

Genomic selection with rapid cycling: Current insights and future prospects

Leonardo Volpato¹, Arthur Bernardeli² and Francisco Gomez^{1*}

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Abstract: *Enhancing the rate of genetic gain in plant breeding program is critical to address global food security in the face of climate change and a growing population. Rapid cycling genomic selection offers a powerful breeding strategy to reduce the breeding cycle and obtain rapid genetic gains in plant breeding programs. In this paper, we discuss theoretical and empirical approaches to deploy and optimize rapid cycling genomic selection in crop improvement programs. We highlight major advantages and challenges associated with rapid cycling genomic selection. Finally, we discuss the trends and general conclusion on this breeding strategy and provide recommendations for future discussions and continued adoption in plant breeding programs.*

Keywords: *Recurrent genomic selection, plant breeding, food security, genetic gain*

INTRODUCTION

Plant breeding is likely to play an important role in sustaining global food security and nutritional quality in the face of climate change and a growing world population, which is projected to reach 9.5 billion by 2050 (He and Li 2020, Qaim 2020). However, to keep pace with these stressors (Wheeler and von Braun 2013, Hummel et al. 2018), global crop production must also be doubled by 2050, which current yield trends are insufficient to achieve in this timeframe (Godfray et al. 2010). Enhancing genetic gain to double production is thus crucial to sustain global food security and nutritional quality. Genomic prediction, proposed almost 20 years ago has revolutionized the design and implementation of plant and animal breeding programs (Meuwissen et al. 2001, Hickey et al. 2017), and has become a promising tool for plant breeding programs to accelerate the rate of genetic gain in crops (Bernardo and Yu 2007, Hickey et al. 2017, Voss-Fels et al. 2018, Cobb et al. 2019, Xu et al. 2020). The widespread adoption of genomic selection in plant breeding programs has been driven by technological developments in genotyping, whole-genome sequencing, and statistical computing. These improvements have enabled plant breeding programs to obtain cheap and abundant single nucleotide polymorphism (SNP) markers for prediction. As private sector and public breeding programs continue to adopt genomic selection, there remains a considerable opportunity to efficiently deploy genomic selection to maximize the rate of crop genetic improvement to address future global food security and nutritional quality.

Genomic selection is a form of marker-assisted selection (MAS) that uses all available molecular markers to predict the overall genomic merit of an individual to make selections (Meuwissen et al. 2001, Bernardo and Yu 2007,



***Corresponding author:**

E-mail: gomezfr1@msu.edu

 ORCID: 0000-0002-2862-7118

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¹ Michigan State University, Department of Plant, Soil, and Microbial Sciences, East Lansing, MI 48824

² Universidade Federal de Viçosa, Departamento de Agronomia, Campus Universitário, 36.570-900, Viçosa, MG, Brazil

Goddard and Hayes 2007). Compared to MAS, in genomic selection all marker effects are estimated simultaneously, avoiding the two-step procedure of determining which markers are “significant,” followed by estimation of their effects using multiple linear regression (Hospital et al. 1997, Lorenz et al. 2012), making it more appealing for genetically complex traits. Initially, a training population is first established of individuals which are phenotyped for the target trait(s) and genotyped with DNA markers across the genome. The training set is used to train a statistical model for associations between molecular markers and traits of interest to derive a prediction equation, which predicts the effect of each marker on the trait, with all marker effects fitted simultaneously (Voss-Fels et al. 2018). This prediction equation is then used to estimate the genetic value of selection candidates using only their genotypic information. The goal is to make a prediction with high enough accuracy to allow parent selection on a testing population based on those predictions, known as genomic estimated breeding values (GEBVs) (Lorenz et al. 2012). Genomic selection can be used in place of phenotyping to drastically restructure breeding program design (Heffner et al. 2009) and increase genetic gain per unit of time without increasing costs (Crossa et al. 2017). Therefore, an appropriate breeding strategy using genomic selection can reduce the breeding cycle, increase the accuracy of estimated breeding values, and improve the selection accuracy (Crossa et al. 2021).

THE BREEDER’S EQUATION – SHORTENING THE BREEDING CYCLE TO ACCELERATE GENETIC GAIN

A useful framework that is commonly used to quantify the effectiveness of a breeding strategy on genetic gain per unit time is the breeder’s equation (Lush 1937). This equation models the expected change in a trait in response to selection and can be approximated in four key parameters written as:

$$R = \frac{i\sigma_a h}{L}$$

where R is the change in trait mean per year or referred to as response to selection, i is the selection intensity, σ_a is the amount of additive genetic variation in the population, h represents the accuracy of selection or heritability, and L is the breeding cycle time (or generation interval). Response to selection can be increased by either increasing the terms in the numerator or by decreasing the breeding cycle time in the denominator. Genomic selection can be used to effectively address each of the four components of this equation (Hickey et al. 2017). Although heritability (accuracy), selection intensity, and additive genetic variance can increase genetic gain, the breeding cycle time can be the most affordable and powerful of these components to increase genetic gain (Cobb et al. 2019). For example, using genomic selection in livestock breeding programs has enabled the shortening of the generation interval, thus increasing the rates of genetic gain (Kasinathan et al. 2015, Hickey et al. 2017). In the context of plant breeding programs, the breeding cycle involves identifying elite breeding material through performance history or evaluation and reusing it as parents for the next breeding cycle. For example, reducing the breeding cycle in a traditional breeding program can simply be achieved by identifying elite parents at earlier stages of the breeding pipeline. However, the chances of identifying elite breeding material only increases with further evaluation and testing. In an excellent review by Cobb et al. (2019), the authors pointed out that accelerating the breeding cycles in a breeding program can be the most efficient way to increase the rate of genetic gain, but it has been underutilized in many breeding programs, which primarily focus on other components of the breeder’s equation. The authors also point out that these components can provide rapid genetic gain initially in a breeding program but are subject to rapidly diminishing returns on investments and can ultimately cost more than shortening the breeding cycle in the long term.

Therefore, an effective breeding strategy that can shorten the breeding cycle is one of the most efficient ways to increase the rate of genetic gain in plant breeding programs. As such, deploying a genomic selection strategy that can reduce the breeding cycle in a breeding program would enhance the rate of genetic gain. Herein, we briefly review breeding schemes that utilize genomic selection to shorten the breeding cycle and accelerate genetic gains in plant breeding programs. Current status, advantages, challenges, and trends in these breeding schemes are highlighted and discussed. We refer to the reader to other focused reviews on the general topic of genomic selection (Voss-Fels et al. 2018, Xu et al. 2020, Crossa et al. 2021, Wartha et al. 2021), training population optimization (Hickey et al. 2014, Akdemir et al. 2015, Isidro et al. 2015, Berro et al. 2019), and model selection (Heslot et al. 2012, Crossa et al. 2017).

CURRENT STATUS OF RAPID CYCLE GENOMIC SELECTION

The development of efficient breeding strategies to incorporate genomic selection in plant breeding programs is an active research field and can drastically change a breeding program. A breeding scheme utilizing genomic selection will depend on the crop species and several subcomponents including the breeding program, integrated breeding platforms, and off-season screening (Xu et al. 2020). To date, several breeding schemes to shorten the generation interval have been evaluated to improve yield and other traits (Massman et al. 2013, Beyene et al. 2015, Gaynor et al. 2017, Vivek et al. 2017, Sleper and Bernardo 2018, Beyene et al. 2019). These population advancement strategies which reduce the breeding cycle have been denoted as rapid cycling genomic selection, rapid recurrent genomic selection, and reciprocal recurrent genomic selection (Figure 1).

To date, many empirical and theoretical studies using rapid cycling genomic selection genomic have shown that these strategies can improve the rate of genetic gain per year when used effectively (Table 1). For example, Massman et al. (2013) reported the first empirical study using rapid cycle genomic selection and demonstrated actual genetic gains achieved in a bi-parental temperate maize (*Zea mays* L.) population. This study evaluated testcrosses of 233 inbreds from distinct heterotic groups between B73 and Mo17 under well-watered conditions and advanced these populations using genomic selection and marker-assisted recurrent selection (MARS). The authors reported superior gains with genomic selection for stover yield as well as stover and grain yield indices by 14 to 50% over MARS. Following this study, Beyene et al. (2015) showed the application of genomic selection to improve eight biparental tropical maize populations for grain yield under drought. The authors compared pedigree selection with genomic selection using three rapid cycles of recombination in a year. They reported an average gain per cycle of 0.086 Mg ha⁻¹ across the eight populations. They also reported that the average gain of hybrids derived from cycle three produced 7.3% (0.176 Mg ha⁻¹) higher grain yield than those developed through the conventional pedigree method.

Similarly, Vivek et al. (2017) reported higher genetic gains for drought stress using genomic selection over phenotypic selection in two bi-parental maize populations. Rapid cycle genomic selection was also applied in a multi-parental

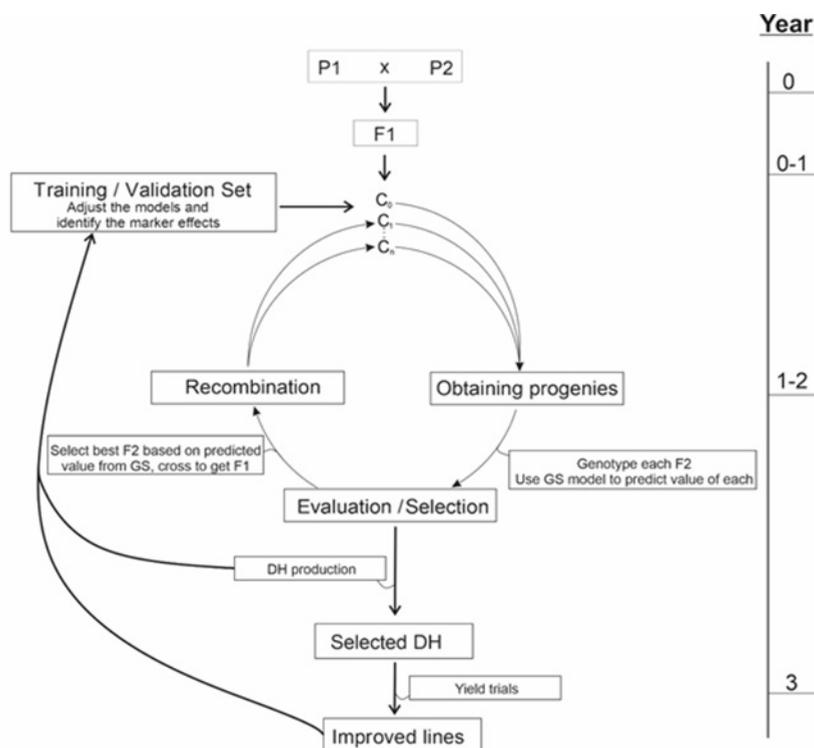


Figure 1. General breeding scheme for recurrent genome selection or rapid cycling genome selection scheme using “n” cycle in a crop breeding program.

Table 1. Summary of parameters and results from published empirical and simulation studies reporting realized genetic gains on recurrent genomic selection

References	Crop	Topology	Trait	Genetic gain [#] (% or efficiency)	Number of genomic selection cycles year ⁻¹
Asoro et al. (2013)	Oat	Empirical	β -glucan concentration	1.12 [*]	2
Beyene et al. (2015)	Maize	Empirical	Yield under drought stress	7.3 [*]	2
Das et al. (2020), Das et al. (2021)	Maize	Empirical	Yield under drought stress	7.5 [*]	2
Gaynor et al. (2017)	Wheat	Simulation	Yield	2.36 - 2.47 [†]	2
Gorjanc et al. (2018)	Wheat	Simulation	Yield	2 - 4 [†]	4
Massman et al. (2013)	Maize	Empirical	Yield + stover index	3.9 [§]	2
Vivek et al. (2017)	Maize	Empirical	Yield under drought stress	24.5 [*]	1
Zhang et al. (2017)	Maize	Empirical	Yield	0.225 [‡]	3

[#] Genomic/phenotypic selection ratio; ^{*} Realized genetic gains from genomic selection compared to phenotypic selection or conventional pedigree breeding method; [†] Two-part strategy (rapid recurrent genomic selection) gains over phenotypic selection; [§] Realized genetic gains from genomic selection compared to marker-assisted recurrent selection (MARS); [‡] Some ratios were not estimated because only realized gains from genomic selection were reported.

tropical maize population (Zhang et al. 2017). In this study the authors reported realized grain yield from cycle 1 to cycle 4 reached 0.100 tons ha⁻¹ yr⁻¹ over a 4.5-yr breeding period from the initial cross to the last cycle with a minimal loss of genetic diversity during the last cycle of genomic selection. Recently, Das et al. (2020) used rapid cycle genomic selection to improve drought and waterlogging tolerance in two multi-parent yellow synthetic maize populations in Asia. This study showed that realized genetic gains after two cycles of rapid cycle recombination of genomic selection under drought stress were 0.110- and 0.135-tons ha⁻¹ yr⁻¹, respectively, and 0.038- and 0.113-tons ha⁻¹ yr⁻¹ under waterlogging in two populations, respectively. The authors also found that genomic selection for drought and waterlogging did not result in any yield penalty under optimal moisture conditions and a genetic diversity analysis of the parents showed an increase in diversity from parents to the first cycle (C₁), but narrowed slightly with the next two cycles of rapid cycling.

The breeding cycle can also be shortened by parental selection in a rapid-cycle recurrent genomic selection program with the aim of improving the breeding value of a given population by decoupling the conventional parent selection from elite breeding populations (Cobb et al. 2019). Similar approaches have been demonstrated for traditional phenotypic recurrent selection programs (Frey et al. 1988, Hallauer et al. 2010). Heffner et al. (2009) suggested the possibility for future elite and parental lines that could be selected based on their GEBVs rather than on their phenotypic performance. Over the past few years breeding schemes using this concept have been described in several crops (Bernardo and Yu 2007, Bernardo 2009, 2010). Computer simulations have become a powerful tool to explore the design of breeding programs and breeding strategies and several studies using them have demonstrated the potential of recurrent genomic selection for long-term population improvement (Jannick 2010, Yabe et al. 2016, Gaynor et al., 2017, Müller et al., 2017, 2018, Gorjanc et al. 2018). Overall these studies determined several important factors that affect long-term genetic see Rembe et al. (2019) for an excellent overview.

Gaynor et al. (2017) proposed a two-part strategy as an extension of the aforementioned studies with the aim to maximize the potential of recurrent genomic selection in a breeding program. This strategy proposes the reorganization of a traditional plant breeding program for inbred or hybrid crops into (i) a population improvement component that develops improved germplasm and (ii) a product development component to identify new inbred varieties or parents for hybrids using traditional breeding program designs (Gaynor et al. 2017, Hickey et al. 2017). The population improvement component uses rapid recurrent genomic selection with the goal to minimize the breeding cycle time to maximize genetic gain per year, while the product development component aims purely at developing inbred lines for releasing as inbred varieties or hybrid parents. The authors used stochastic simulations of entire breeding programs based on the structure of a winter wheat (*Triticum aestivum* L.) breeding program producing double haploids and using a restricted budget for all breeding programs to allow direct comparison using different breeding strategies. The breeding programs included a traditional phenotypic selection wheat breeding program without genomic selection, two breeding programs using the proposed two-part breeding strategy, and three breeding programs using alternative genomic selection strategies. Genomic prediction models were updated using the phenotypic and genomic data generated during the product development component. The authors found that the two-part strategy generated a rate of genetic gain between 2.36 and 2.5 times

that of a conventional program and between 1.31 and 1.46 times more than a standard genomic selection breeding strategy which only increases selection accuracy. The results from this study demonstrate that the two-part strategy is a cost-effective and aggressive strategy to implement genomic selection in plant breeding programs by reducing the breeding cycle. Ultimately, adopting this breeding strategy would require a breeding program to run on solely genomic selection and would need large costly training populations to achieve acceptable prediction accuracy, which may not be feasible in smaller breeding programs for some years (Cobb et al. 2019). While some commercial breeding programs may be leading the way on this breeding strategy, to date few public breeding programs have reported any empirical results for the two-part strategy.

While the previous studies have evaluated recurrent genomic selection schemes, few breeding programs have yet to adopt them or have been reported. For example, in a recent study, Bernardo (2021) mentions that the reluctance for maize breeders to adopt recurrent genomic selection is the compromise between higher genetic gains and the lengthier period required to develop hybrids whose performance reflects such gains. In this same study, the author used computer simulations to assess if a two-cycle genomic selection can increase genetic gains in maize using similar resource allocation compared to a one-cycle genomic selection and phenotypic selection breeding scheme. This study found that the two-cycle genomic selection scheme can increase genetic gains without increasing the cost or time in a maize breeding program. Furthermore, the largest gains from the two-cycle genomic selection were 124-178% of the largest gains from phenotypic selection and 112-135% of the largest gains from one-cycle genomic selection. The author concluded that the two-cycle genomic selection is a compromise to the one-cycle genomic selection with similar time and costs. Overall, results demonstrate that incorporating a single recombination step can lead to increase gains leveraging cost-efficient genotyping over more costly phenotyping.

ADVANTAGES AND CHALLENGES OF RAPID CYCLING METHODS

In a conventional breeding program, rapid cycling genomic selection can shorten the breeding cycle and reduce the cost of phenotyping, while increasing the rate of genetic gain. However, rapid cycling genomic selection can have a profound impact on genetic diversity as revealed by simulation studies (Jannink 2010, Gaynor et al., 2017). For example, in Gaynor et al., (2017) the differences in genetic variance depended on multiple factors including the breeding strategy used, the effective population size, selection intensity, selection accuracy, and the number of cycles per year for each breeding program. As mentioned earlier in this review, genomic selection can effectively address several parameters of the breeder's equation which can ultimately impact loss in genetic variance. As a result, Gorjanc et al. (2017) discussed some important factors when considering rapid cycling genomic selection to ensure large genetic gains: number of cycles ($C_0, C_1 \dots C_n$) used, size of the population, number of parents, accuracy of genomic prediction, maintenance of genetic diversity, and costs. While the author was referring to the two-part strategy approach proposed by Gaynor et al. (2017), these factors should be considered in many of the rapid cycling schemes mentioned in this review. Increasing the number of cycles in a rapid cycling genomic selection scheme can increase the costs required to genotype many selection candidates as well as other operating costs. Managing the size of the training population and the number of parents will also need to be balanced in order to achieve an acceptable prediction accuracy for a breeder to make selections on. Increasing the number of cycles can also reduce the amount of genetic diversity and ultimately reduce long-term genetic gains in a breeding program. For example, in the simulation performed by Gaynor et al. (2017), all breeding programs lost genetic variance over time. However, the rate of loss differed depending on the breeding strategy. While the breeding strategies using genomic selection without reducing the breeding cycle showed a large drop in initial genetic variance relative to the conventional approach, the two-part strategy led to a larger initial decrease followed by a more rapid decrease in genetic variance. Thus, Gorjanc et al. (2018) proposed an optimal cross selection strategy to reduce the loss of genetic diversity and reduce the drop of genomic prediction accuracy with rapid cycling. Furthermore, in an optimal breeding pipeline, the genetic diversity should not be affected after cycles of GS, as mentioned by Dias et al. (2020). On the other hand, the increase in population size at the expense of performing several parental crosses and fewer recombination cycles comprises the selection performed under more narrow selection intensity. It tends to deliver greater genetic gains as well, despite the increase in overall genotyping costs. Therefore, a major challenge in the rapid cycling genomic selection method will be to balance the long-term genetic gains, maintain the genetic diversity, and handle increasing genotyping costs.

GENERAL CONSIDERATIONS FOR THE FUTURE

While rapid cycling genomic selection can potentially increase the rate of genetic gain in public-sector breeding programs. Breeding programs must also have the capacity to undertake several changes and meet specific criteria to successfully deploy genomic selection. For example, breeding programs should 1) have an optimal breeding pipeline for population improvement and line development; 2) have the capacity to collect high quality phenotypic data through proper experimental design; 3) be able to analyze phenotypic or pedigree analysis; 4) have the appropriate resources for collecting genotypic information for their crop. Meeting these requirements prior to evaluating genomic prediction should maximize the potential of genomic selection in a breeding program. If genomic selection is successful in a breeding program, moving towards a more aggressive breeding strategy such as rapid cycling genomic selection can be considered after computer simulated assisted scenarios to help re-design a breeding program based on resource allocation and crop biology. Ultimately, through a series of steps breeding program can evolve to adopt these breeding genomic-assisted breeding strategies.

Rapid cycling genomic selection has tremendous potential to increase the genetic gains in plant breeding programs. However, these methods have not been adopted due to genotyping costs that are still considerably high for several public-sector plant breeding programs or smaller breeding programs without the resources of capacity to undertake a large genotyping effort. Therefore, more effort is needed to evaluate rapid cycling in different crop species and model breeding program in terms of resource allocation to redesign current breeding programs to integrate genomic selection. Efforts like this and that of CGIAR centers like the International Maize and Wheat Improvement Center (CIMMYT) to utilize rapid cycling genomic selection in Africa (Beyene et al. 2015) and Asia (Vivek et al. 2017) provide excellent examples in public-sector breeding programs that will help increase the rate of genetic gain in maize and other important crops.

CONCLUSIONS

Reducing the breeding cycle will likely increase the rate of genetic gain in plant breeding programs. However, methods to reduce the breeding cycle have not been adopted as routinely as other components of the breeder's equation to increase the rate of genetic gain per year. Plant breeding programs continue to struggle to re-design breeding programs to fully integrate genomic selection and alter breeding pipelines all together. While the incorporation of simulation tools will allow for more computational based decision making within breeding programs to deploy genomic selection, most plant public-sector breeding programs in both developed and countries may still find bottlenecks in the cost of genotyping or managing large training populations. Continued investment to modernize plant breeding programs is required to adopt modern technologies in order to maximize the rate of genetic gain. Ultimately, rapid cycling genomic selection offers an effective breeding strategy to achieve rapid genetic gains to critically meet future food security in the face of climate change.

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