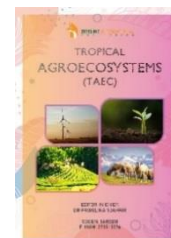




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## RESEARCH ARTICLE

# GENOMIC SELECTION: FUTURE OF POTATO CROP IMPROVEMENT

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## ABSTRACT

Crop improvement through plant breeding is fundamental to meet the food demand of the increasing population estimated to reach more than 9 billion by 2050. Potato is the third most important food crop globally and is considered imperative for global food security. The demand for improved potato cultivars for enhanced yield, quality, and disease resistance is increasing. Conventional potato breeding is less efficient and time-consuming, which takes more than a decade to improve desirable traits in the selected population. However, Genomic selection (GS) is evolving as an efficient tool for potato breeding which provides opportunities to increase the genetic gain of complex traits per unit time and cost. The genomic prediction model has shown promising results in various traits like yield, maturity, processing qualities, and diseases resistance. This study is designed to understand the basics of GS and the application of genomic selection in potato crop improvement.

## KEYWORDS

Potato Breeding, Genetic Gain, Genomic predictions, Prediction accuracy.

## 1. INTRODUCTION

Potato (*Solanum tuberosum*) is the world's most vital non-grain food crop and produces about twice the quantity of calories per hectare compared to cereals (Ortiz, 2020). By 2050, a global population of 9.7 billion people will demand 70% more food than is consumed today (FAO, 2018). This population growth is going to place enormous pressure on agriculture. Today's food system is insufficient to meet the growing demand for food in an environmentally sustainable way to the world's population (Wu et al., 2018). To feed this expanded population nutritionally and sustainably demands substantial improvement in food production. Being considered space-efficient food crops (Sverrisdóttir et al., 2017) and its essential attributes bearing a significant amount of carbohydrates, protein, vitamins, and minerals prove its importance for global food security (Wijesinha-Bettoni & Mouillé, 2019). An increase in productivity will depend on improved potato varieties with higher yield potential and resistance to pests and diseases, greater use of quality seed potatoes, and improved pest and disease management (Lutaladio & Castaldi, 2009). Thus, considering these aspects, major emphasis nowadays lies on plant breeding. It is one of the major driving forces for enhancing the productivity, quality, and development of resistance against diseases of the food crops (Joshi, 2017).

The two techniques employed in plant breeding are conventional and marker-assisted breeding (MAB). MAB has two approaches i.e., marker-assisted selection (MAS) and Genomic selection (GS) (Bhat et al., 2016). But, conventional potato breeding approaches are hampered by several factors, including costly seed tubers, tetrasomic inheritance, long breeding cycles, and inbreeding depression (Habyarimana et al., 2017). MAS in potato breeding also has setbacks because it only captures the variance

from a limited number of quantitative trait locus (QTLs) which are not suitable for the economic traits of potatoes controlled by a large number of genes (Sverrisdóttir et al., 2017). Because of this limitation of MAS, methods based on genome-wide high-density markers are emphasized for these complex traits (Wang et al., 2018).

Genomic selection (GS) is an upgraded form of MAS that predicts breeding values. In contrast to MAS, it can efficiently capture all genetic variance of smaller to larger genes (Bhat et al., 2016). Thus, GS is seen to be promising in potato breeding for predicting its quantitative, complex traits regulated by multiple genes (Sverrisdóttir et al., 2017). Genetic gain in complex traits, such as yield, has been slow to nonexistent in conventional breeding (Jansky, 2009). These low annual gains from potato breeding compared to other grain crops is due to potato's polyploidy and highly heterozygous nature (Stich & Van Inghelandt, 2018). However, GS has shown a high genetic gain per year compared to conventional breeding (Bhat et al., 2016). Furthermore, the heterozygous nature of potatoes is making a prediction of the outcome of a sexual cross particularly challenging (Xu et al., 2011). In response to that, GS has demonstrated exciting results regardless of the ploidy level, and some breeders and breeding programs have found promising results to circumvent these problems (Stich & Van Inghelandt, 2018). Thus, GS can be a potential breeding tool to improve the complex and important traits of potatoes.

The main objective of this review is to provide readers with the basics of GS in potatoes and its implications in potato breeding. We are hopeful that the broad application of this technology provides an alternative to traditional selection methods and will increase efforts towards discovering desirable genes that could be used to improve current breeding objectives.

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## 2. OVERVIEW OF POTATO BREEDING

Potatoes are polyploid species, highly heterozygous, with basic chromosome number 12 (Watanabe, 2015). Cultivars mostly used in potato breeding are diploid and tetraploid species (Ortiz, 1998). Because of the extremely heterozygous and autotetraploid character of the potato, its breeding is more difficult than other grain and pasture crops. Furthermore, additional market-specific qualities are also taken into considerations which makes its breeding cumbersome. Environment strongly influenced the many target traits, like as yield, tuber quantity, tuber size, specific gravity, and processing quality, which varies greatly (Jansky, 2009). The degree of environmental effect on the expression of the target characteristics, as well as the genetic control of each feature, are crucial to know and will determine which technique should be utilized for choosing better phenotypes and genotypes. Some characteristics are governed by a single gene, whereas others are governed by a more complicated set of genes (Slater et al., 2016).

Nowadays, along with the yield improvement, the fundamental breeding goals for potatoes are focused on the market-specific traits (i.e., yield, tuber number, tuber size), a pleasing visible aspect (i.e., shape, depth of eyes, skin, and flesh color), and cooking suitability, processing quality (i.e., chemical composition, specifically for low, reducing sugars and appropriate specific gravity or dry matter content) and with the host plant resistance to many pathogens and pests affecting potato elsewhere, and suitability for being grown and stored (Ortiz, 2020). More recently, the potato industries are likewise asking for starch quality (amylose: amylopectin ratio), bioactive compounds such as antioxidants, micronutrients (vitamins, Fe, Zn) (Ortiz, 2020). These most of the economic characteristics are controlled by a large number of genes, which are defined as complex traits (Sverrisdóttir, 2017).

One of the breeding methods; conventional potato breeding, is not effective for such complex and low heritable traits (Tuberosa, 2012). Besides, it involves screening genotypes across several clonal generations and in a number of appropriate locations for a range of desirable characters, which can take over 10-15 years (Haltermann et al., 2016; Jansky, 2009). MAS, an alternative of traditional breeding, is also efficient only for those traits that are controlled by fewer numbers of QTLs having the major effect on trait expression, whereas, for complex quantitative traits which are governed by a large number of minor QTLs, the method is even inferior to conventional phenotypic selection (Zhao et al., 2014).

## 3. GENOMIC SELECTION IN POTATO BREEDING

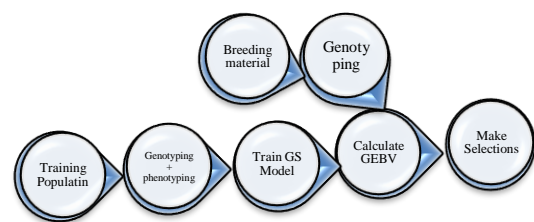
The promising approach for exploiting molecular genetic markers to design novel breeding programs and develop new markers-based models for genetic evaluation is GS. GS was first proposed by Meuwissen et al., (2001) as a potential alternative to traditional breeding, which offers new opportunities to increase plant breeding's efficiency (Meuwissen et al., 2001). Another type of MAS is GS, which successfully captured all the genetic variance since it jointly analyses all marker data. It is efficient for the complex traits controlled by a large number of QTLs (Jannink et al., 2010). GS provides opportunities to increase the genetic gain of complex traits per unit time and cost (Bhat et al., 2016). The cost-benefit balance is an essential consideration for GS to work in crop plants during breeding. Availability of genome-wide high-throughput, low ascertainment bias, cost-effective and flexible markers, having suitable for large population size and both models and non-model crop species with or without the reference genome sequence was the most crucial factor for its success effective implementation in crop species (Kirst et al., 2011; Metzker, 2010; Poland & Rife, 2012; Toonen et al., 2013)

Based on the genotypic and phenotypic data, GS develops the prediction model of the training population (TP), which is used to derive genomic estimated breeding values (GEBVs) for all the individuals of the breeding population (BP) from their genomic profile (Meuwissen et al., 2001). As molecular marker profile of individuals to perform better and suitable either as a parent in hybridization or for next-generation advancement of the breeding program is similar to that of other plants of TP that have been recorded to perform better in the particular environments, the GEBVs allow us to predict individuals that will perform better (Bhat et al., 2016). Unobserved individuals' genetic effect values may be predicted using this approach, avoiding the removal of small-effect markers that would fail the significance test. Even if each marker's influence is modest, a vast amount of marker data spanning the entire genome can explain genetic variations. A significant number of loci must be genotyped to undertake crop genomic prediction. For that, Next-generation sequencing (NGS) technologies have provided novel Single Nucleotide Polymorphisms (SNP) genotyping platforms (Manivannan et al., 2018) especially genotyping by sequencing. With the rapid advancement of the potato genome sequence and

identifying a large number of genome-wide Single Nucleotide Polymorphisms (SNPs) (Uitdewilligen et al., 2013), a unique application of genomic selection in the potato can be expected in the near future.

Genetic gain can be improved by using GS. However, the heterozygous nature of potatoes will require some considered strategies (Slater et al., 2016). GS can be attractively integrated into potato breeding, particularly in early clonal generations, to predict and select for traits with low heritability, which would otherwise require more testing years, environments, and resources (Habyarimana et al., 2017b). GS allows for prediction of the performance of individuals and subsequent selection of breeding candidates in the absence of direct phenotyping, potentially reducing the breeding cycle while improving gain from selection and reducing costs associated with phenotyping (Heffner et al., 2010; Sverrisdóttir, 2017). The variety of parameters, including trait heritability, the size of the training population, and the genetic connection between individuals, influences the accuracy of genomic prediction (Dhankhar, S.K, and Koundinya, 2020).

The main objective of GS is to reduce field testing and, thereby, the costs involved in the varietal development. Application of genomic prediction in breeding programs for tetraploid potato has a high potential for increasing the gain from the selection. Hence, using the established GS schemes, higher genetic gains can be achieved cost-effectively.



Source: (Heffner et al., 2009)

Figure 1: Diagram of genomic selection (GS) processes

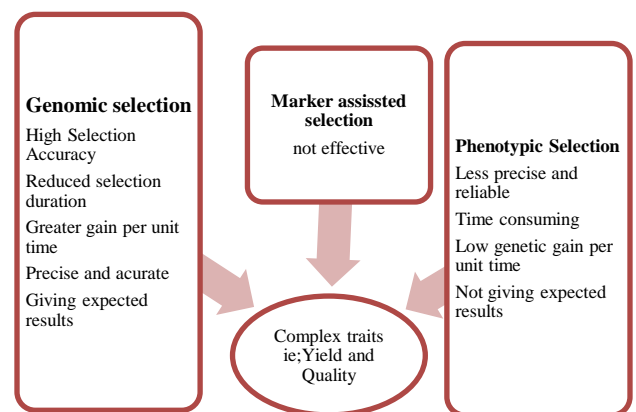


Figure 2: Illustrating the benefits of genomic selection over Phenotypic selection and marker-assisted selection in complex traits of potato.

## 4. APPLICATIONS OF GENOMIC SELECTION IN POTATO

### 4.1 Genomic Prediction for Yield, Processing, Nutritional Quality, and Disease Resistance

One of the fascinating applications of GS in potato breeding can be its implementation in early clonal generations to predict and select for traits with low heritability, such as yielding ability and tuber grades, which can only be evaluated based on the average performance of many plants in several environments, over several seasons. GS is expected to shorten the time to cultivar development, reduce the number of clones to be field-tested and the cost of current breeding programs and help avoid committing resources on plant materials that will not meet breeding and market standards. The good prediction ability for tuber grades and tuber dry matter content is exciting as it offers the possibility to identify commercially relevant clones that can be leveraged earlier with GS than conventional potato breeding strategies. The possibility to predict cross-

validation accuracy using information from previous results will help breeders significantly reduce the costs associated with comparative and multi-location varietal testing (Habyarimana et al., 2017b).

Genomic prediction models showed promising results for starch content and chipping quality (Habyarimana et al., 2017b) and disease resistance for Common scab and late blight (Douches et al., 2018) suggesting that genomic selection is a feasible breeding strategy in tetraploid potato. GS could be promising for rapid cycling selection to resist late blight and common scabs in tetraploid potato (Enciso-Rodriguez et al., 2018). Slater et al. (2016) estimated a genetic gain over 20 years, almost nine times as high as the expected genetic gain using phenotypic selection, using only 5000 populations. Even when using merely 500 individuals, the genetic gain is expected to more than double compared to phenotypic selection. Sverrisdóttir et al. (2017) generated genomic prediction models for starch content, dry matter, chipping quality, yield, and late blight resistance and obtained high cross-validated prediction accuracies for the starch content dry matter within each population, while prediction accuracies for chipping quality were generally observed slightly lower. These findings suggest that the application of genomic prediction in breeding programs for tetraploid potato encompasses a high potential for increasing the genetic gain from the selection and low heritability of the trait and a high proportion of non-additive genetic effects signifying the more challenging predictions of quantitative resistance.

Table 1: Results of recent research findings on genomic prediction of breeding values in potato		
Traits	Main findings	References
Starch content	Cross prediction validation correlation of 0.56	(Sverrisdóttir et al., 2017)
Host plant resistance Late blight	Prediction accuracy 0.8 (tetraploid German breeding clones, genomic heritability (0.46 ± 0.04) and prediction correlation 0.31 in tetraploid breeding clones	(Stich & Van Inghelandt, 2018)
Common scab	Genomic heritability of 0.45 ± 0.02 with estimated prediction correlation of ca. 0.27–0.31 in advanced US tetraploid breeding clones	(Enciso-Rodriguez et al., 2018)
Tuber fresh color	Prediction accuracy (after cross-validation) above or equal to 0.7	(Habyarimana et al., 2017b)
Tuber dry matter or specific gravity	prediction accuracy ranging between 0.25 and 0.63 in unselected US F1 tetraploid breeding population	(Sverrisdóttir et al., 2018)
Frying chipping quality	Prediction accuracy ranging between 0.4 and 0.45 when using different pedigree depth in unselected US F1 tetraploid breeding population  Cross-prediction validation correlation of 0.73 in training panel but between 0.42 and 0.43 in test panel from tetraploid mapping population of the breeding program in Denmark	(Sverrisdóttir et al., 2018)  (Sverrisdóttir et al., 2017)
Stem number per plant	Average prediction accuracy (cross-validation) across models of 0.05 (0.01–0.13) in European cultivars	(Habyarimana et al., 2017b)
Tuber yield and components	prediction accuracy ranging between 0.06 and 0.63 in unselected US F1 tetraploid breeding population. Average prediction accuracy (cross-validation) across models of 0.37 (0.22–0.41), 0.32 (0.15–0.41), and 0.17 (0.13–0.23) for total yield, size (as measured by diameter) and number, respectively, in European cultivars	(Endelman et al., 2018)  (Habyarimana et al., 2017b)
Maturity	Prediction accuracies between 0.19 for yield and 0.78 for maturity.	(Slater et al., 2016)

## 4.2 Increasing the Range of Traits That Can Be Evaluated or Selected

The advent of GS use in breeding programs assists in developing new cultivars with improved drought tolerance. Genomic selection will also allow improvement and expansion of the range of traits, such traits that are evaluated late in the breeding process or that have recently become a priority, such as low acrylamide levels, which have been the subject of recent attention (Bethke & Bussan, 2013) or they could be new abiotic or biotic stresses, including drought, heat, salinity, or specific and more productive genotypes, such as efficient nutrient or water use. GS is unique in this case as it allows for targeted phenotypic assessment of key lines to maximize prediction accuracy to apply to genotyping seedlings (Slater et al., 2016).

## 4.3 Progeny Test for Multiple Traits

Progeny test for multiple traits (visual preference, late blight tuber, and foliar resistance, white cyst nematode resistance, and fry color for processing) have been employed by (J E Bradshaw et al., 2003; John E Bradshaw, 2007), resulting in the identification of superior clones and parental types with improved disease resistance, as well as a 14% increase in yield (John E Bradshaw, 2007; John E Bradshaw et al., 2009).

## 4.4 Genome Sequencing of Wild Varieties

The genome sequence of a wild species of potato, *Solanum commersonii*, was assembled using the potato genome sequence as a reference (Aversano et al., 2015). This species has interesting sources of freezing resistance and cold acclimation, and resistance to the potato's essential diseases. When this species was used in breeding potatoes for resistance to bacterial wilt, increased resistance levels were observed (Carputo et al., 2009). Thus, wild varieties can be employed in genomic selection as a potential source of the biotic and abiotic resistance in commercial cultivars.

## 5. PROSPECTS OF GENOMIC SELECTION

Genomic selection is still in its infancy in plant breeding. One of the most significant barriers to applying GS in practical breeding is the high start-up expenses. Several studies, however, have demonstrated that GS can dramatically increase genetic gain while using less expensive per unit time than traditional breeding (Sverrisdóttir et al., 2017). Also, genotyping costs are steadily declining, and it has become more convenient than it was only a few years ago (Lorenz et al., 2011). Higher prediction accuracy in GS can be achieved using larger training sets closely linked to the target breeding and selection populations. Modeling GE (Genotype × Environment) and borrowing knowledge from similar environments can also help to improve prediction accuracy (Heffner et al., 2009). Furthermore, some researchers have found that genetic gain can be enhanced in GS with optimized breeding designs (Lin et al., 2017; Slater et al., 2016).

## 6. CONCLUSIONS

Slow breeding gain is one of the significant problems in potato breeding. The breeding process can speed up through molecular breeding. Genomic selection using genome-wide molecular markers is becoming increasingly applicable to crops as the genotyping costs continue to reduce, making it an attractive breeding alternative. It allows for the prediction of the performance of individuals and subsequent selection of breeding candidates in the absence of direct phenotyping. The development of a GS-based approach would radically enhance potato breeding by enabling early-stage selection for complex traits, thereby facilitating faster identification of elite breeding parents with desirable traits. GS would lead to rapid improvement in commercial varieties and reduced time in getting these to market, enabling the Potato breeding industry to remain competitive and grow its market share.

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