 doi:10.20944/preprints202009.0308.v1

Review

Accelerating tomato breeding by exploiting genomic selection approaches

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Department of Agricultural Sciences, University of Naples 'Federico II', Portici, Italy, Running title: Tomato genomic selection; Elisa Cappetta (elisa.cappetta@unina.it); Giuseppe Andolfo (giuseppe.andolfo@unina.it); Antonio Di Matteo (antonio.dimatteo@unina.it); Amalia Barone (ambarone@unina.it); Luigi Frusciante (fruscian@unina.it); Maria Raffaella Ercolano (ercolano@unina.it)

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Abstract: Genomic selection (GS) is a predictive approach that was build up to increase the rate of genetic gain *per* unit of time in breeding programs. It has emerged as a valuable method for improving complex traits that are controlled by many genes with small effect. GS enables the prediction of breeding value of candidate genotypes for selection. In this work we address important issues related to GS and its implementation in tomato breeding context. Genomic constrains and critical parameters affecting the accuracy of prediction in such crop such as phenotyping, genotyping training population composition and size and statistical method should be carefully evaluated. Comparison of GS approaches for facilitating the selection of tomato superior genotypes during breeding program are also discussed. GS applied to tomato breeding has already shown to be feasible. We illustrated how GS can improve the rate of gain in elite lines selection, descendent and in backcross schemes. The GS schemes begin to be delineated and computer science can provide support for future selection strategies. A new breeding framework is beginning to emerge for optimizing tomato improvement procedures.

Key word: Tomato; genetic breeding value; training population; genotyping; marker effect; phenotyping; selection schemes

1. Background

Tomato (*Solanum lycopersicum*) is one of the most important vegetable crops worldwide. It possesses unique properties, offering a rich source of minerals (potassium, magnesium, phosphorus) and antioxidant compounds, which prevents cardiovascular, cancer diseases and strengthens our immune system [1]. Tomato is an autogamous diploid species, with a modest genome size (~900 Mb) and a relatively short life cycle. As a model plant, numerous genetic and molecular tools have been developed for tomato species, including a high-quality draft genome sequence, high-density genetic maps, high-throughput molecular markers, introgression lines and mutant collections (Tomato Genome Consortium- [2]). In addition, hundreds of genomes from landraces, cultivars, and wild relatives have been re-sequenced, revealing a relatively low molecular diversity but high rate of chromosome rearrangements due to traces of wild introgressions [3].

Tomato crop genetic basis became narrow along the process of domestication, preventing intra-populational breeding strategies to provide satisfactory genetic gains [4]. Besides the low genetic variability that limits breeding gains of conventional and modern selection schemes, tomato is tolerant to inbreeding and this allows the generation and maintenance of inbred lines. Therefore, the

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recombination of the genetic variability has been an excellent alternative for obtaining superior genotypes [4]. Moreover, the retaining of genome segments from wild relatives, used for introgressing agronomically relevant traits such as resistance to diseases and quality traits [5,6], largely contributes to the genetic variability within the cultivated tomato gene pool.

In the early 1980s, the development of different molecular marker systems drastically changed the fate of plant breeding. Molecular markers were mainly integrated in traditional phenotypic selection (PS) by applying marker-assisted selection (MAS) to improve the plant selection process through the inclusion of chromosomal segments containing quantitative trait loci (QTLs) or single genes [7,8,9]. Several research articles concerning the identification of tomato QTLs and major genes conferring resistance to biotic and environmental stresses have been reviewed in [5,10]. Molecular markers have been also used in tomato to map genes or QTLs for environmental stresses and some flower and fruit-related traits (reviewed in [11]). However, MAS is more suitable for application concerning simple traits with a few major-effect genes than for complex traits controlled by a large number of minor genes [12,13].

Genomic selection (GS) provides new opportunities for increasing the efficiency of plant breeding programs for traits with polygenic inheritance [13,14,15]. The potential breeding value of an individual is estimated using genomic-based data such as single nucleotide polymorphisms (SNP). Recent high-throughput genotyping (HTG) systems helps to generate several thousand of SNP markers allowing entire genomes to be scanned at a reasonable cost. Genomic screening of breeding populations can accelerate the genetic gain obtained at each cycle, especially when selection is performed for traits with low heritability. Although the effect of each marker is very small, a large amount of genome-wide marker information has the potential to explain all the genetic variance [16].

The development of statistical methods capable of accurately predict marker effects has led to the breakthrough of GS increasing the rate of genetic gain per unit of time. GS combines genotypic and phenotypic data from a training population (TRN) in a training set (TRS) to obtain the genomic estimated breeding values (GEBVs) of a testing set (TST) which has been genotyped but not phenotyped. The GS model will be then employed to predict breeding values of not phenotyped individuals in the next selection step (Figure 1).

 doi:10.20944/preprints202009.0308.v1

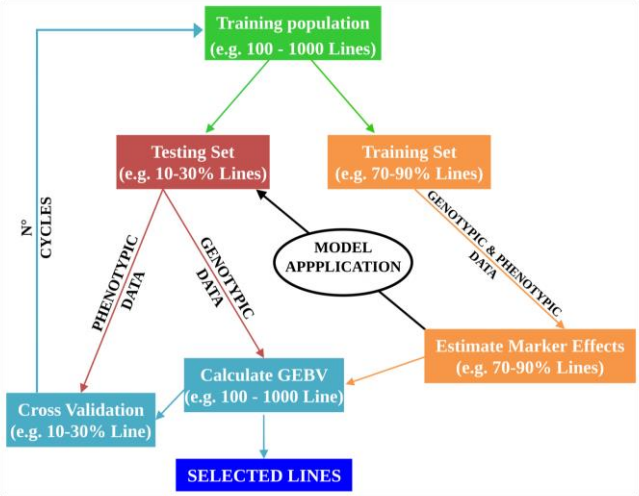

Figure 1. Flowchart of a genomic selection (GS) breeding program. GS overview with cross validation using a training set (70-90% out of 100-1000 lines) to estimate marker effects in order to get a genomic estimated breeding value (GEBV) of lines in the testing set (10-30% out of 100-1000 lines). Finally, phenotypic and genotypic data of the training set are used to setup the prediction model.

In tomato, pioneer studies concerning the application of GS for yield-related traits were reported for fresh market varieties and wild related species [17,18]. More recently, Yamamoto et al. [19] assessed the potential of GS to increase soluble solids content and fruit weight in F1 tomato varieties, whereas Liabeuf et al. [20] reported the implementation of a GS approach to develop bacterial spot resistant

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tomato lines. GS models were widely exploited for predicting phenotypes of progeny and parents, although the efficiency varied depending on the parental cross combinations and the selected traits [21]. Optimized and validated GS protocols are still needed in tomato. Several GS programs in tomato are still in progress, thus the impact of factors affecting the implementation and the accuracy of the model have not yet been evaluated while their optimization for tomato breeding is still required. Among these factors, phenotyping procedures, TRN size, genetic relationship between individuals in TRS and TST, genotyping platforms, marker quality metrics and design of GS schemes should be further investigated. Here we discussed the application in tomato breeding schemes of GS within and across breeding generations, as well as its potential to select parents based on their assessed GEBV.

2. Tomato GS schema implementation

Recent studies have demonstrated that the establishment of GS experiment optimal parameters requires a careful evaluation of key factors. Selection response depends on the precision of the phenotyping and genotyping methods used to obtain the GEBVs (including size of TRN, marker density, marker technology), knowledge of the genome structure and marker linkage disequilibrium [21].

The success of modern breeding programs based on genomic techniques strictly depends on precision of measurements related to phenotyped traits [22]. Digital instruments with scalable technologies can improve the precision of phenotyping [23] and accelerate the selection. Recent technologies have being used to acquire specific data on tomato traits with the aim of boosting the precision and the throughput of measurements, the size of analyzed plant populations and, thus, enhancing the accuracy of the predicted phenotypic value and the genetic gain [24,25].

The appropriate TRN size and composition are also critical for gaining high prediction accuracy. A positive correlation between prediction accuracy and TRN size was confirmed in several species [26,27]. However, the optimal TRN size seems to be highly influenced by the relatedness of TRS and TST [28,20,29]. The highest prediction accuracies were found using TRS with a strong relationship to the TST [15,30,31]. Indeed, when the TRS and TST are unrelated, marker effects could be inconsistent due to the presence of different alleles, allele frequencies, and linkage phases. Developing *ad hoc* TRN is crucial and update the TRN at each cycle could improve the prediction accuracy since that the segregating population could accumulate genetic diversity and gene frequencies may change at each selection cycle [20].

To capture as much informative loci as possible an appropriate abundance of markers is required [32]. In this regard, genotyping-by-sequencing (GBS) can be used to efficiently generate high-density marker panels. Alternately, the cDNA-based GBS technique (RAR-seq restriction site associated RNA sequencing) may detect conserved SNPs associated to a candidate mutation directly at the expression level [33]. Recently, a customizable method for tomato targeted genotyping, named single primer enrichment technology (SPET) was developed for improving the panel design and increasing the multiplexing levels of tomato genotyping [34]. Previous GS data can help to design an optimized suite of markers for next steps. Liabeuf et al. [20] reduced the initial "SolCAP array" of 7,700 SNPs [35] to screen populations with limited recombination. Moreover, the prediction accuracy may be also affected by minor allele frequency threshold (MAF) [32]. Establishing methods for efficiently transferring validated genome signatures within tomato breeding selection procedures is also relevant. Linkage drag caused by recombination suppression can be reduced by estimating the effects of relevant markers improving prediction performance. Indeed, large gene introgression fragments in tomato cultivars from *Solanum* wild species caused drastic chromosome landscape changes. The *Solanum peruvianum* introgression carrying the tomato mosaic virus (ToMV) resistance gene *Tm2* can cover up to 79% of chromosome 9 in modern varieties [3].

In the framework of GS, several statistical methods have been developed to estimate the marker effects in tomato [20]. The choice of the most appropriate method should be finalized to the specific context, considering the model complexity (genetic architecture, population size and heritability) and the computation requirements [36,37]. Ridge regression best linear unbiased prediction (RR-BLUP) and genomic best linear unbiased prediction (G)BLUP [38] are suggested when assessing a trait that

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is affected by many small-effect genes using close TRN relatives. On the other hand, when traits are controlled by major-effect QTLs or when considering prediction of unrelated individuals, a higher prediction accuracy can be obtained by Bayesian methods [39]. However empirical studies suggest that there are no major differences between regression-based methods and Bayesian GS in tomato [20].

3. Applying GS in tomato crop improvement

Several constraints can affect the genetic gain of a GS program in tomato. The implementation of GS requires the optimization of field trial management and agricultural practices, seed production, phenotyping, sample collection and sequencing [40]. Moreover, as discussed above, parameters such as inbreeding level of populations, number of individuals to be assessed, and marker metrics, should be carefully evaluated to effectively run a GS-assisted breeding scheme. It can be estimated that, for tomato breeding programs, the genotyping work to complete GEBV predictions requires approximately three months. Once these issues have been addressed, the GEBVs can be calculated both to perform parental line selection and to evaluate the overall performance of the progenies in a descendent selection or backcross schemes. The selection decision will be achieved based on the higher GEBVs for each tested trait on the overall average of traits or as 'indices' of GEBV from several traits following selection priorities.

4. Evaluation of Elite lines

The first step in tomato F1 hybrid variety development is the selection of elite parents to maximize the genetic variability exploitation. Elite germplasm represents a core collection of cross-compatible genotypes enriched for some favorable alleles [41]. In a GS-assisted breeding scheme for tomato F1 hybrid development, the decision to select parental lines is based on their breeding value (i.e., the mean performance of the progeny of a given parent) that consequently requires to be estimated accurately. Consistently, Yamamoto and collaborators [19] used a set of 96 big-fruited F1 tomato varieties to develop GS models, and the segregating populations obtained from crosses were used to validate the models. Consequently, the GS models were used to successfully predict parental combinations generating superior hybrids using progeny genotypic and phenotypic data for soluble solids content and total fruit weight. However, the efficiency of predictions varied depending on traits and parental combinations. While the need for fixing favorable alleles in the gene pool leads to increase inbreeding, the GS selection gain is dramatically reduced in small populations with narrow genetic variability. The managing of elite genetic diversity to increase the frequency of favorable alleles over time can highly benefit from GS approaches [41]. The prediction accuracy of parent cross ability could improve with the assessment of a higher number of selfing progenies. Thanks to the advances made in tomato genome knowledge and genotyping technologies, breeders can easily identify valuable alleles in elite germplasm [42,43] and create new lines combining these valuable alleles using a set of validated markers.

5. Descendent selection schemes

In tomato, breeders commonly take advantage of useful genetic variability by recycling the best-performing varieties that have been successful for a given area by Single Seed Descendent (SSD) schema where each generation derived from the former, taking only one seed from each parent plant. Nearly all steps can be conducted in the greenhouse, making this a method of choice for accelerating breeding in areas that do not benefit of a growing season long enough [43]. In the classical SSD scheme, the choice of tomato parental lines is very critical to ensure a higher additive breeding value since self-fertilization increases inbreeding level by 1⁄2 at each cycle. In the SSD scheme, no selection is conducted until the last generation (generally F6-F7), so the phenotyping of a larger number of lines could be challenging. The integration of the GS approach in the SSD could result in reducing the number of selfing generations thus shortening the overall schema and decreasing the phenotyping effort (Figure 2). Because the prediction accuracy is generally higher when LD is high, an increase of the breeding gains is expected when applying GS in the earliest heterozygous

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segregating generations (i.e., F2-F4). Therefore, these generations could be successfully used for developing the GS model, and subsequently GS prediction could assist selection in the following generations. Genomic data can accurately track the best performing plants along the generations, and the approach can successfully lead to the selection of individuals with the highest GEBV.

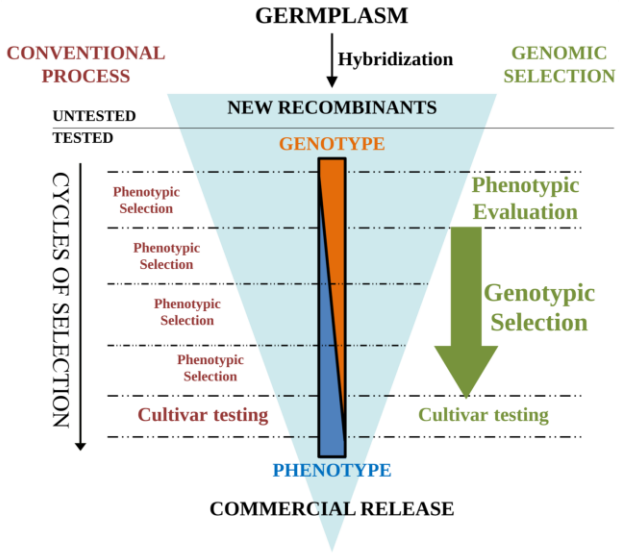

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Figure 2. Comparison of genomic selection (GS) and conventional selection in tomato breeding programs. Screening of recombinant lines through GS approaches optimizes the genetic gain obtained in each selection cycle. Breeding cycles (horizontal dashed lines) are shortened by removing phenotypic evaluation of lines before training population (TRN) evaluation for the next cycle.

6. Backcross schemes

Backcrossing is a quite popular breeding scheme where a valuable trait is introgressed from a donor parent into the genomic background of a recurrent parent. In tomato breeding, backcrossing schemes with exotic or elite materials are widely used to introduce favorable traits. However, the constant introduction of novel alleles and the linkage drag, the crossing with old varieties or exotic material with low breeding value as well as the extended breeding cycles deriving from complex crossing scheme, can reduce the genetic gain *per* year. The response to genetic selection achieved through the selection of lines with high breeding value in a segregating population can be certainly improved by GS (Figure 2). A variant of the classical backcross scheme, where lines of each generation are selected based on recurrent parent breeding value, allowed obtaining high rates of genetic gain [44,45]. By combining GS with single-marker assays, genes with major effects can be also selected within each offspring following the cross with the recurrent line. In this way, the GS approach is expected to additively increase the genetic gain at each generation. Candidate genotypes for selection, carrying specific alleles (i.e, resistance traits) can be identified using genotyping platforms that include gene specific diagnostic markers or integrate single locus data obtained with different technologies. In addition, among markers used in the GS model implementation, a subset of them identifying undesirable segments of wild donor can be selected. In fact, large wild genome segments (between the 30 and 70% of the whole chromosome) were found to be incorporated due to resistance gene introgressions on specific chromosome in cultivated tomatoes [3]. As an extension of this approach, genome-wide selection with high-throughput markers in BC1 could be even more efficient and the recovering of the recurrent parent genome could be increased from generation BC1 to BC3 without affecting favorable trait introgression.

7. Conclusions

The evaluation of complex traits such as disease resistance genes and QTLs for quality traits with high efficiency in a segregating population can be a difficult task for tomato breeders. The implementation of GS in breeding schemes, supporting the selection of improved genotypes, can accelerate genetic achievable gain. Major GS implementation challenges were highlighted here, including model development, genotyping quality, optimal GS incorporation stage and indications for overcoming these issues were also discussed. While the methodological procedures begin to be delineated, the optimal way to incorporate GS in a breeding scheme remains to be empirically defined. Important features for the success of GS under different breeding scenarios should be assessed. Advancements in genotyping efficiency and phenotyping technologies will facilitate the adoption of GS in tomato breeding. A future update of existing selection schemas may be achieved using computer simulations for investigating different strategies to face the selection process gaps.

Author Contributions: EC was centrally involved in writing the manuscript and in drafting figures. GA revised the manuscript and produced the figures. ADM revised the text. AB provided important suggestions for improving the manuscript. LF critically revised the manuscript. MRE conceived the study, coordinated work and contributed to manuscript writing. All of the authors read and approved the final manuscript.

Funding: This work was supported by the Italian Ministry of University and Research and carried out within TomGEM Project that has received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No 679796.

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Conflicts of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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