Optimizing QTL introgression via stochastic simulations: an example of the IRRI rice breeding program

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Research Article

Keywords: genomic selection, qualitative traits, breeding value, selective sweep, background recovery,

Posted Date: July 6th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1780978/v1

Optimizing QTL introgression via stochastic simulations: an example of the IRRI rice breeding program

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ABSTRACT

A key limitation in the ability of breeding programs to leverage benefits of major-gene marker-assisted selection is the availability of those genes in appropriate elite germplasm. In this context, our study compared three strategies to develop new recipients for QTL introgression (Background recovery (BG), Selective sweep (SS), and Breeding values (BV)) in a short-term breeding program (over five breeding cycles). Furthermore, we evaluated two different numbers of recipients (10 and 20) in the introgression process and how they influence the population performance and the QTL fixation over cycles. Finally, we used rice as a model of a self-pollinated crop and implemented stochastic simulations. Each strategy was simulated and replicated 40 times. Regardless of the selection strategy used, the QTL introgression resulted in substantial penalties in yield performance. However, introducing fewer new parents to the augmentation process minimized this effect. Conversely, the time required to achieve fixation of target QTLs showed substantial differences, with selection for BV during augmentation out-performing other methods. Overall, the BV_10 strategy (10 parents selected based on genomic estimated breeding values) displayed the best trade-off between reduced penalty from introducing new QTLs with a reasonable speed at which those QTLs can achieve fixation over subsequent breeding cycles.

Keywords: genomic selection; qualitative traits; breeding value; selective sweep; background recovery;

DECLARATIONS

Funding: AGGRi Alliance (Accelerated Genetic Gain in Rice in South Asia and Africa - OPP1194889) - Bill and Melinda Gates Foundation (BMGF).

Conflicts of Interest: The authors declare no conflict of interest.

Availability of data: all the data is available as supplementary information.

Code availability: all the scripts are available as supplementary information.

Ethical standards: Not applicable

AUTHOR CONTRIBUTION STATEMENT

JDP and RFN contributed equally to developing the hypothesis, analyzing, interpreting the results, and writing. All authors read and approved the final manuscript.

ACKNOWLEDGMENTS

To IRRI Breeders, Dra Amelia Henry, Dr. Waseem Hussain, and the Excellence in Breeding - CGIAR platform for the comments and suggestions.

KEY MESSAGE

Selecting recipients based on breeding values during the augmentation process is best for QTL introgression in breeding populations.

INTRODUCTION

Modern farming is facing major challenges in the coming years. Increases in population and standards of living are projected to double the demand for grain crops by 2050. At the same time, the effects of climate change are already being felt. Temperatures have already risen by 0.95ºC in the decade 2009 to 2018 (Ting and Vasel-Be-Hagh 2022) extreme weather events such as droughts, heat waves, and typhoons are predicted to increase in frequency. At the same time, crops are increasingly being grown on more marginal land, both due to expanding cropping area, displacement from urban growth, and degradation of existing farmland. Disease pressures shift as cropping intensity and opportunities for spread to new regions increase. In all, rice production is predicted to require an increase of 117% by 2050 to offset these various pressures (Ray et al. 2013). Current trends in productivity due to breeding are 1% or less (Ladha et al. 2021; Khanna et al. 2022), far short of the 2.4% predicted to be required to meet these demands.

Clearly, a major revolution in the speed and effectiveness of breeding for major crops is required. Therefore, many initiatives have increased genetic gains to 2.4% or higher (Ladha et al. 2021; Nayak et al. 2022). These initiatives emphasize mechanisms to reduce the breeding cycle time, increase selection accuracy, increase selection intensity, etc. Adopting modern breeding methods based on quantitative genetics, such as enabling genomic predictions, help address many of these parameters. However, concomitant with these quantitative genetics approaches, substantial value also lies in more qualitative genetics systems. Selection for major genes and QTLs enables rapid improvement of a particular trait, reducing the time required to produce new varieties substantially better than previously available (Kumar et al. 2014). Major-gene selection is also typically applied at different stages of the breeding process, so it is at least partially decoupled from selection for traits under polygenic control, allowing gains in a wider variety of traits per breeding cycle (Hospital and Charcosset 1997). Crucially, the relative simplicity of selection for major genes allows these to be moved around rapidly within and between breeding programs, providing agility that will be essential in meeting the rapidly changing demands of climate change.

A key limitation in the ability of breeding programs to leverage these benefits of major-gene marker-assisted selection is the availability of those genes in appropriate elite germplasm (Bhatia et al. 2016; Janaki Ramayya et al. 2021). Studies on current breeding programs have shown that about half of the genes and QTLs

that could be useful are not found in current elite material; a further 15% or so are present at very low levels (Cobb et al. 2019b, a; Juma et al. 2021). Furthermore, these genes are mostly only available from very poorly-performing landraces or occasionally very old breeding material. This means breeders who use these major genes will face a major decrease in the performance of the resulting material (negative genetic gains for yield). Thus, breeders currently must choose between making short-term genetic gains for yield versus the long-term potential for agility in improving a range of traits.

The standard approach to offset this tradeoff is (marker-assisted) introgression of the target gene/QTL into elite genomic backgrounds. While this takes a dedicated effort, the result is clean material in an elite genomic background that can then be used to introduce the new gene into mainstream breeding efforts. Key quality measures in this process include the size of introgression (eliminating linkage drag) and recipient recovery rates (RPR, eliminating drag from the undesirable donor genome) (Hospital and Charcosset 1997). However, this approach suffers two major drawbacks: first, introgression is often a tedious and expensive process, especially if coming from a particularly poor-quality landrace or a related wild species. Thus, the initial introgression typically focuses on a single introgression population and will only produce one or a small number of converted lines with the new gene. Breeders cannot use these too extensively in their crossing program lest the overall genetic diversity of their program become depleted from the repeated use of the same parent. This means the penetration of the new gene into mainstream breeding will take multiple breeding cycles, which often last four years or more.

The second major drawback of current introgression processes is they will always take several generations to eliminate the highly undesirable genome of the original donor landrace (Koudandé et al. 2000). This means even if they start with the best, most cutting-edge material from breeding programs as a recipient, by the time introgression is complete, the performance of the current breeding cohorts has improved, and the yield performance of the converted recipient is no longer within the range desired for current parents.

To overcome these drawbacks, a 2-stage process has been proposed to introduce new genes into the mainstream breeding process (Cobb et al. 2019b, a). Firstly, deployment (or conversion) creates a high-quality conversion of a modern elite background. Deployment is heavily focused on quality: ensuring no undesirable genomic contribution of the original landrace donor remains in the final product. However, as mentioned, this

suffers from the above two drawbacks. To overcome this, the second stage, which is described as line augmentation, aims to rapidly introgress the new gene into a wide variety of elite genomic backgrounds as quickly as possible to enable rapid and wide-ranging impact in the breeding program. Line augmentation is thus focused primarily on quantity and speed rather than quality; it cannot address issues of breaking linkage drag, fertility problems, or eliminating the undesirable genomic background. It requires high-quality donor material from the deployment process (or existing elite donors if available).

This concept of line augmentation as a separate and distinct activity appears to be fairly new, and many questions remain on optimizing the process to achieve maximum results (Cobb et al. 2019a). Besides scale and speed, other quality control parameters for line augmentation could include recovery of the (new elite) recipient background. The aim is to minimize the influence of the first elite donor on reducing genetic diversity in the elite breeding program and to have? recombinant selection around the target genes to embed these in additional elite haplotypes, thus avoiding selective sweeps. Selective sweep refers to a process by which a new advantageous mutation eliminates or reduces variation in linked neutral sites as it increases in frequency in the population (Nielsen et al. 2005). In this context, another option for a fast line augmentation process is the application of new methods such as genomic prediction (Ødegård et al. 2009), in order to select parents to be introgressed in the breeding population, having the target gene/QTL. This selection approach disregards the similarity between recombinant lines with the donors but prioritizes their genomic breeding values. For that, marker effects estimated based on the elite breeding population would be used. Therefore, it might reduce the well-known penalty in quantitative traits, such as grain yield, caused by introgressions in elite populations (Dar et al. 2018).

Based on the above, the raised question is which measures or methods will ensure the most rapid utilization of target genes in the mainstream breeding program. Unfortunately, comparing all these possibilities using empirical data would be impractical, costly, and time-consuming. Also, it will be difficult to detangle the specific germplasm background effect on the conclusions, not allowing extrapolation of the results to more general applications or rules of thumb. Hence, the objective of this study was to use stochastic simulations to examine the effectiveness of three methods in promoting the uptake and fixation of new genes in the mainstream breeding program.

MATERIAL AND METHODS

Our study compared three strategies to develop new recipients for QTL introgression in a short-term breeding program. For that, we used rice (*Oryza sativa* L.) as a model of self-pollinated crop and stochastic simulations performed by the *AlphaSimR* package (Gaynor et al. 2021). Furthermore, we evaluated two different numbers of recipients in the introgression process and how the population performance and the QTL fixation over breeding cycles was influenced.

Historical population and genetic parameters

The historical rice founder population was simulated as 3,000 unique diploid inbred individuals, with 12 chromosome pairs each, using a Markovian Coalescent Simulator (MaCS) (Chen et al. 2009). For that, 1,644 biallelic segregating sites were considered, uniformly distributed across chromosomes and 360 segregating loci randomly sampled as quantitative trait nucleotides (QTN), and 994 segregating loci as single-nucleotide polymorphism (SNP) (Arbelaez et al. 2019). The genome size (cM) and chromosome sizes follow those values described by (Li et al. 2008).

The target of the simulation was a quantitative trait (such as grain yield, GY) and three qualitative traits (for instance, QTL controlling biotic stress resistance or abiotic stress tolerance). For the former, the genetic parameters obtained by (Li et al. 2008) were used. Each QTN received randomly allocated additive and dominance effects. Genetic values for each genotype were obtained by summing all additive and dominance effects for all QTN. Additive effects (a) were sampled from a gamma distribution with scale and shape parameters equal to 1 and randomly assigned for each QTN. Similarly, dominance effects (d) for each QTN were computed by multiplying the absolute value of its additive effect (a_i) by locus-specific dominance degree (δ_i). Dominance degrees were sampled of a Gaussian distribution with $\delta_i \sim N(\mu_\delta, \sigma_\delta^2)$, where μ_δ is the average dominance degree equal to 0.22 and σ_δ^2 is the dominance variance equal to 0.50. Dominance effects were assigned for each QTN according to the equation below:

$$d_i = \{0, \quad if\ QTN\ is\ homozygous\ \delta_i \times |a_i|, \quad if\ QTN\ is\ heterozygous$$

Phenotypic values for the quantitative trait were obtained by adding a random error sampled of a Gaussian distribution with mean equal to 0 and variance (σ_e^2) equal to 1, which was defined by broad-sense ($H^2 = 0.53$) and narrow ($h^2 = 0.50$) heritabilities.

We consider three independent characteristics regarding the qualitative traits, each controlled exclusively by one additive QTL, with heritability equal to 1.0. Also, we consider that all the traits were independent in terms of segregation and genetic correlations (Koudandé et al. 2000).

Base population and burn-in phase

In order to obtain the base populations, we selected two sets of 60 individuals from 3,000 lines of the historical population based on their superior phenotypic values for the quantitative trait (Fig. 1). The former, without any favorable allele for the three QTLs, and the latter with two copies for the favorable QTLs. As a starting point to consider a program representative of current 4-year rice breeding programs, we ran three traditional recurrent selection cycles, totaling 12 years of breeding in the burn-in stage. First, these 60 parental lines were crossed to generate 30 F_1 plants, which were selfed to produce 230 F_2 plants from each cross (Cobb et al. 2019b). Then, SSD was conducted during the line fixation stage, from F_2 until the F_6 generation, where the best individuals were selected based on their phenotypic values to find the next breeding cycle. Finally, after three recurrent breeding cycles, we obtained the two base populations to evaluate the augmentation/introgression schemes.

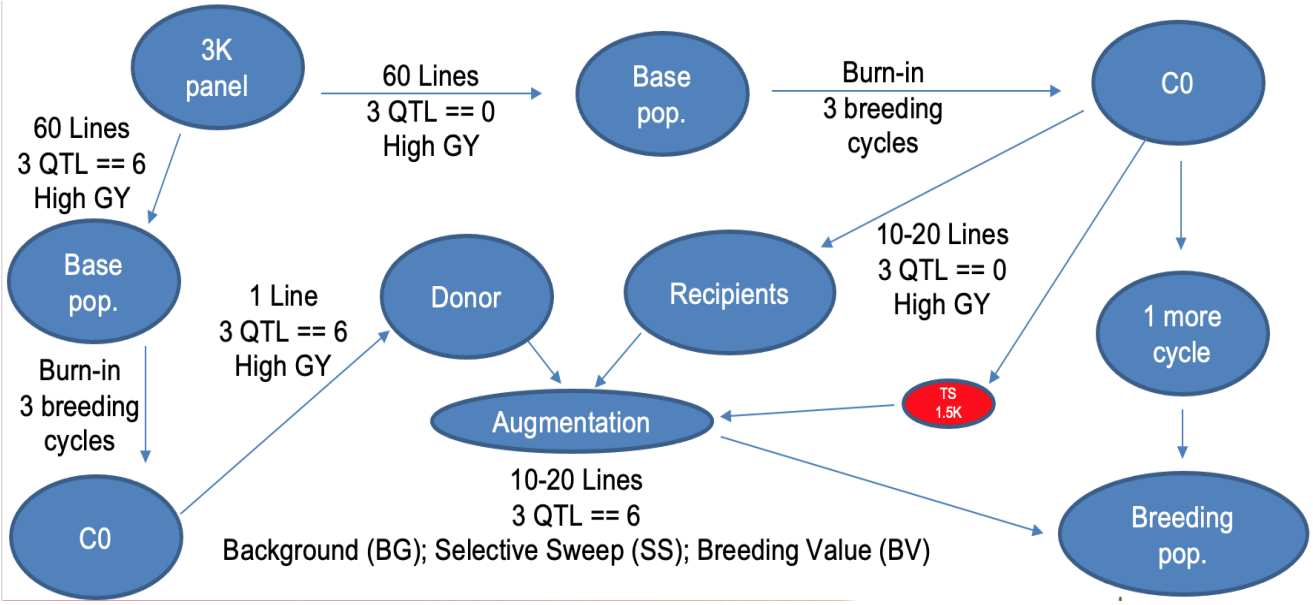

Fig. 1. Base population development, donors and recipients, and the methods used for augmentation. (C0: Breeding cycle zero; 3K panel: rice germplasm panel with 3,000 individuals; TS 1.5K: Genomic prediction training set composed of 1,500 individuals).

We selected only the best line from the donor population (QTL == 6), representing a donor with an elite genetic background. On the other hand, from the recipient population, we considered two scenarios, 10 or 20 superior lines, to develop the newest recipients in the augmentation process.

Line augmentation

The objective of line augmentation is to diversify the range of elite genomic backgrounds containing new QTLs as rapidly as possible in order to introduce this as parental material in the wider breeding program. The starting point is an elite donor line in which effects such as linkage drag and elimination of highly unfavorable genomic background have already been eliminated (Platten et al. 2019; Cobb et al. 2019a)To minimize the time required for delivery of products, introgression schemes focused on a single backcross with recipient lines, with BC_1F_3 fixed lines used as the material to introduce to breeding programs. During the augmentation framework (Fig. 2), in addition to the requirement of possessing the three target QTLs, we

compared three possible methods to select favorable progeny and, ultimately, the upgraded elite lines that can be used as donor parents in further ongoing breeding efforts (Fig. 1).

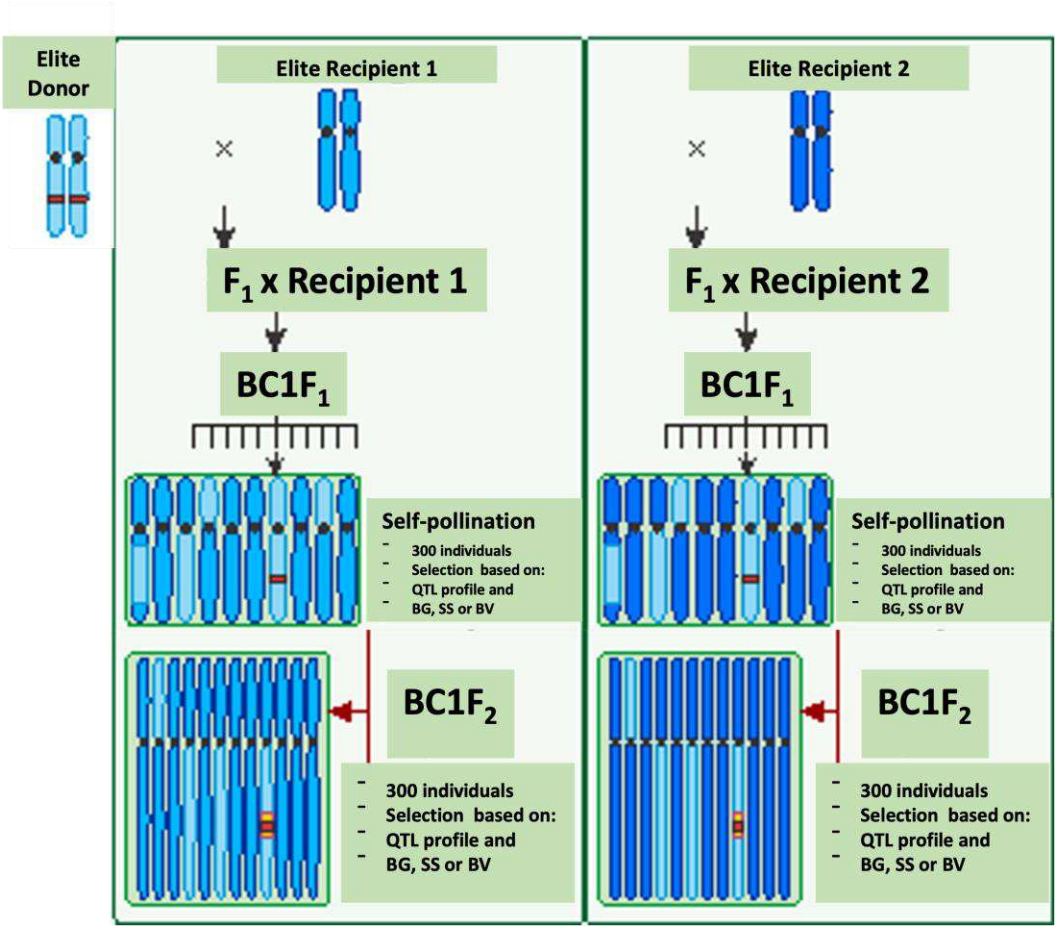

Fig. 2 Scheme used for line augmentation across a different number of elite recipients (Damien et al. 2019; Cobb et al. 2019a).

Background recovery (BG): introgression workflows typically aim to maximize recovery of the elite recipient background. Thus, individuals were selected based on the genetic similarity with the original recipient parent under this scheme.

Selective sweep (SS): individuals were selected to reduce selective sweeps associated with the introgressed genes, in other words, shrinking the genomic region surrounding the target QTL. We used the four nearest SNP near the QTL to inform recombinant selection on either side of the target locus in an opportunistic manner.

Breeding values (BV): also known as recipient background (RPRR), the base training set (TS) was composed of 1,536 inbred lines originated by 30 crosses, between 60 individuals (parents), with near to 52 plants per cross, from the base population after the burn-in stage. Markers effects were predicted using the ridge-regression best linear unbiased prediction (RRBLUP) (Endelman 2011) according to the equation below:

$$y = 1\mu + Z_u u + \varepsilon$$

where y is the vector of individual phenotypic values from the TS; μ is the mean (intercept); u is the vector of marker effects, where $u \sim N(0, I\sigma_u^2)$; and ε is the vector of random residuals. 1 is the vector of ones and Z_u is the incidence matrix of TS genotypes for m markers. Z_u is coded as 1 for homozygous A_1A_1, -1 for homozygous A_2A_2, and 0 for heterozygous A_1A_2.

To perform the GS, the genomic estimated breeding value (GEBV) was estimated using the following equation: $GEBV = Mu$, where M is the incidence matrix of selection candidate genotypes, and u is the vector of predicted marker effects. The GEBV was calculated for BC_1F_1 and derived BC_1F_2 material that had been pre-selected for the target QTLs as above. In this context, we considered the 1K-Rica SNP panel to perform the genomic predictions (Arbelaez et al. 2019).

QTL introgression and its effects on a breeding population

After developing the newest elite donor lines, these can be used in the mainstream breeding program to introduce the target QTLs to the wider, mainstream breeding effort. For that, as a representative self-pollinated crop, simulations were based on the rice breeding program structure from the International Rice Research Institute (IRRI) (Collard et al., 2019) (Fig. 3). For all scenarios, the line fixation phase was conducted by the single-seed descent (SSD) method, which collects one seed from each segregating plant to advance to the next stage until it reaches a high homozygosity level.

Six schemes were compared: three methods and two recipients (Fig.1). Also, two methods (traditional and drift) were used as baselines. In the introgression, we removed the 10 to 20 worst parents for the quantitative trait, then included the elite augmentation products as new parents into the crossing block. It is important to highlight that the augmentation products are one cycle back in terms of genetic improvement due to the time spent developing them (Fig 1). Therefore, to evaluate the effect on the population, we monitor two parameters over short-term breeding: the quantitative trait's performance and the QTL frequency in the breeding population. Each strategy was simulated over five breeding cycles and replicated 40 times considering the current rice breeding framework used in IRRI (Fig.3).

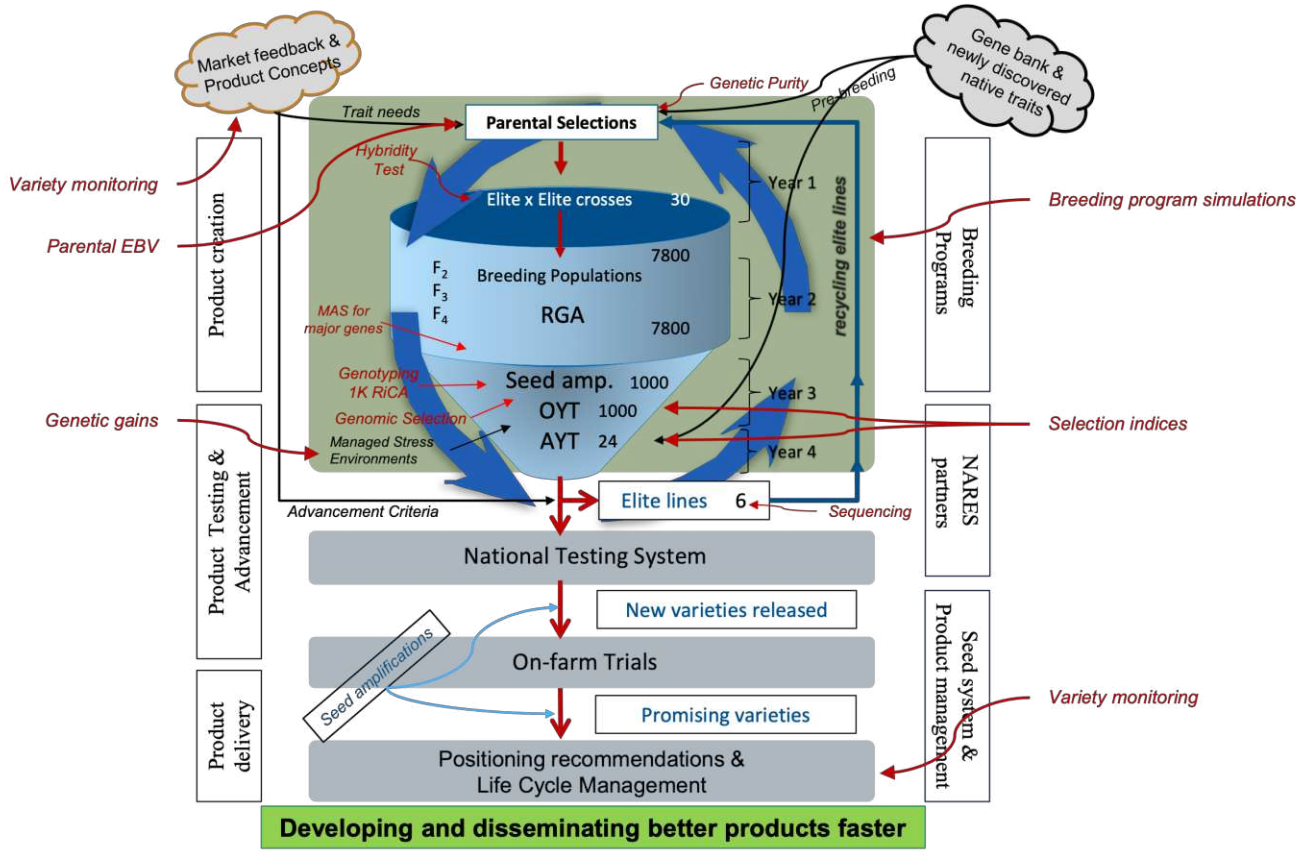

Fig. 3 Current rice breeding framework used in IRRI (Collard et al. 2017, 2019; Cobb et al. 2019b).

RESULTS

In this study, we used stochastic simulations to examine the effectiveness of three methods in promoting the introgression and fixation of new QTLs in the mainstream breeding program, background recovery, selective sweep, and genomic selection. Furthermore, we simulate the current scenario in IRRI, where the donor and recipients are elite lines (improved by breeding), not as usually a landrace as the donor. For that, we used a different approach regarding the number of populations "running in parallel" in breeding (Figure 1). This method provided elite populations for the quantitative trait with similar performances, differing only by the presence of the target QTLs.

Simulation of breeding programs clearly showed a substantial penalty associated with introducing new material, even when this material was only one breeding cycle less advanced than the current parents (Figure 4a). There was little difference between different selection strategies. Therefore, maximizing background recovery (BG), selective sweeps (SS), or breeding value (BV), will produce almost identical penalties that persist over several breeding cycles. Though maximizing background recovery was arguably slightly worse in later cycles. A difference was observed when using either 10 or 20 new parents derived from the augmentation process. Introducing 20 new parents consistently performed worse than introducing only 10 new parents. This is consistent with the size of the penalty being directly proportional to the extent of "older" genetic material being introduced to the crossing program. More variability in the extent of penalty was seen when introducing 10 new parents, with maximizing background recovery (BG_10) being substantially worse than other strategies, on a par with SS_20. In contrast, the BV_10 and SS_10 strategies had almost half the penalty in population mean performance compared to other strategies.

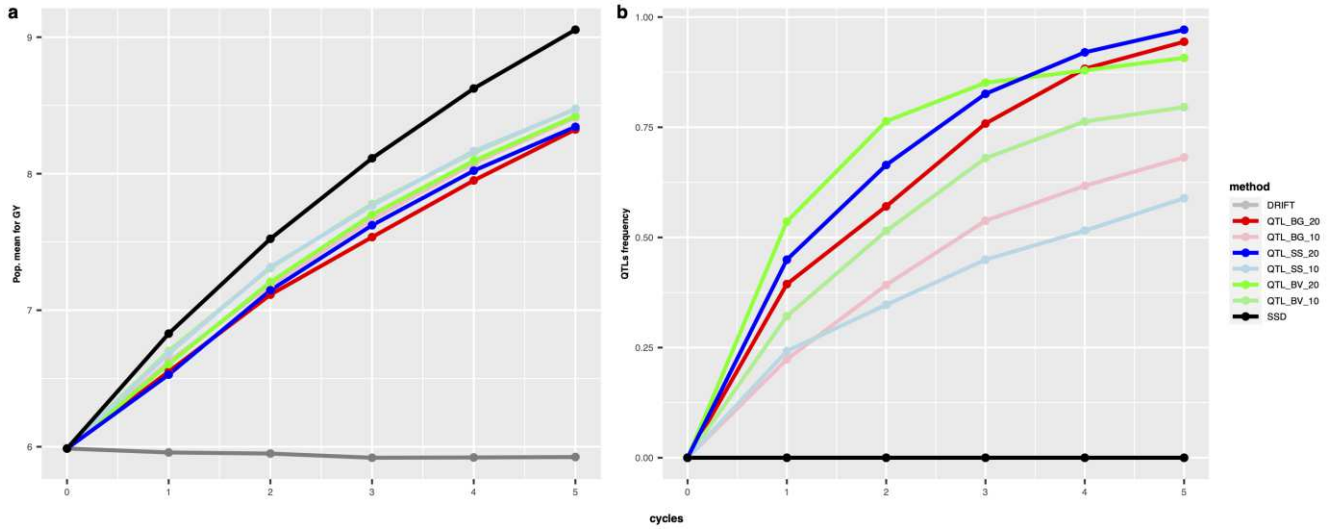

Fig. 4 Population mean performance for yield (a) and QTL frequency (b) over five breeding cycles. Each colored line represents a selection method (background recovery – BG; Selective sweep – SS; Breeding value – BV) and the number of recipients (10 or 20).

In contrast to the situation with the mean performance of the breeding program, the time required to bring new QTLs to fixation in the breeding program was substantially faster when introducing 20 new parents rather than 10 (Figure 4b). However, substantial differences were also observed between the different augmentation selection strategies. For both 10 and 20 new parents introduced, maximizing the breeding value of augmentation selections resulted in faster fixation of the target QTLs. At the other extreme, maximizing recovery of the recipient background produced the slowest fixation of target QTLs when using 20 parents, while minimizing selective sweeps performed the poorest when introducing 10 new parents. As a result, introducing 10 new parents always took longer than introducing 20, but the BV_10 strategy did not take much longer than the BG_20 strategy and achieved a frequency of approximately 70% after only 3 breeding cycles.

DISCUSSION

Modern breeding strategies focus on rapid-cycle recurrent selection achieved through intercrossing the best elite lines identified in each breeding cycle. A drawback often highlighted in this approach is that it produces (indeed relies on) a breeding program that is effectively closed; it is difficult to introduce new genetic variation from external sources, as these typically do not have equivalent performance with current elite cohorts (Juma et al. 2021). This becomes a problem when the breeding program lacks key variations for major QTLs, such as major disease resistance or abiotic stress tolerance genes (Cobb et al. 2019a). These often stem from landraces or other highly un-adapted genomic backgrounds, so introducing these to the crossing program introduces substantial penalties in performance for other traits such as yield. The standard strategy for introducing these into the breeding program involves the backcrossing of the target gene(s) into one or more elite backgrounds, maximizing recovery of the elite genomic background to avoid penalties from the unfavorable donor genome, and in some cases also recombinant selection around the target gene to minimize the probability of linkage drag. This one-stage process suffers a tradeoff. However, it is difficult to simultaneously achieve both high-quality introgressions across a range of elite genomic backgrounds. Hence in practice, programs often focus on either producing a single, high-quality introgression in one background, or a modest number of lower-quality introgressions in multiple backgrounds. To overcome this tradeoff, a 2-stage introgression process has been developed (Cobb et al., 2019b), whereby the initial deployment of a gene focuses on producing one high-quality elite introgression donor. This deployment product is then used as the donor in the line augmentation, to rapidly introduce the new gene into a variety of elite backgrounds. Genomic penalties and linkage drag having already been minimized, the focus of augmentation is speed and quantity of introgressions rather than quality.

The objective of this study was to examine the optimum strategy for selecting segregants during the augmentation pipeline. The typical strategy of maximizing the recovery of the recipient genomic background (BG) was contrasted with strategies to minimize selective sweeps with recombinant selection (SS) and a new approach to maximize the breeding value of segregants (BV). In the last process, segregants are selected based on the most favorable genomic composition as judged by genomic predictions (Sonesson et al. 2012); priority is

given to segregants displaying the highest breeding value irrespective of which parent (elite donor or elite recipient) contributed to any given portion of the genome.

Simulation results clearly showed that irrespective of selection strategy, substantial penalties in performance for yield were associated with introducing introgression products as new parents in the breeding program (Figure 4). This is presumably due to introgression products being at least one breeding cycle less advanced than the most recent breeding cohort. In general, only modest differences were observed between the various selection strategies. However, there was clearly less penalty associated with introducing *fewer* new augmentation products as parents. In particular, introducing 10 augmentation products as parents using either SS or BV selection methods introduced half the penalty of introducing 20 parents or 10 parents using the traditional BG selection method. This penalty associated with introducing introgression products is almost inherent in any introgression procedure; introgression takes time, so even if the recipients represent the absolute best performers in the current cohort at the outset, the final introgression products will always be a step behind the most advanced material by the time they are finished (Hospital and Charcosset 1997; Koudandé et al. 2000). Therefore, it is perhaps counter-intuitive that BV selection did not out-perform other methods in reducing the penalty associated with introducing augmentation products. This highlights the need to minimize the time taken for introgression (augmentation in particular), thus minimizing the divergence between augmentation products and current breeding cohorts.

In contrast to the situation seen for yield performance, the time required to achieve fixation (or near fixation) of the target QTLs was minimized when introducing more parents with the target QTLs. As might be expected, introducing 20 parents with the new QTLs always resulted in faster fixation in the breeding program than introducing only 10 new parents. For this parameter, the different augmentation selection strategies showed substantial performance differences. Of particular interest, selection based on breeding value (BV) always out-performed the SS and BG methods. Minimizing selective sweeps out-performed background selection when introducing 20 parents, though, with 10 parents, the opposite effect was seen. This suggests that the improved performance of augmentation segregants selected based on BV (relative to segregants selected based on SS or BG, though not segregants of the current breeding cohort) increases their chances of being

selected as parents in subsequent breeding cycles, thus increasing the QTL frequency faster than augmentation products selected based on SS or BG.

The superior outcomes when selecting via BV may be due to the use of marker effects estimated based on the elite breeding population. It favors those individuals genetically more related to the current population and those with the best haplotype combinations (Won et al. 2020). In other words, it reduces the penalty in grain yield because we can select the best breeding values (almost the same LD and linkage phase) and accelerate the gene/QTL fixation because the target ones are present and in favorable haplotypes. Furthermore, it shifts the paradigm that the donor genome is inherently and always unfavorable. In the augmentation pipeline, the donor line already has a high BV, if not as high as the most advanced elite lines. Thus, some portions of the donor genome would be expected to be favorable, even compared to the recipient genome, and crucially are also represented in the current elite breeding pool. By selecting on overall BV, the most favorable fragments/haplotypes are selected irrespective of whether they are contributed by the donor or recipient parents. Hence, the progeny could, in principle, outperform both parents. If this were true, it is not fundamentally opposed to the usual paradigm of maximizing recipient parent recovery rates; in typical MABC procedures, the donor parent is highly unfavorable, and so in the vast majority of cases, the donor parent haplotype in any given interval would decrease breeding value. In turn, since the BV of progeny is higher, it improves the chances that these will be selected as parents for future breeding cycles, thus speeding the fixation of target genes. Finally, stochastic simulations may help select the most important factors to be adjusted. Furthermore, it is a fast and inexpensive approach to testing a wide range of scenarios and factors (Faux et al. 2016).

CONCLUSION

Selection strategies during line augmentation can produce substantially different outcomes as products are introduced into the breeding program as a source of new QTLs. Substantial work has been done on optimizing many aspects of the breeding process, but this appears to be the first attempt to quantify optimal strategies for introducing new genes and QTLs to the mainstream breeding process. In particular, the introduction of introgression products resulted in substantial penalties in yield performance, largely regardless of the selection strategy used. However, introducing fewer new parents to the augmentation process minimized this effect. In addition, the time required to achieve fixation of target QTLs showed substantial differences, with selection for BV during augmentation out-performing other methods. Overall, the BV_10 strategy (10 parents selected based on genomic estimated breeding values) displayed the best trade-off between reduced penalty from introducing new QTLs with the reasonable speed at which those QTLs can achieve fixation over subsequent breeding cycles.

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