
Vmt 16-1	-16.11				
Sm/13-129	-16.47				
Lby-11	-16.56				
Sm/09-13	-17.18				
Vmt 14-3	-17.88				
Sm/00-42	-18.22				
Hr 2-2	-18.94				
Sm/13-131	-19.07				
Sm/09-161	-21.1				
Sm/92-168	-21.11				
Ks/96-725	-21.61				
Vmt 16-3	-21.81				
Hr 9-5	-22.67				
Sm/14-19	-23.68				
Hr 2-4	-24.45				
Kufri Chipsona-1	-25.13				
Vmt 12-7	-25.4				
Sm/15-27	-25.61				
Vmt 11-1	-26.2				
Sm/10-253	-27.03				
Sm/98-239	-27.72				
Hr 2-1	-27.92				
Sm/95-43	-29.28				
Sm/90-45	-29.43				
Hr 2-6	-33.18				
Vmt 2-4	-35.68				
Sm/09-153	-36.12				
Kufri Lauvkar	-36.12				
Sm/09-02	-38.23				
Sm/96-127	-39.15				
Sm/09-14	-40.4				
Sm/93-237	-41.07				
Kufri Girdhari	-41.93				
Sm/94-44	-43.14				
Vmt 16-7	-43.83				
Hb/82-372	-45.27				
Sm/09-54	-46.86				
Lby-14	-47.06				
Sm/10-75	-47.81				
Sm/01-07	-58.29				
Sm/10-220	-58.64				
Kufri Surya	-59.14				

Cont...

Genotype	TTY	Genotype	LB	Genotype	SG
Sm/08-21	-61.91				
Sm/11-120	-64.07				
Sm/05-75	-71.17				
Sm/02-01	-77.95				
Sm/12-02	-82.65				
Sm/04-20	-85.25				
Sm/09-99	-91.79				
Sm/03-45	-95.29				
Sm/03-23	-97.92				
Sm/02-08	-103.27				
Sm/03-13	-103.85				
Sm/03-32	-106.43				
Sm/03-16	-106.81				
Sm/05-170	-117.16				