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ORIGINAL ARTICLE

Effect of genomic prediction on response to selection in forest tree breeding

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Abstract

Through stochastic simulations, estimates of breeding values accuracies and response to selection were assessed under traditional pedigree-based and genomic-based evaluation methods. More specifically, several key parameters such as the trait's heritability (0.2 and 0.6), the number of QTLs underlying the trait (100 to 200), and the marker density (1 to 10 SNPs/cM) were evaluated. Additionally, impact of two contrasting mating designs (partial diallel vs. single-pair mating) was investigated. Response to selection was then assessed in a seed production population (seed orchard consisting of unrelated selections) for different effective population sizes ($N_e = 5$ to 25). The simulated candidate population comprised a fixed size of 2050 individuals with fast linkage disequilibrium decay, generally found in forest tree populations. Following the genetic/genomic evaluation, top-ranked individuals were selected to meeting the predetermined effective population size in target production population. The combination of low h^2, high N_e, and dense marker coverage resulted at maximum relative genomic prediction efficiency and the most efficient exploitation of the Mendelian sampling term (within-family additive genetic variance). Since genomic prediction of breeding values constitutes the methodological foundation of genomic selection, our results can be used to address important questions when similar scenarios are considered.

Keywords GBLUP · Seed orchards · Genomic selection · Response to selection · Effective population size

Introduction

The effectiveness of genomic selection (GS) is contingent on populating the genome with dense marker coverage to exploit the associations between markers and causal variants (a.k.a. linkage disequilibrium (LD)) for selection and breeding purposes (Meuwissen et al. 2001). From its inception, GS has garnered increased attention and acceptance for its potential in predicting individuals' genetic values and the delivery of greater gains per unit time and cost. The impetus of GS coincided with the development of efficient, accurate, and relatively affordable high throughput single-nucleotide polymorphism (SNP) genotyping technologies (Elshire et al. 2011; Peterson et al. 2012; Truong et al. 2012). GS is a significant paradigm shift with an inconceivable repercussion as the models' unit of quantitative genetics analyses have shifted from being the line of descent to the allele. Thus, the traditional approach of genetic evaluation which fundamentally is based on the pedigree expected relationship is replaced with the actual realized relationship (Wright 1922; VanRaden 2008). Genomic best linear unbiased prediction (GBLUP) has been used to estimate the genomic estimated breeding values (GEBVs) of various complex traits in human, plant, and animal populations (Yang et al. 2010; Heffner et al. 2009; Villanueva et al. 2005; VanRaden 2008) ranging from cattle to aquacultures (Sonesson and Meuwissen 2009; Ødegård and Meuwissen 2015; Vela-Avitúa et al. 2015). Several studies described how genomic BLUP differs from

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the traditional pedigree BLUP and dissected the genetic features captured by the genomic relationship matrix (Habier et al. 2007, 2013). Coefficients of the pedigree-based relationship matrix describe expected additive genetic relationships (Malécot 1948) among individuals at quantitative trait loci (QTL) conditional on pedigree information. According to Habier et al. (2013), it is not obvious to what extent the genomic relationship matrix explains genetic covariance at QTL level, despite the fact that several authors called the genomic relationship matrix the actual (Hill and Weir 2011) or realized relationship matrix (Lee et al. 2010) as it describes the identity-by-descent (IBD) at SNPs (Hayes et al. 2009) with the assumption of an ancient founder population. This variety of terms might be misleading as only the genetic relationships at QTL matter in quantitative genetic analyses.

Genetic relationships derived from pedigrees (basis of BLUP) ignore the random sampling of the two possible alleles from each parent at each locus during meiosis. This phenomenon is defined as the Mendelian sampling term. Van Arendonk et al. (1994) suggested that large numbers of DNA markers covering the genome could lead to more accurate estimation of genetic covariance, as opposed to the pedigree-based relationship, as the realized genetic covariance would be based on the actual proportion of the genome that is identical by decent (IBD) between any two individuals. Additional to tracing IBD alleles, DNA markers also identify those identical by state (IBS) (Powell et al. 2010). The major difference between the realized and expected relationships is the ability of the former to estimate the actual fraction of total DNA that two individuals share and utilize this information in predicting of genetic merit of non-phenotyped individuals (Zapata-Valenzuela et al. 2013).

GS has potential in forest trees recurrent selection breeding program as it eliminates progeny phenotypic testing; however, there are challenges that cannot be ignored. These include the unquestionable need for balance between genetic gain and diversity, long generation intervals, very large effective population size (N_e), fast linkage disequilibrium decay, and extremely large genome sizes requiring dense SNP genotyping for a large number of individuals (Neale and Savolainen 2004). Using a deterministic approach, Wong and Bernardo (2008), Grattapaglia and Resende (2011), and Iwata et al. (2011) have demonstrated GS potential and all concluded that it could radically increase tree breeding efficiency. In these studies, the impact of several factors, such as heritability, number of QTLs, marker density, and effective population size on the accuracy of GEBVs and selection efficiency was evaluated. Currently, genomic selection models were also used to decompose the genetic variance to its additive and non-additive components using both simulation and empirical data yielding more realistic heritability and breeding value estimates, leading to improved prediction accuracy (Denis and Bouvet 2013; Bouvet et al. 2015; de Almeida Filho et al. 2016; El-Dien et al. 2016). While most of the abovementioned studies were assessing similar parameters in plant breeding, there is a limited knowledge on GBLUP efficiency in the context of seed orchards under variable mating designs and effective population sizes balancing genetic gain and diversity. Similarly, studies concerning stochastic variation connected to such scenarios are also lacking.

In this study, through stochastic simulations, the impact of selection strategy in conjunction with traditional BLUP vs. GBLUP on response to selection was assessed. Specifically, we evaluated the impact of several key parameters such as the trait heritability (h^2), the number of QTLs underlying the trait (N_{QTL}), and the marker density (fixed low LD; monitored LD decay across a single generation under various marker densities) on the accuracy of BLUP and GBLUP and the response to selection in a production population (i.e., seed orchard). Response to selection was evaluated for several effective population sizes to show the impact of N_e on final results. Additionally, the impact of alternative mating design on results was investigated. Finally, run-to-run (200 iterations) absolute genetic gains were assessed to show the extent of gain variability. Genetic gain variability is of interest as in most cases, breeders are confronted with only one outcome of their program; thus, gain variability should show the extent of a program's uncertainty.

Methods

We developed a stochastic simulation model utilizing two commercial software tools, namely, ASReml (Gilmour et al. 2006) and Gurobi Optimizer (Gurobi Development Team 2014) within the R system (R Core Team 2017). We created two populations (parental and offspring). In the parental population, allelic frequencies were generated using the function "glSim" implemented within the R package "adegenet" (Jombart and Ahmed 2011) assuming the following: (1) no population structure, (2) all markers were considered as non-structural, (3) individuals were considered as diploids, (4) based on forest tree LD decay knowledge, the linkage disequilibrium (LD) between neighboring markers was set at 0.5 (fast LD decay: specified by parameter θ extending from 0 (very slow LD decay) to 0.5 (fast LD decay) (Savolainen et al. 2007; Jansson and Ingvarsson 2010; Porth and El-Kassaby 2014), and (5) LD decay block size within was modeled as constant using the setting block.minsize = block.maxsize (Jombart and Ahmed 2011). The offspring population was generated using a partial diallel mating design with 50 full-sib families, each with 20 offspring (White et al. 2007). The population, parents and offspring, was fixed at a size of 2050 individuals. Population of the same size was alternatively simulated under single-pair mating design (SPM), which exhibits noticeably lower connectedness and larger family sizes (25 families and

80 offspring individuals per family). Bi-allelic marker data were simulated for the full-sib families using the function "genomesim" implemented within the R package "pedantics" (Morrissey and Wilson 2010). To investigate the effect of marker density on prediction accuracy and potential gains, the number of markers (SNPs) per centiMorgan (cM) was set to 1, 2, 5, and 10 covering the chromosome length of 120 cM; in total, two chromosomes (linkage groups) were simulated, comparably to previous studies (i.e., Denis and Bouvet 2013), with the maximum number of markers equal to 2400. QTL effects were randomly assigned to selected loci and were sampled from a standardized normal distribution (mean = 0; variance = 1) to emulate traits following Fisher's infinitesimal model. To avoid the overestimation of cumulative QTL additive effects, the QTL loci were removed from final marker data prior to each evaluation. For each marker density, 200 independent runs were conducted and statistical inference was drawn across these runs.

To evaluate the impact of traits' genetic architecture, we modeled variable QTL number (N_{QTL} = 100, 150, and 200). The phenotypic data were generated as the sum of allelic effects across all QTL loci with the addition of residual effects reflecting two distinct heritability levels (h^2 = 0.2 and 0.6). These heritability estimates were selected as representative of two commonly studied traits with contrasting values (e.g., height and wood density as proxies to fitness and productivity, respectively (El-Dien et al. 2016)).

For pedigree- (ABLUP) and genomic-based (GBLUP) relationships, separate genetic evaluations were conducted to predict offspring breeding value (BV; i.e., forward selection) using the animal model in the REML framework (Gilmour et al. 2009; Mrode 2014) as follows:

$$y = X\beta + Zu + e$$

where y is the vector of phenotypes, β is the vector of fixed effects (intercept), u is the vector of random breeding values following $\mathrm{var}(u) \sim N\left(0, \sigma_a^2 A\right)$, where σ_a^2 is the additive genetic variance and A is the average numerator relationship matrix which is substituted by the marker-based relationship matrix G when GBLUP scenario is performed, e is the vector of residuals following $\mathrm{var}(e) \sim N\left(0, \sigma_e^2 I\right)$, where σ_e^2 is the residual variance and I is the identity matrix, and X and Z are the incidence matrices assigning effects in the vector β and u to phenotypes in vector y, respectively. Marker-based relationship matrix G was constructed on the basis of VanRaden (2008) as follows:

$$G = \frac{ZZ'}{2\sum p(1-p)}$$

where Z is M-P, where M is the marker matrix containing genotypes coded as 0, 1, and 2 for the first allele homozygote and heterozygote and second allele homozygote and P is the vector of doubled allele frequencies, and p is the allelic frequency at the loci.

Breeding value accuracies were calculated as the correlation between their predicted (genetic evaluation ABLUP/GBLUP) and true (as determined by the sum of simulated allelic effects) respective values. Selection response was calculated as a sum of true breeding values divided by the given number of selected individuals. Following the genetic evaluation, a set of unrelated offspring representing the best individuals based on their breeding values were selected to meet predetermined effective population sizes (N_e = 5, 10, 20, and 25), so the genetic response is maximized. These selected individuals were used to form various production populations corresponding to the predetermined N_e (seed orchards). To avoid any build-up of co-ancestry (i.e., inbreeding depression), in the seed orchards, selection was restricted to unrelated and non-inbred individuals using a mathematical programming method developed by Lstibůrek et al. (2015).

The efficiency of GBLUP relative to ABLUP was determined (termed R_G thereafter), for the various genetic architectures (i.e., heritability and QTL) and studied marker density, by dividing the mean selection response across the GBLUP 200 iterations by those from the ABLUP. This was done to illustrate how R_G varies in a range of target effective population sizes (N_e = 5, 10, 20, and 25).

Results

Accuracies of predicted breeding values

First, we investigated the effect of marker density on the accuracies of breeding values. Under GBLUP, a steady increase in BV's accuracy was reported with higher h^2 and higher marker density, while respective accuracies were more sensitive to increasing marker density as N_{QTL} further increased (> 100). Across all N_{QTL}, the BV's accuracy under GBLUP reached a saturation level under marker density ≥ 5/cM (Table 1).

Second, we analyzed the effect of N_{QTL} on the BV's accuracy. While the accuracy was robust across the range of N_{QTL} under ABLUP, the opposite trend was observed under GBLUP, irrespective of h^2 value (Table 1). BV's accuracy under GBLUP was greater than that under ABLUP under all investigated scenarios, when marker density reached at least 2 SNPs/cM (Table 1).

Third, we investigated the impact of an alternative mating design (single-pair mating; SPM). As shown in Table 2, BV's accuracy increased moderately under h^2 = 0.2 in all reported N_{QTL} and marker densities under both ABLUP and GBLUP. Table 2 also outlines the same scenarios under h^2 = 0.6, where the accuracies increased only under GBLUP.

Table 1 BV's accuracies with corresponding standard errors for the two h^2 levels (0.2 and 0.6), three N_{QTL} (100, 150, and 200), and four marker densities (1, 2, 5, and 10 SNPs/cM)

Marker density	$h^2 = 0.2$						$h^2 = 0.6$					
	$N_{QTL} = 100$		$N_{QTL} = 150$		$N_{QTL} = 200$		$N_{QTL} = 100$		$N_{QTL} = 150$		$N_{QTL} = 200$	
	ABLUP	GBLUP	ABLUP	GBLUP	ABLUP	GBLUP	ABLUP	GBLUP	ABLUP	GBLUP	ABLUP	GBLUP
1	0.684 (0.003)	0.611 (0.003)	0.689 (0.003)	0.552 (0.004)	0.685 (0.003)	0.415 (0.004)	0.832 (0.002)	0.711 (0.001)	0.835 (0.002)	0.628 (0.003)	0.832 (0.002)	0.465 (0.003)
2		0.720 (0.003)		0.713 (0.003)		0.694 (0.003)		0.850 (0.001)		0.838 (0.002)		0.817 (0.002)
5		0.769 (0.002)		0.771 (0.002)		0.763 (0.002)		0.906 (0.001)		0.906 (0.001)		0.902 (0.001)
10		0.784 (0.002)		0.782 (0.002)		0.783 (0.002)		0.918 (0.001)		0.917 (0.001)		0.917 (0.001)

Response to selection

Generally, under all investigated scenarios, the relative genetic gain efficiency of GBLUP (R_G) was higher at lower h^2 (see R_G at $h^2 = 0.2$ vs. 0.6; Table 3), highlighting the usefulness of GS under low h^2 traits. Heritability of 0.6 generally showed decreased R_G, even though GBLUP still outperformed the ABLUP in most of the presented scenarios, indicating that model saturation was reached more frequently at the higher h^2 with N_e playing a minor role (Table 3, Fig. 1).

R_G was sensitive to N_e under all scenarios, except at lower N_e values (see $N_e = 5$ vs. 10); R_G values are products of complex interactions among the studied parameters, i.e., (see the interplay among h^2, N_e, N_{QTL}, and marker density in Table 3). R_G was most sensitive to marker density under high N_e, thus under $N_e = 25$ sparse marker coverage led to minimum R_G (18%), while dense marker coverage resulted in maximum R_G (188%). At lower marker density (1 marker/cM), GBLUP generally produced lower R_G (in all cases below 100%). Differences in response to selection (in original absolute units) between GBLUP and ABLUP scenarios were statistically significant (pairwise t test, $\alpha = 0.05$), except for several values under $N_{QTL} = 100$ and 150, $h^2 = 0.6$, and 2 SNPs/cM (Table 3). Generally, differences were still significant at $N_e > 10$.

Above described trends were also present under the SPM design, with comparable R_G to partial diallel scheme in the majority of reported scenarios. When h^2 is low, SPM exhibits greater or comparable R_G values under N_e below 25 (with a single exception under $N_e = 5$ and lowest marker density). Higher heritability changes the relations only slightly and the impact of N_{QTL} is emphasized. Therefore, SPM does not increase R_G under $N_{QTL} = 200$ and 5 SNPs/cM. Generally, the moderate increase of accuracy seems to diminish, when the selection response is assessed related to a production population (Table 4).

A considerable run-to-run variability was observed across all simulation scenarios as observed by plotting the adjusted relative genetic gain efficiency (R_{GA}) values of the 200 individual stochastic iterations (i.e., random realization of a given simulation scenario). Due to high variability captured in 200 iterations, some of the absolute gains dropped below zero, which made it impossible to compare relative gain efficiency of the minimum and maximum scenario. Correspondingly, we added a constant 100. While the R_G values in Table 3 represent the average of the 200 iterations, all individual iterations of two most contrasting scenarios, i.e., minimum and maximum, were plotted in Fig. 2. Individual R_{GA} varied from 87.1 to 97.0% and from 99.3 to 114.3% under the minimum and maximum scenarios, respectively (Fig. 2). It is interesting to note that both extreme values were reached under the highest simulated N_e (25).

Table 2 SPM-BV's accuracies with corresponding standard errors for the two h^2 levels (0.2 and 0.6), two N_{QTL} (100 and 200), and two marker densities (1 and 5 SNPs/cM). Only one higher marker density (5 SNPs/cM) is presented in the table

Marker density	$h^2 = 0.2$				$h^2 = 0.6$			
	$N_{QTL} = 100$		$N_{QTL} = 200$		$N_{QTL} = 100$		$N_{QTL} = 200$	
	ABLUP	GBLUP	ABLUP	GBLUP	ABLUP	GBLUP	ABLUP	GBLUP
1	0.706 (0.003)	0.678 (0.003)	0.700 (0.003)	0.501 (0.002)	0.834 (0.002)	0.756 (0.001)	0.830 (0.002)	0.545 (0.001)
5		0.791 (0.003)		0.787 (0.002)		0.909 (0.001)		0.906 (0.001)

Discussion

As noted in numerous studies on several organisms, including forest trees, the genetic architecture of adaptive traits is complex and controlled by many loci contributing to these traits' variances, thus conforming to Fisher's (1918) infinitesimal model. The present study corresponded to the general findings in animal and plant breeding programs, where the primary genetic response to genome-based selection is jointly influenced by many factors, including population genetic structure, marker density, extent of LD, number of contributing loci, and their respective (differential) effects, effective population size, and trait's heritability (Grattapaglia and Resende 2011). Additional factors contributing to the breeding efficiency include selection intensity, mating design, progeny test size, and genetic gain and diversity trade-off (El-Kassaby et al. 2012). Here, we clearly demonstrated the role of heritability, number of QTLs underlying the trait, and marker density interplay and extended the work to determine the response to selection and its relative genetic gain efficiency with establishing seed production populations with a continuum of effective population sizes of 5 to 25. We confirmed the superiority of the GBLUP to ABLUP on breeding value accuracy and more notably the drastic role of marker density and the number of loci underlying the trait's genetic architecture. Additionally, we highlighted the diminishing role of genomic prediction in terms of relative genetic gain efficiency under low marker density and high heritability. Moreover, we investigated the impact of mating design on accuracy and relative gain efficiency under both strategies and highlighted the variability among stochastic iterations.

Generally, tree breeders are often unaware of the specific genetic architecture of the target traits (i.e., the extent of heritability). Further, initial sampling of parents and population structure, including marker-QTL associations, is unique and so is the respective sampling of alleles and their effects. Thus, when reporting accuracy of genomic predictions of a given trait, such values should always be viewed as a unique realization of the specific selection experiment (i.e., stochastic iteration of a given strategy in this study). The same holds for the actual genetic gains, where the variability is even much larger. Naturally, the more factors are contributing to the system, the more complicated prediction of the response becomes, i.e., high uncertainty of the predicted gains. Thus, with many unknown factors, one may not accurately predict the anticipated genetic response (Clark et al. 2011). Most forest tree genomic-based studies focus on the prediction accuracy in a given population/trait, but the accuracy is not a simple indicative of the actual response to selection in production

Table 3 Relative gain efficiency (R_G) between GBLUP and ABLUP for combinations of h^2 (0.2 and 0.6), N_{QTL} (100, 150, 200), N_e (5, 10, 20, 25), and marker density (1, 2, 5, 10 SNPs/cM)

	$N_{QTL} = 100$				$N_{QTL} = 150$				$N_{QTL} = 200$			
$h^2 = 0.2$												
Marker density	$N_e = 5$	$N_e = 10$	$N_e = 20$	$N_e = 25$	$N_e = 5$	$N_e = 10$	$N_e = 20$	$N_e = 25$	$N_e = 5$	$N_e = 10$	$N_e = 20$	$N_e = 25$
1	89	86	80	76	73	70	60	49	54	53	41	32
2	108	111	116	127	107	110	113	121	105	105	107	118
5	118	124	132	143	119	123	132	146	122	124	134	144
10	122	126	134	151	129	133	152	180	127	134	155	188
$h^2 = 0.6$												
	$N_e = 5$	$N_e = 10$	$N_e = 20$	$N_e = 25$	$N_e = 5$	$N_e = 10$	$N_e = 20$	$N_e = 25$	$N_e = 5$	$N_e = 10$	$N_e = 20$	$N_e = 25$
1	75	72	61	49	63	59	48	34	45	42	30	18
2	101	100	99	99	100	99	97	95	97	95	91	87
5	111	112	114	117	112	113	115	117	112	112	114	117
10	112	114	117	122	113	116	122	127	115	116	122	127

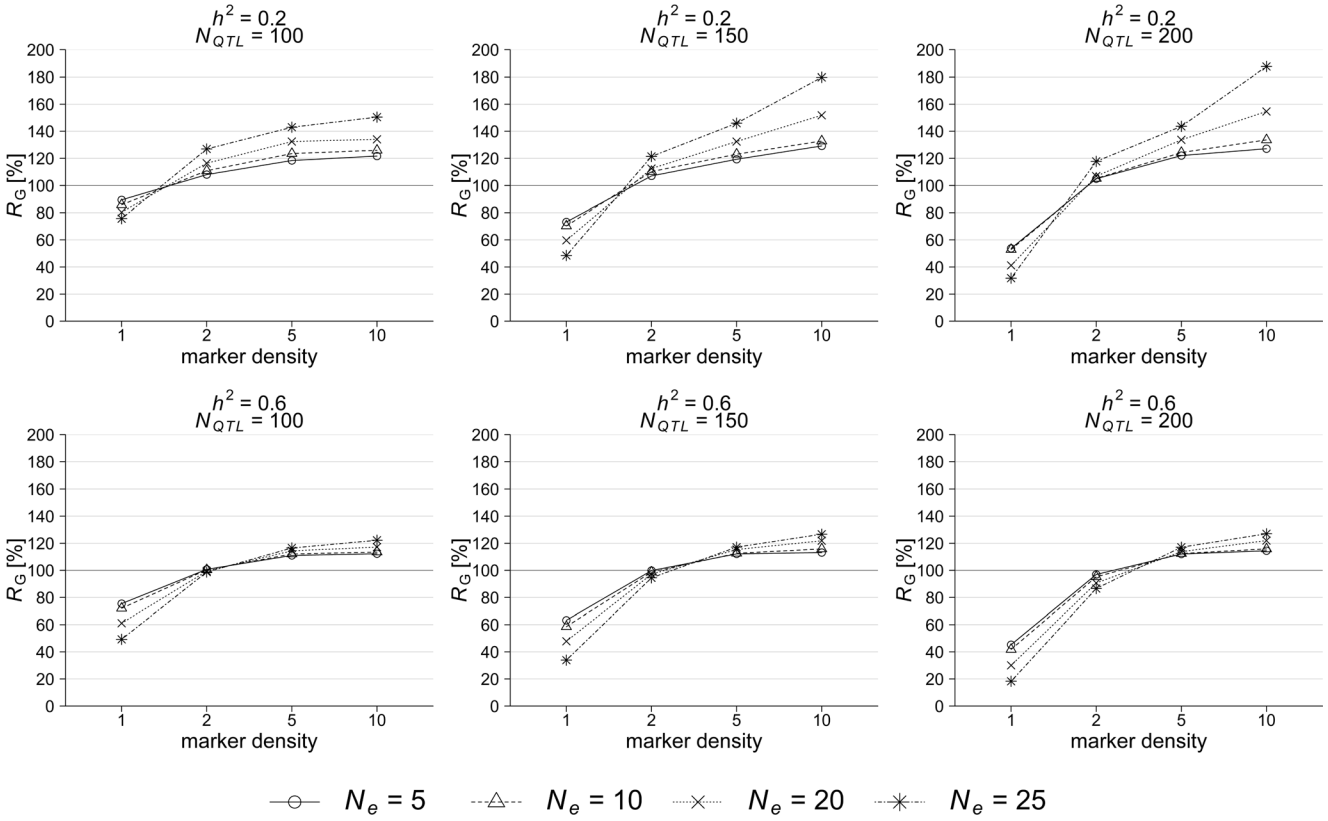

Fig. 1 Plotted R_G for variable h^2 (0.2 and 0.6), N_{QTL} (100, 150, 200), N_e (5, 10, 20, 25), and marker density (1, 2, 5, 10 SNPs/cM)

populations (i.e., seed orchards) due to added constraints on relatedness and effective population size along with other biological factors specific to the production population's reproductive biology (El-Kassaby and Askew 1991; El-Kassaby 1995). Here, we aimed at assessing the production population's potential genetic gain under various effective population size scenarios with emphasis on avoiding relatedness to minimize the impact of inbreeding depression in seed orchards' crop (Chaisurisri and El-Kassaby 1994). We clearly demonstrated the variability in genetic response for a given accuracy, where the respective ranking and selection response is highly dependent on the target N_e (= census number when unrelated selections are made).

As reported, the impact of mating design on our study results was rather minor. We deliberately chose two highly contrasting mating schemes that are still operationally feasible. It seems that GBLUP is slightly more efficient under the SPM design, as it capitalized on the larger family sizes (actually four times larger), where the Mendelian sampling can be exploited more efficiently. This relative benefit diminishes under $h^2 = 0.6$, where both ABLUP and GBLUP remained more comparable to the original partial diallel mating scheme. To our knowledge, this comparison has not been presented elsewhere, but it is clear that the impact of the additionally observed parameters on final results is more relevant as opposed to the mating design alone. These results show a different perspective compared to earlier research on mating design impact (i.e., Huber et al. 1992). As reported here, the SPM design has provided higher accuracies and comparable genetic

Table 4 SPM-relative gain efficiency (R_G) between GBLUP and ABLUP for combinations of h^2 (0.2 and 0.6), N_{QTL} (100 and 200), N_e (5, 10, 20, 25), and marker density (1and 5 SNPs/cM). Results presented in the table correspond to 1 and 5 SNPs/cM

Marker density	$h^2 = 0.2$							
	$N_{QTL} = 100$				$N_{QTL} = 200$			
	$N_e = 5$	$N_e = 10$	$N_e = 20$	$N_e = 25$	$N_e = 5$	$N_e = 10$	$N_e = 20$	$N_e = 25$
1	88	89	81	70	63	57	44	26
5	121	124	134	141	123	126	135	145
	$h^2 = 0.6$							
	$N_{QTL} = 100$				$N_{QTL} = 200$			
	$N_e = 5$	$N_e = 10$	$N_e = 20$	$N_e = 25$	$N_e = 5$	$N_e = 10$	$N_e = 20$	$N_e = 25$
1	77	74	62	53	51	44	31	18
5	111	112	115	117	110	112	114	116

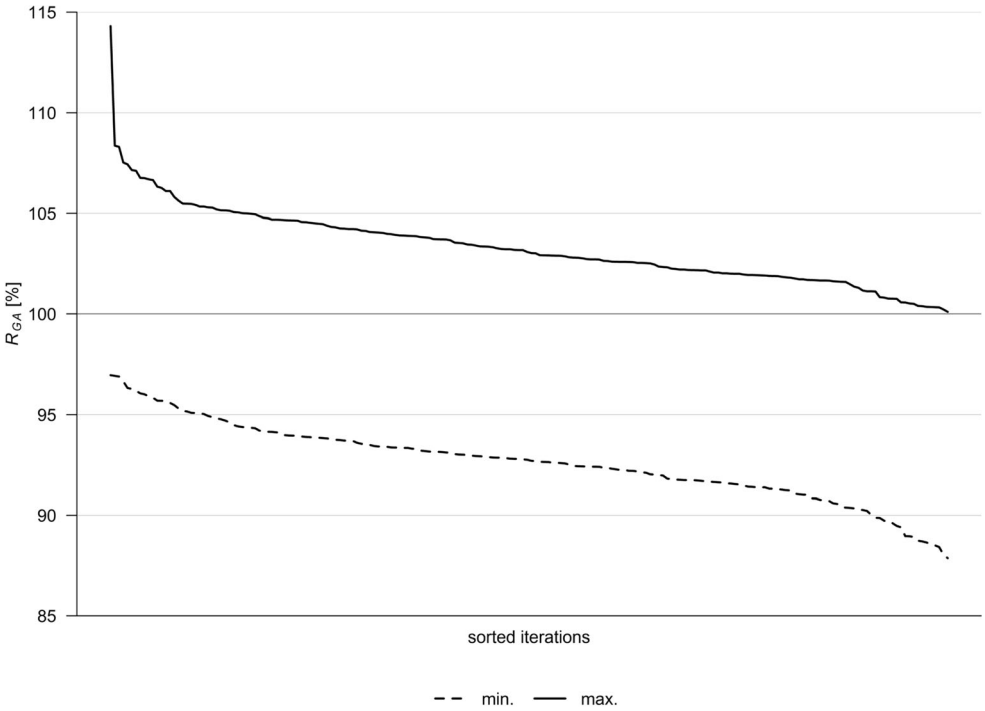

Fig. 2 Sorted adjusted relative gain efficiency (R_{GA}) across the 200 iterations for $N_{QTL} = 200$, $h^2 = 0.2$, and 10 SNPs/cM (max.) compared to $h^2 = 0.6$ and 1 SNP/cM (min.)

response under GBLUP scenarios, which further enhances its operational feasibility.

The main added value of the GBLUP evaluation is its ability to capitalize on capturing within-family additive genetic variance and unmasking cryptic relatedness (Habier et al. 2007, 2013). Our results suggest that under higher N_e, most selections are captured within the central part of the normal curve in the progeny trial. It is obvious that higher accuracy is needed to identify the top-ranking individuals, thus satisfying the relatedness restrictions in the central part of the distribution. Under such realistic scenarios in forestry (high N_e), additional gains due to GBLUP are substantial (up to 188% of ABLUP), making the GBLUP evaluation particularly suitable, as it allows much more efficient exploitation of the within-family variance. However, sufficient marker coverage is critical to capitalize on GBLUP evaluation advantage. In case the trait is influenced by large number of loci, as most growth and adaptive attributes, then the marker density increment may not increase the accuracy of breeding values unless the reference population is very large (Clark et al. 2011). This unavoidable trend is apparent even under the lowest QTL number (100), where ABLUP is more efficient under the lowest reported marker density. This suggests that marker density is critical under typical genetic architecture of quantitative traits in forest trees where the genome size itself might be the limiting factor for GBLUP application.

Here, we found that absolute gains in production populations are reduced at higher N_e (i.e., lower selection intensity). At the same time, the relative efficiency of GBLUP is the greatest. However, the benefit is only obtained under higher marker density due to the fast LD decay. Therefore, the investment of the implemented genomic resources is critical. In contrary, under low N_e, individual phenotype might be sufficient to determine the top-ranking extreme observation within the tail of the normal curve; thus, the relative efficiency of GBLUP is reduced under low N_e.

Conclusion

The present study confirms that, in general, the use of genomic information is of upmost importance for traits with low heritability. The combination of low h^2, high N_e, and dense marker coverage leads to the maximum relative efficiency of the GBLUP (compared to ABLUP) under the most typical forestry scenarios. The benefits of quantitative genomic assessment were highlighted at the production population level where the actual genetic gain is captured. We demonstrated the advantage of less complex mating design generating larger families under the same training population size, leading to more efficient exploitation of the within-family additive genetic variance and generating comparable response to selection.

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Data archiving statement In our study, we described a stochastic simulation model and conducted a comparison of hypothetical breeding strategies. No real-world data of any species have been used throughout the study. Output data have been outlined and published in tables and figures included in the manuscript. The complete R script is provided in the online Appendix.

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