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Comparative Analysis of Pedigree-Based BLUP and Phenotypic Mass Selection for Developing Elite Inbred Lines, Based on Field and Simulated Data

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Abstract: Pedigree-based best linear unbiased prediction (pBLUP) is an effective method for genetic evaluation. The objective of this study was to assess the efficacy of pBLUP to develop superior inbred lines, using field and simulated data. This study was based on the data of 30,986 plants from six S_0 generations and eight inbred progeny trials (S_1–S_4), performed over eight years. We measured the grain yield and the expansion volume (EV). We also simulated the EV and grain yield of 5000 plants (S_0–S_4) in two in silico populations, assuming 300 and 400 genes distributed across 10 chromosomes of 200 cM, respectively, and 10% of pleiotropic genes. We selected selfed plants based on the predicted additive value for EV by fitting the individual model in inbred population. The use of pBLUP provided total genetic gains in EV in the range of 1 to 45%, inversely proportional to the level of improvement of the population, and indirect changes in grain yield in the range of −17 to 3%. Only from the analysis of the in silico populations, assuming selection based on the true additive value and genetic gain computed from the genotypic values, there was evidence that pBLUP is superior to phenotypic mass selection.

Keywords: genetic evaluation; pedigree-based BLUP; genetic variances; genetic gains

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1. Introduction

The best linear unbiased prediction (BLUP) is a statistical approach that allows the prediction of a non-observable random variable, as the additive genetic value [1]. Its features make BLUP suitable for genetic evaluation under a wide variety of situations [2]. Advances in computing algorithms have led animal breeders to accept BLUP as a standard procedure for genetic evaluation in animal breeding, based on frequentist and Bayesian approaches [3]. The initial and the most significant application of BLUP in plant breeding is the prediction of non-assessed single crosses [4]. It is impressive that the initial proposition was based on relationship information from molecular markers. In our opinion, the most significant aspect of BLUP in animal and plant breeding, as well as in human genetics, is the prediction of the additive or genotypic values of individuals that cannot be measured for a sex-limited trait or that are too young to be measured for a trait, or of a subset of individuals that were not measured for a trait because quantification is too expansive. However, this remarkable feature depends on a key basic aspect of BLUP: relationship information [5].

The most important models for genetic assessment in animal breeding, such as the animal, sire, and gametic models, among others, have application in plant breeding, but denominated individual, half-sib progeny, and full-sib progeny models, respectively [6,7]. The individual model is used for the prediction of individual additive value using individual phenotype. The half-sib progeny model aims to predict the common parent additive value using the average phenotypic value of their progeny. The full-sib progeny model is used for the prediction of the parents' additive values using the average phenotypic value of their progeny. Since 2001, when Meuwissen et al. [8] proposed the use of a high number of single nucleotide polymorphisms (SNPs) and a limited number of phenotypic records to predict the genetic merits of a sample of selection candidates (genomic selection), BLUP allowed animal and plant breeders to reach a higher level of efficacy, permitting fast genetic gains under a decreasing cost, keeping comparable accuracies relative to previous more expensive procedures, as progeny test [9,10]. Note, however, that the only innovation in genomic BLUP (GBLUP) was the use of a genomic relationship matrix (observed) instead of a pedigree-based relationship matrix (expected) [11]. However, this was a very significant innovation. The use of SNPs for measuring relationship allows discrimination among equivalent relatives and prediction of non-relatives based on identity by state and linkage disequilibrium between SNPs and genes [12].

In recent years, few studies, especially on plant breeding, have published results from genetic assessment based exclusively on pedigree-based BLUP. In these few papers, pedigree-based BLUP was regularly compared with a least squares approach. In most papers using GBLUP, especially in animal breeding, this approach was commonly compared with pedigree-based BLUP. In a survey based on the results from 50 recently published papers (2018–2022), in approximately 50% of the studies the authors emphasized that GBLUP, especially the single-step procedure, provided superior prediction accuracy [13]. Velazco et al. [14] observed in sorghum that a combined pedigree-genomic relationship matrix provided the largest increases in predictive ability and the largest reductions in prediction bias. Comparing pedigree-based and genomic BLUP, Suontama et al. [15] concluded that a significant increment in the breeding value prediction accuracy and genetic gains was possible by implementing genomic selection for wood properties in *E. nitens*. On the contrary, in the study of Kainer et al. [16], pedigree-based BLUP performed best across eight traits of *E. polybractea*. Using a simulated dairy cattle population, Seno et al. [17] did not observe significant differences between pedigree-based and genomic BLUP.

Thus, pedigree-based BLUP is an effective method for genetic evaluation in plant and animal breeding. To our knowledge, most studies using pedigree-based BLUP in animal and plant populations focused on the estimation of genetic parameters (components of genetic variances, heritability, and genetic/genotypic correlation) and assessment of the selection process efficacy, from the estimation of prediction accuracy and genetic gains. In plant breeding, these investigations generally involved a single cycle of selection. In animal breeding, these studies involved a huge amount of data from several generations of a single population. By using field and simulated datasets over four generations of selfing, our objective was to assess the efficacy of pedigree-based BLUP to develop superior inbred lines.

2. Materials and Methods

2.1. Populations and Trials

This study was based on data from six S_0 generations and eight inbred progeny trials, performed over the growing seasons 2013/2014 (S_1 progeny test) to 2020/2021 (S_4 progeny test) in an experimental area at Federal University of Viçosa, Minas Gerais, Brazil. Due to a low stand in the flowering time or a reduced number of selfed plants, the S_1 and S_4 progeny trials were replicated twice (2013/2014 and 2014/2015, and 2019/2020 and 2020/2021). Note that the progeny were replicated, not the plants. Distinct groups of S_2 and S_3 progeny were assessed over two years (2015/2016 and 2016/2017, and 2017/2018 and 2018/2019, respectively). The S_1 progeny were obtained over the growing seasons 2011/2012 and 2012/2013 from a tropical synthetic and five temperate populations. The synthetic was generated from the recombination of 30 inbred lines from the tropical populations Viçosa and Beija-Flor. The other populations (UFV-1 to 5) were obtained from recombining the single crosses P622, P625, P802, AP2501, and AP4502, developed by the Agricultural Alumni Seed, Indiana, USA. All trials were designed as completely randomized with 40–70 replicated inbred lines (twice). Each plot corresponded to a 5 m row with an ideal stand of 25 plants, spaced by 0.2 m. The space between plots was 0.9 m. In each plot, at least one plant was selfed, if available. The number of progeny assessed per population ranged from 32 to 840. The number of selfed plants per progeny ranged between 1 and

47 (four, on average). For each selfed plant (S_0 to S_4), we measured the grain weight of the selfed ear (g) and the expansion volume (EV; mL/g), a measure of popcorn quality. To assess EV, we used a 27 L microwave oven (900 W) and samples of 10 g. The processed dataset includes information from 30,986 plants with 145 and 1689 missing data for grain weight and EV, respectively.

Regarding the selection process, over the years we did not process the data and the criterion for selecting a selfed plant was an EV higher than or equal to 40 mL/g. Because we accomplished mass selection based on EV, it was possible to compare pedigree-based BLUP and phenotypic mass selection. To carry out a more accurate assessment on the relative efficacy of pedigree-based BLUP, compared with phenotypic mass selection, we included two other populations, generated using simulation. These populations will be referred to as in silico. We used the software REALbreeding (available upon request), which has been developed in Xojo (https://www.xojo.com/, accessed on 5 September 2022). REALbreeding has been used to provide simulated data in investigations in the areas of genomic selection, GWAS, QTL mapping, linkage disequilibrium, population structure, heterotic grouping/genetic diversity, and quantitative genetics. The current version allows the inclusion of digenic epistasis, genotype x environment interaction, and multiple traits, including pleiotropy. Details on the theoretical background and the stages for simulating individual genotypes for markers and genes and phenotypes can be found in a series of papers published by the main author (the software's developer) since 2013, including Viana and Garcia [18]. REALbreeding can also be used for research on human genetics, animal genetics and breeding, population genetics, and evolution.

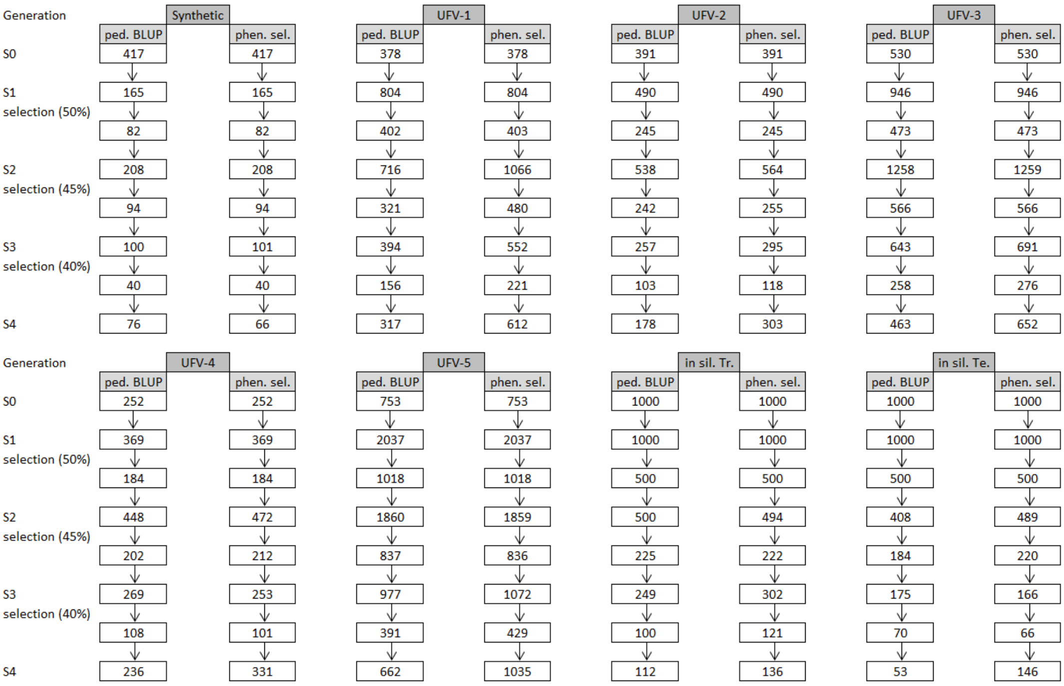
We simulated EV (mL/g) and grain yield (g/0.18 m^2) assuming 300 and 400 genes distributed across 10 chromosomes of 200 cM, respectively, 10% of pleiotropic genes (30 genes), and no epistasis. The minimum and maximum genotypic values for EV and grain yield were 60 and 15, and 90 and 20, respectively. The minimum and maximum phenotypic values were 70 and 5, and 100 and 10. The non-inbred populations were defined assuming 0.4 and 0.6 as the average frequency of the favorable genes for EV in the in silico tropical (low EV) and in silico temperate (high EV). Concerning grain yield, for both in silico populations, we assumed 0.3 as the average frequency of the favorable genes. We assumed bidirectional dominance (average degree of dominance: 0.01) for EV and positive dominance (average degree of dominance: 0.57) for grain yield. The sample size from S_0 to S_4 was 1000 plants, assuming 0 to 10 selfed plants per progeny, with an average of four. We maximized the linkage disequilibrium (LD) in the populations and the number of positive (in silico tropical) and negative (in silico temperate) LD values (for D, r^2, and D′). This led to significant positive and negative genotypic correlations between the traits. The heritabilities at the individual level for EV and grain yield were 30 and 20%, respectively.

2.2. Efficacy of Pedigree-Based BLUP and Statistical Analysis

Assume a single biallelic gene (A/a) and a non-inbred population in Hardy–Weinberg equilibrium. The genotype probabilities are p^2 AA: 2pq Aa: q^2 aa, where p and q are the allele frequencies. The population mean is $M = m + (p - q)a + 2pqd$. The parameters m, a, and d are the mean of the genotypic values of the homozygotes, the deviation between the genotypic value of the homozygote of greater expression and m, and the dominance deviation, respectively [19]. After $n - 1$ generations of selfing under selection, the genotype probabilities in generation n can be defined as $p^2 + pqF + \Delta_{AA}$ AA: $2pq(1 - F) + \Delta_{Aa}$ Aa: $q^2 + pqF + \Delta_{aa}$ aa, where Δ is the change in the genotype probability due to selection and F is the inbreeding coefficient. Note that $\Delta_{AA} + \Delta_{Aa} + \Delta_{aa} = 0$. Assuming no selection ($\Delta_{AA} = \Delta_{Aa} = \Delta_{aa} = 0$), the inbred population mean is $M_F = M - 2Fpqd$, where $-2Fpqd$ is the change in the non-inbred population mean due to inbreeding. If the selection changed the allelic frequencies, the mean of the generation n is $M_{Fs} = M_F + \Delta_{AA}(m + a) + \Delta_{Aa}(m + d) + \Delta_{aa}(m - a) = M_F + [(\Delta_{AA} - \Delta_{aa})a + \Delta_{Aa}d] = M_F + \Delta_g$, where $\Delta_g = M_{Fs} - M_F$ is the true genetic gain. Using phenotypic values, we have a predicted genetic gain of $D_g = (avP_{Fs} -$

avP$_F$)·h^2, where avP stand for the average phenotypic value and h^2 is the heritability. This is a standard function for the estimated genetic gain: selection differential times heritability.

We adopted a selection process based on the predicted additive value by fitting the individual model in inbred population [20]. The percentages of selected plants by phenotypic mass selection were approximately 60, 50, 60, and 90, from S$_1$ to S$_4$. However, in this study, we assumed 50, 45 and 40% of selected S$_1$, S$_2$, and S$_3$ plants for both selection processes (Figure 1). Because there was selection based on EV, we computed the increment in the genetic gain due to pedigree-based BLUP, relative to the gain attributable to phenotypic mass selection, given by iD$_g$ = (avP$_{Fsb}$ − avP$_{Fsp}$)·h^2, where the first mean refers to the individuals selected by pedigree-based BLUP and the second mean refers to the individuals selected by phenotypic mass selection. Because *REALbreeding* provides the parametric population means and genetic variances and covariances, and the true additive and dominance genetic values per generation, in the in silico populations the relative efficacy of pedigree-based BLUP selection was based on the parametric genotypic values (iΔ$_g$ = avG$_{sb}$ − avG$_{sp}$), where avG$_{sb}$ and avG$_{sp}$ are the average genotypic values of the selected plants under pedigree-based BLUP and phenotypic mass selection, respectively.



Generation	Synthetic ped. BLUP	Synthetic phen. sel.	UFV-1 ped. BLUP	UFV-1 phen. sel.	UFV-2 ped. BLUP	UFV-2 phen. sel.	UFV-3 ped. BLUP	UFV-3 phen. sel.
S0	417	417	378	378	391	391	530	530
S1	165	165	804	804	490	490	946	946
selection (50%)	82	82	402	403	245	245	473	473
S2	208	208	716	1066	538	564	1258	1259
selection (45%)	94	94	321	480	242	255	566	566
S3	100	101	394	552	257	295	643	691
selection (40%)	40	40	156	221	103	118	258	276
S4	76	66	317	612	178	303	463	652

Generation	UFV-4 ped. BLUP	UFV-4 phen. sel.	UFV-5 ped. BLUP	UFV-5 phen. sel.	in sil. Tr. ped. BLUP	in sil. Tr. phen. sel.	in sil. Te. ped. BLUP	in sil. Te. phen. sel.
S0	252	252	753	753	1000	1000	1000	1000
S1	369	369	2037	2037	1000	1000	1000	1000
selection (50%)	184	184	1018	1018	500	500	500	500
S2	448	472	1860	1859	500	494	408	489
selection (45%)	202	212	837	836	225	222	184	220
S3	269	253	977	1072	249	302	175	166
selection (40%)	108	101	391	429	100	121	70	66
S4	236	331	662	1035	112	136	53	146

Figure 1. Sample size and number of selected plants in S$_1$, S$_2$, and S$_3$ generations, in each popcorn and in silico populations, under pedigree-based BLUP and phenotypic mass selection.

The covariance between relatives in inbred populations, assuming linkage equilibrium and no epistasis, was derived by Cockerham [21]. Assuming biallelic genes, the covariance between relatives with self-fertilization depends on the additive (σ_A^2) and dominance (σ_D^2) variances, the covariance between the a and d deviations (D$_1$), and the variance of the dominance deviations (D$_2$). Ignoring the components D$_1$ and D$_2$, the diagonal and off-diagonal elements of the additive and dominance relationship matrices were computed from the covariances $c_{ggg} = (1+F_g)\sigma_A^2 + \left(1-F_g^2\right)\sigma_D^2$ and $c_{tgg'} = (1+F_t)\sigma_A^2 + \left[(1+F_t)(1-F_g)\left(1-F_{g'}\right)/(1-F_t)\right]\sigma_D^2$, respectively, where t, g, and g' are the generations. We used t as the first common ancestor (S$_0$ plant). Thus, for example, c_{011} is the covariance between two S$_1$ plants derived from the same S$_0$ plant and c_{012} is the covariance between a S$_1$ and a S$_2$ plant derived from the same S$_0$ plant. Although the elements of the additive and dominance relationship matrices are easy to compute, since they are a function of the inbreeding coefficient, the process is not available in known R packages such as AGHmatrix, ggroups, pedigree, and pedigreemm. We used a REALbreeding tool (Relationship) to compute the additive and dominance relationship matrices.

We performed the statistical analyses fitting the linear mixed model $y = \mu 1 + X\beta + Zu + \epsilon$ using ASReml-R v.4 [22], where y is the vector of phenotypes, μ is the general mean, β is the matrix of fixed effects of years and generations, u is the vector of additive values within generations, with $u \sim N(0, \Sigma_g)$, and ϵ is the error vector, with $\epsilon \sim N(0, I\sigma^2_\epsilon)$. Σ_g is a diagonal matrix with an additive variance for each generation. 1 is a vector of ones and X and Z are incidence matrices. We estimated the components of variance using the Residual Maximum Likelihood (REML) [23].

3. Results

The in silico tropical population shows similar means for EV and grain yield with Synthetic UFV. The in silico temperate population shows an EV comparable to the temperate populations. However, both in silico populations show much lower phenotypic variability relative to all other populations (Table 1). In the in silico populations, because of bidirectional dominance, the inbreeding had no significant effect on the EV mean of the inbred generations. Due to positive dominance, the grain yield decreased by 16% with inbreeding, on average. The inbreeding increased the genotypic variability for both traits. Note also that the inbreeding did not significantly affect the genotypic correlation between the traits. The values were significantly negative and positive for the temperate and tropical in silico populations, respectively. These results are consistent with no selection.

Table 1. Number of progeny, sample size, mean (M/M$_F$), phenotypic (σ^2_P), additive (σ^2_A), dominance (σ^2_D), and error (σ^2_E) variances, covariance between additive and dominance values ($\sigma_{A,D}$), and genotypic correlation (σ_g), per generation, in the popcorn (estimates) and in silico (estimates in the 2nd row) populations, relative to EV (mL/g) and grain yield (g/0.18 m^2).

Pop.	**Gen.**	**Prog.**	**Size**	**EV**						**Grain Yield**						σ_g
				M/M$_F$	σ^2_P	σ^2_A	σ^2_D	$\sigma_{A,D}$	σ^2_E	**M/M$_F$**	σ^2_P	σ^2_A	σ^2_D	$\sigma_{A,D}$	σ^2_E	
Synthetic	S_0	-	417	30.8	60.1	44.25	-	-	11.34	52.9	309.5	155.13	-	-	148.16	−0.05
	S_1	32	165	41.0	79.3	97.42	-	-	11.34	40.6	228.2	50.93	-	-	148.16	−0.21
	S_2	59	290	39.3	51.0	43.91	-	-	11.34	32.3	209.8	36.10	-	-	148.16	0.57
	S_3	75	360	39.0	23.8	10.82	-	-	11.34	30.4	201.3	39.29	-	-	148.16	−0.11
	S_4	76	367	43.3	11.8	0.50	-	-	11.34	36.9	168.2	11.86	-	-	148.16	0.11
UFV-1	S_0	-	378	40.8	76.2	32.11	-	-	17.90	42.8	195.2	52.92	-	-	141.26	−0.25
	S_1	215	804	43.9	73.0	69.59	-	-	17.90	39.3	186.0	30.61	-	-	141.26	−0.40
	S_2	317	1130	40.7	54.0	37.82	-	-	17.90	35.9	225.7	46.58	-	-	141.26	0.02
	S_3	276	1134	39.6	25.4	3.85	-	-	17.90	29.8	166.6	15.68	-	-	141.26	−0.58
	S_4	427	1981	43.1	17.3	0.26	-	-	17.90	36.2	177.0	17.62	-	-	141.26	−1.00
UFV-2	S_0	-	391	42.0	74.5	34.96	-	-	20.21	37.9	215.8	44.68	-	-	142.84	−0.17
	S_1	168	490	45.2	67.0	47.00	-	-	20.21	37.6	194.0	29.96	-	-	142.84	−0.13
	S_2	169	617	41.2	48.2	24.72	-	-	20.21	36.6	219.6	30.72	-	-	142.84	−0.16
	S_3	183	706	39.2	24.9	2.30	-	-	20.21	29.5	177.1	17.08	-	-	142.84	−0.20
	S_4	315	1468	42.7	20.3	0.70	-	-	20.21	36.7	173.8	17.23	-	-	142.84	0.03
UFV-3	S_0	-	530	42.0	48.4	26.06	-	-	16.82	37.1	145.9	0.00	-	-	146.75	-
	S_1	310	946	44.7	59.8	46.83	-	-	16.82	41.0	214.8	42.22	-	-	146.75	−0.23
	S_2	357	1330	40.4	55.9	36.47	-	-	16.82	35.4	225.7	28.09	-	-	146.75	0.13
	S_3	337	1421	39.3	27.7	7.18	-	-	16.82	29.9	167.1	14.45	-	-	146.75	−0.44
	S_4	502	2433	42.9	17.1	0.80	-	-	16.82	36.4	183.5	19.15	-	-	146.75	−0.02
UFV-4	S_0	-	252	40.7	56.8	24.13	-	-	20.84	37.5	205.1	71.60	-	-	133.33	−0.10
	S_1	101	369	43.5	72.2	53.12	-	-	20.84	41.5	206.3	47.47	-	-	133.33	−0.03
	S_2	116	517	40.6	61.6	38.44	-	-	20.84	35.5	218.1	32.94	-	-	133.33	0.12
	S_3	144	603	39.0	30.3	5.32	-	-	20.84	30.6	170.0	17.74	-	-	133.33	−0.29
	S_4	218	1107	42.6	20.2	0.50	-	-	20.84	36.2	154.5	12.18	-	-	133.33	−0.41
UFV-5	S_0	-	753	42.4	52.8	35.73	-	-	12.11	40.6	168.4	39.58	-	-	126.92	−0.53
	S_1	546	2037	43.9	67.5	78.68	-	-	12.11	36.6	132.6	9.63	-	-	126.92	−1.00
	S_2	600	1913	40.7	51.7	41.12	-	-	12.11	35.1	231.3	50.00	-	-	126.92	−0.26
	S_3	533	2163	39.8	29.8	13.21	-	-	12.11	28.8	151.6	15.92	-	-	126.92	−0.63
	S_4	840	3914	43.2	12.6	0.59	-	-	12.11	37.0	191.3	46.52	-	-	126.92	−1.00

Table 1. *Cont.*

Pop.	Gen.	Prog.	Size	EV						Grain Yield						σ_g
				M/M$_F$	σ_P^2	σ_A^2	σ_D^2	$\sigma_{A,D}$	σ_E^2	M/M$_F$	σ_P^2	σ_A^2	σ_D^2	$\sigma_{A,D}$	σ_E^2	
In silico temperate	S$_0$		1000	42.9	14.0	4.04	0.17	0.00	9.84	48.2	26.5	4.40	0.30	0.00	18.82	−0.65
				42.8	13.4	1.11	-	-	12.32	48.4	23.2	0.09	-	-	23.16	−1.00
	S$_1$	247	1000	42.5	18.4	5.38	0.16	−0.01	12.87	44.9	30.2	6.01	0.54	−0.28	23.93	−0.61
				42.5	16.3	3.13	-	-	12.32	44.5	16.74	3.44	-	-	23.16	−0.74
	S$_2$	250	1000	42.3	20.0	5.91	0.12	−0.02	13.96	43.2	31.8	6.69	0.44	−0.43	25.09	−0.65
				42.1	16.6	4.05	-	-	12.32	43.3	16.32	3.60	-	-	23.16	−0.60
	S$_3$	220	1000	42.2	20.6	6.13	0.09	−0.03	14.40	42.4	32.2	7.00	0.35	−0.50	25.39	−0.65
				42.0	16.5	3.36	-	-	12.32	42.1	17.37	5.16	-	-	23.16	−0.59
	S$_4$	243	1000	42.1	20.9	6.23	0.08	−0.03	14.58	42.0	32.4	7.14	0.30	−0.53	25.49	−0.52
				41.6	16.4	3.57	-	-	12.32	42.1	16.88	4.00	-	-	23.16	−0.36
In silico tropical	S$_0$	-	1000	33.9	14.8	4.31	0.12	0.00	10.33	49.2	32.2	6.08	0.36	0.00	25.76	0.78
				34.0	15.3	2.77	-	-	12.49	49.0	32.9	2.04	-	-	30.87	1.00
	S$_1$	243	1000	33.8	19.3	5.71	0.11	−0.01	13.51	45.5	41.6	8.19	0.64	−0.28	33.06	0.75
				34.1	20.4	5.34	-	-	12.49	45.9	41.0	6.28	-	-	30.87	1.00
	S$_2$	227	1000	33.7	21.0	6.25	0.08	−0.02	14.68	43.6	43.9	9.06	0.49	−0.43	34.76	0.80
				33.9	21.0	4.87	-	-	12.49	43.9	44.9	8.29	-	-	30.87	0.75
	S$_3$	237	1000	33.9	21.7	6.48	0.06	−0.02	15.15	42.7	44.5	9.43	0.37	−0.50	35.20	0.81
				33.9	22.5	5.15	-	-	12.49	42.6	43.3	6.74	-	-	30.87	0.67
	S$_4$	217	1000	33.6	22.0	6.58	0.05	−0.02	15.36	42.2	44.7	9.60	0.30	−0.53	35.34	0.82
				34.0	23.7	5.45	-	-	12.49	42.9	42.4	6.11	-	-	30.87	0.62

In regard to the popcorn populations, there is some evidence that the phenotypic mass selection improved EV, with a significant EV increase in Synthetic UFV and a substantial decrease in the phenotypic variability over the selfing generations (Table 1). This is also supported by the considerable decrease in the estimates of the additive variances for EV over the selfing generations. However, there is, in general, no evidence of significant indirect changes in grain yield. The results for grain yield are, in general, those expected with inbreeding. However, changes occurred in the estimated genetic correlations over the selfed generations. Because only BLUP provided the estimates of the additive variances for EV and grain yield, the accuracies for phenotypic mass selection and pedigree-based BLUP are very similar (Table 2). Thus, the experimental evidence is that both processes are equally efficient. Based on the same two accuracies, this is also true for the in silico populations. Comparing the accuracies in the tropical and temperate in silico populations, the general conclusion is that both selection processes have similar efficiencies.

Table 2. Accuracies [1] of phenotypic mass selection and pedigree-based BLUP based on EV, percent of selected plants (%S), and increments of direct (iDgd; mL/g) and indirect (iDgi; g/plant) genetic gains per generation with pedigree-based BLUP, relative to phenotypic mass selection, in the popcorn and in silico populations.

Pop.	Gen.	Ac$_1$	Ac$_2$	Ac$_3$	Ac$_4$	Ac$_5$	%S	iDgd	iDgi
Synthetic	S$_0$	-	0.89	-	-	0.88	0	-	-
	S$_1$	-	0.95	-	-	0.92	50	0.00	0.00
	S$_2$	-	0.89	-	-	0.85	45	−0.58	0.16
	S$_3$	-	0.70	-	-	0.55	40	0.45	−0.17
	S$_4$	-	0.20	-	-	-[2]	-	-	-
UFV-1	S$_0$	-	0.80	-	-	-[2]	0	-	-
	S$_1$	-	0.89	-	-	0.62	50	0.13	−0.08
	S$_2$	-	0.82	-	-	-[2]	45	−0.20	−0.38
	S$_3$	-	0.42	-	-	-[2]	40	0.06	0.10
	S$_4$	-	0.12	-	-	-[2]	-	-	-

Table 2. *Cont.*

Pop.	Gen.	Ac_1	Ac_2	Ac_3	Ac_4	Ac_5	%S	iDgd	iDgi
UFV-2	S_0	-	0.80	-	-	0.75	0	-	-
	S_1	-	0.84	-	-	0.85	50	−0.01	0.03
	S_2	-	0.74	-	-	0.69	45	−0.04	−0.05
	S_3	-	0.32	-	-	- [2]	40	0.02	0.46
	S_4	-	0.18	-	-	- [2]	-	-	-
UFV-3	S_0	-	0.78	-	-	0.76	0	-	-
	S_1	-	0.86	-	-	0.86	50	0.00	−0.01
	S_2	-	0.83	-	-	0.83	45	0.05	−0.01
	S_3	-	0.55	-	-	- [2]	40	0.00	0.18
	S_4	-	0.21	-	-	- [2]	-	-	-
UFV-4	S_0	-	0.73	-	-	0.68	0	-	-
	S_1	-	0.85	-	-	0.86	50	−0.25	−0.10
	S_2	-	0.80	-	-	0.80	45	0.06	−0.07
	S_3	-	0.45	-	-	- [2]	40	0.05	−0.04
	S_4	-	0.15	-	-	- [2]	-	-	-
UFV-5	S_0	-	0.86	-	-	0.84	0	-	-
	S_1	-	0.93	-	-	0.94	50	−0.01	0.00
	S_2	-	0.88	-	-	0.87	45	−0.04	0.00
	S_3	-	0.72	-	-	0.49	40	0.15	−0.01
	S_4	-	0.21	-	-	- [2]	-	-	-
In silico temperate	S_0	0.54	0.29	0.52	0.52	0.28	0	-	-
	S_1	0.54	0.45	0.52	0.67	0.42	50	0.07	−0.04
								0.46 [3]	−0.31 [3]
								1.16 [4]	−0.68 [4]
	S_2	0.54	0.50	0.49	0.72	0.45	45	0.14	−0.04
								0.41 [3]	−0.16 [3]
								0.32 [4]	−0.27 [4]
	S_3	0.54	0.46	0.51	0.78	0.34	40	0.29	−0.20
								0.83 [3]	−0.96 [3]
								2.05 [4]	−1.74 [4]
	S_4	0.55	0.47	0.48	0.78	0.34	-	-	-
In silico tropical	S_0	0.54	0.43	0.56	0.56	0.42	0	-	-
	S_1	0.54	0.55	0.53	0.71	0.58	50	0.02	0.02
								0.15 [3]	0.23 [3]
								0.75 [4]	0.48 [4]
	S_2	0.55	0.53	0.54	0.79	0.49	45	0.03	−0.01
								0.15 [3]	−0.06 [3]
								0.54 [4]	0.30 [4]
	S_3	0.55	0.54	0.56	0.82	0.48	40	0.26	0.31
								0.96 [3]	0.86 [3]
								1.25 [4]	0.81 [4]
	S_4	0.55	0.55	0.57	0.83	0.48	-	-	-

[1] Ac_1: root square of the parametric narrow sense heritability; Ac_2: root square of the estimated narrow sense heritability; Ac_3: correlation between the parametric additive value and the phenotypic value; Ac_4: correlation between the predicted and parametric additive values; $Ac_5 = \sqrt{1 - \left(PEV/\hat{\sigma}^2_A\right)}$, where PEV is the prediction error variance [24]. [2] $PEV/\hat{\sigma}^2_A > 1$. [3] Increment due to selection based on predicted additive value and gains computed using the genotypic value. [4] Increment due to selection based on true additive value and gains computed using the genotypic value.

In complete agreement with the accuracy analysis, the estimated increments in the genetic gain for EV with pedigree-based BLUP selection, relative to phenotypic mass selection, indicate a similar efficacy for the popcorn populations. The total increments were close to zero, in the range of −0.14 to 0.10 mL/g. However, slightly higher efficacy occurred in the in silico populations. The total increments were 0.30 and 0.50 mL/g (Table 2). The true total increments were 1.26 and 1.70 mL/g for the tropical and temperate populations, respectively. These values are associated with correlations between the predicted and parametric additive values of approximately 0.7, 0.7–0.8, and 0.8 in the generations S_1, S_2, and S_3, respectively. However, selecting based on the parametric additive values instead of the predicted additive values, the true total increments were 2.54 and 3.53 mL/g, respectively.

In regard to the indirect increments for grain yield, we observed small values in the popcorn populations, in the range of −0.36 to 0.44 g/0.18 m^2 (Table 2). In the in silico populations, the true indirect increments were 0.47 and −0.29 g/0.18 m^2 for the tropical and temperate populations, respectively. The true changes due to inbreeding were 1.59 and −2.69 g/0.18 m^2, respectively. To confirm a higher efficacy of pedigree-based BLUP, relative to phenotypic mass selection, observed from a single simulation, we also computed the true increments in other nine simulations of the in silico temperate population, assuming selection based on the predicted and true additive values (Table 3). The average direct total increments, 0.34 and 1.74 mL/g for selection based on the predicted and true additive values, confirm that pedigree-based BLUP is superior to phenotypic mass selection. The average total indirect increments in grain yield are also negative with small magnitude, indicating that pedigree-based BLUP provides slightly different indirect changes in grain yield, relative to phenotypic mass selection. It is important to emphasize that the average true direct increments with pedigree-based BLUP selection in the S_1, S_2, and S_3 generations are proportional to the correlation between the predicted and parametric additive values. In S_3, the accuracy was 26% lower than the maximum value and the true direct increment was 54% lower relative to the maximum value.

Table 3. Average additive and error variances per generation for EV, percent of selected plants (%S), accuracy [1], and increments in the direct (mL/g) and indirect genetic gains (g/0.18 m^2) with pedigree-based BLUP based on EV, relative to phenotypic mass selection, in the in silico temperate population (minimum and maximum values between brackets).

Gen.	σ^2_A	σ^2_E	Ac	%S	iDgd	iDgi
S_0	1.99 [0.83, 3.42]	11.80 [10.71, 12.94]	0.54 [0.52, 0.58]	-	-	-
S_1	4.29 [3.06, 5.37]	11.80 [10.71, 12.94]	0.71 [0.63, 0.75]	50	−0.48 [−0.93, 0.59] [2]	0.25 [−0.37, 0.74]
					0.08 [−0.28, 1.16] [3]	−0.03 [−0.68, 0.35]
S_2	4.36 [3.16, 5.35]	11.80 [10.71, 12.94]	0.75 [0.71, 0.81]	45	0.32 [−0.04, 1.03] [2]	−0.23 [−0.77, 0.11]
					0.33 [0.06, 0.66] [3]	−0.28 [−0.71, 0.04]
S_3	4.57 [3.15, 6.76]	11.80 [10.71, 12.94]	0.78 [0.72, 0.82]	40	0.50 [−0.40, 0.93] [2]	−0.33 [−1.12, 0.59]
					1.33 [0.80, 2.21] [3]	−0.76 [−1.74, 0.18]
S_4	4.32 [3.03, 5.87]	11.80 [10.71, 12.94]	0.80 [0.73, 0.83]	-	-	-

[1] Ac: correlation between the predicted and parametric additive values. [2] Increment due to selection based on predicted additive value and gains computed using the genotypic value. [3] Increment due to selection based on true additive value and gains computed using the genotypic value.

Only in Synthetic UFV we observed a significant estimated genetic gain for EV, with pedigree-based BLUP selection (approximately 14 mL/g) (Figure 2). The genetic gains in the other populations ranged from approximately 0.5 to 4.6 mL/g. This cannot be solely due to the reduced S_4 size (76 plants), since the number of S_4 plants in the in silico temperate population was only 53. Remember that the proportion of selected plants was kept constant in each population. Note that, as theoretically expected, higher gains were observed in the tropical populations (less improved). As expected, the selection process decreased the variability in the populations in similar proportions, between −58 and −92%. The selection for EV in Synthetic UFV also provided the highest indirect change in grain yield, of approximately −18 g/0.18 m^2. This is surprising since the genotypic correlations ranged between −0.1 and 0.2, approximately. In the in silico populations, with significant positive and negative genotypic correlations, the indirect changes were also negative. The change in the variability for grain yield was not consistent, varying from −67 to 28%.

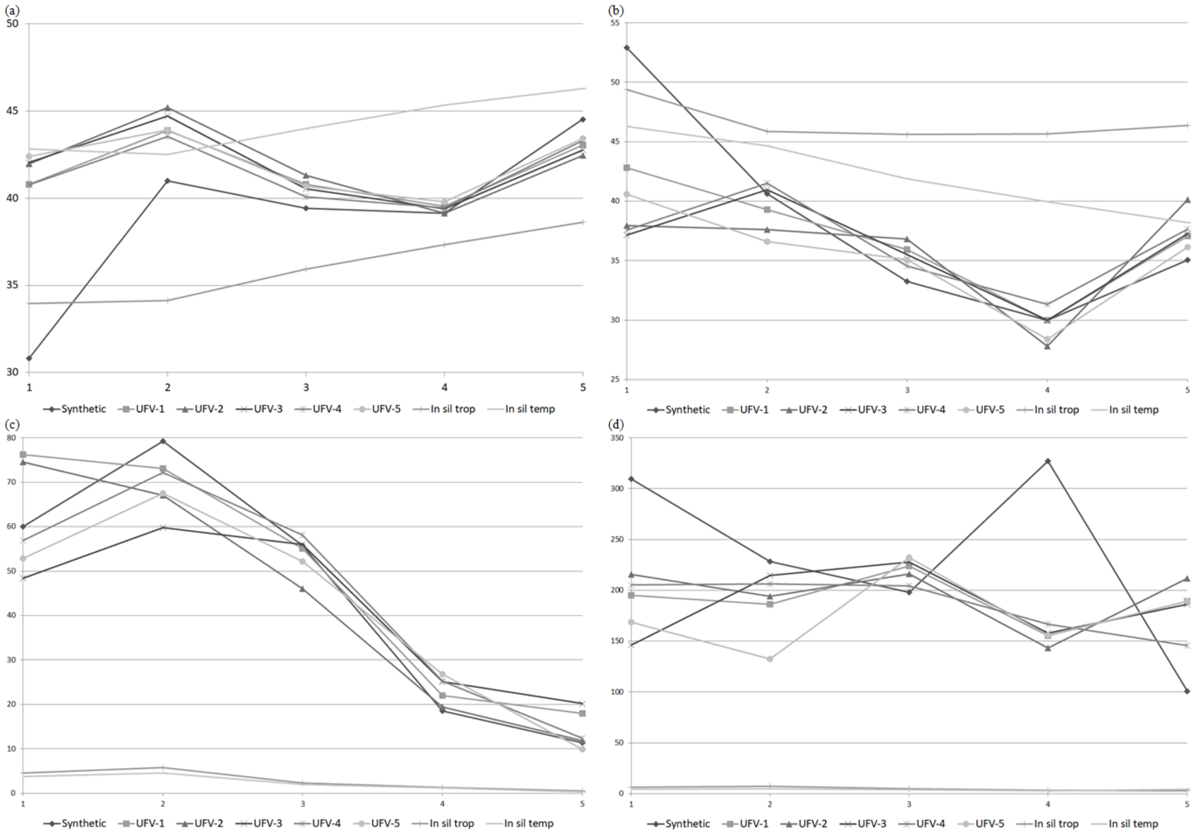


Figure 2. Changes in the populations means (**a**,**b**) and variances (**c**,**d**) over generations (S_0 = 1) with pedigree-based BLUP, using the predicted or true additive (for the in silico populations) values in the generations S_1, S_2, and S_3, relative to EV ((**a**,**c**); mL/g) and grain yield ((**b**,**d**); g/0.18 m^2).

4. Discussion

In a vast amount of studies on animal and plant breeding, distinct statistical approaches were compared, such as least squares (no relationship information), pedigree-based BLUP, and GBLUP, especially single-step GBLUP in recent years. Based on the results, it cannot be definitely stated that pedigree-based BLUP is superior to least squares and that GBLUP is superior to pedigree-based BLUP, in any situation [25–28]. However, taking into account the BLUP principles, the theoretical advantages of including relationship information, and the huge amount of favorable field results from genetic assessment in plant and animal breeding [5], there is no reason to not use BLUP for genetic evaluation and for the prediction of complex traits. Using a simulated population, Seno, Guidolin, Aspilcueta-Borquis, do Nascimento, da Silva, de Oliveira and Munari [17] investigated the efficacy of phenotypic selection, pedigree-based BLUP, and GBLUP over 25 years of selection. They observed equivalence for the two BLUP approaches concerning the rates of gain and average inbreeding coefficient. However, both methods yielded superior genetic gains relative to phenotypic selection.

When pedigree-based BLUP was applied to the recurrent genetic assessment of inbred lines, it was not possible to fit the additive-dominance model. This occurred not because of a problem with the additive and dominance relationship matrices (both well-conditioned) but due to singularities in the average information matrix. Theoretically, fitting the complete model would be advantageous since in inbred populations additive and dominance genetic values are correlated [19]. However, as shown from the analysis of the simulated data, even ignoring dominance, the correlation between the predicted and true additive values ranged from 0.5 (S_0) to 0.8 (S_4), proportional to the amount of relationship information. Velazco, Malosetti, Hunt, Mace, Jordan and van Eeuwijk [14] observed that the impact of including genealogy information to improve predictions was stronger for the lower heritability traits, such as grain yield and stay green. The analysis of the simulated data also showed comparable estimated and true values for the genotypic correlation between EV and grain yield.

For the popcorn and the in silico populations, we generally observed equivalence between the prediction accuracies based on estimated heritability and on prediction error variance [24]. However, only in the third selection cycle did we observe a positive correlation between the prediction accuracy and the genetic gain with pedigree-based BLUP (0.48). This does not mean that estimating accuracy is useless, since it is an appropriate measure for assessing and comparing selection processes and statistical approaches. Viana et al. [29] observed that the efficacy for identifying the superior 9% untested single crosses achieved 0.71 under a prediction accuracy of 0.92. In the study of Viana et al. [30], the efficacy of identification of the superior 6–9% of the untested testcrosses reached 0.76 when the prediction accuracy was 0.94. Note that, because recurrent selection provides theoretically lower genetic gains over selection cycles, only with a decrease in the prediction accuracy due to a decline in the genetic variability, under similar environmental conditions, will the correlation be positive. In the in silico populations, the prediction accuracies showed comparable or higher values for the correlation between the predicted and parametric additive values over the selection cycles, associated with decreasing true genetic gains. The genetic gains due to pedigree-based BLUP in S_1 to S_3 were 1.8, 1.4, and 1.3 mL/g for the tropical population and 1.5, 1.3, and 0.9 mL/g for the temperate population. Using simulation, Jibrila et al. [31] observed a slight decrease in the genetic gains in subsequent generations by increasing the intensity of preselection. They assumed genetic gain as the difference between the average true breeding values of the selected individuals in two subsequent generations.

Probably due to sampling, the analysis of the increments in the genetic gain with pedigree-based BLUP using the predicted additive value, relative to phenotypic mass selection, showed that the procedures were equivalent. However, the analysis of the increments in the non-replicated tropical and the replicated temperate in silico populations, assuming selection based on the predicted and true additive values, clearly showed that pedigree-based BLUP was superior to mass phenotypic selection. The breeders should not be disappointed with the magnitude of the genetic gains with pedigree-based BLUP because they are proportional to the percentage of selected plants. Note that even assuming 50, 45, and 40% of selected plants, there was a significant decrease in the genetic variability for EV in the populations. Using pedigree-based BLUP, Suontama, Klapste, Telfer, Graham, Stovold, Low, McKinley and Dungey [15] observed genetic gains for several growth, form, and wood quality traits across two *E. nitens* orchards. For most traits, the genetic gains were comparable (at least 80%) to those obtained with GBLUP.

Concerning the indirect changes in grain yield, the analysis of the alterations in the in silico population means due to inbreeding under no selection and inbreeding under indirect selection shows that inbreeding and indirect selection induced comparable changes. Because negative correlation in the in silico temperate population, the decrease in grain yield due to inbreeding and indirect selection was 1.9 times greater than the decrease due to inbreeding. On the contrary, because of the positive correlation in the in silico tropical population, the decrease in grain yield due to inbreeding was 2.1 times greater than the decrease due to inbreeding and indirect selection. El-Attrouny et al. [32] investigated the effects of pedigree-based selection for Japanese quail bodyweight at four weeks on bodyweight and bodyweight gain across four generations and observed significant indirect genetic gains. Because of moderate heritabilities, the strong positive genotypic correlation between spawn weight and number of eggs in the spawn and individual egg size traits, and the lack of correlation between the number of eggs in the spawn with egg size traits and female body weight, D'Ambrosio et al. [33] concluded that selection for growth will not induce indirect improvements in female reproduction traits. In the study of Cobo et al. [34] with rainbow trout, the genetic progress curves of the index MAT and litter weight (LW) indicated that the selection based on MAT gave a positive correlated response on LW. This occurred due to a high correlation between the traits (0.85).

Concluding, the use of pedigree-based BLUP in eight populations, over four generations of selfing, provided total genetic gains in EV in the range of 1 to 45%, inversely proportional to the level of improvement of the reference population, and indirect changes in grain yield in the range of −17 to 3%, values that correspond to approximately half of the values assuming inbreeding and indirect selection. The analysis of the in silico populations, assuming selection based on the true additive value and genetic gain computed from the genotypic values, proved that pedigree-based BLUP is superior to the phenotypic mass selection. The average direct total increments were 0.34 and 1.74 mL/g for selection based on the predicted and true additive values, respectively. The equivalence between both selection processes observed in the popcorn populations are due to sampling, as observed in the replications of the in silico temperate population. Based on our results, then, we strongly recommend the use of pedigree-based BLUP for genetic evaluation of inbred progeny.

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