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Simultaneous trait selection strategies applied to genome-wide selection for the identification of superior genotypes

Abstract – The objective of this work was to evaluate the efficiency of direct and indirect selection in genome-wide selection (GWS) and to compare multivariate strategies applied to GWS via selection indices. Ten F2 populations with 800 individuals were simulated, considering four traits with different heritabilities. The simulated data were subjected to genomic selection analyses. The five following strategies of selection indices were developed and applied to GWS: weighting of marker effects by residual variance; coding and standardization of marker effects; application of the average to the marker effects; application of the Mulamba & Mock index to genomic genetic values; and coding and standardization of phenotypic values before the GWS analyses. The GWS methods were more efficient than phenotypic selection. The multivariate strategies provide a higher selection efficiency than the direct and indirect phenotypic selections and than the direct and indirect selections based on genomic genetic values and on the phenotypic selection index.

Index terms: heritability, multivariate analysis, quantitative genetics, selection index.

Estratégias de seleção simultânea de características aplicadas à seleção genômica ampla para identificação de genótipos superiores

Resumo – O objetivo deste trabalho foi avaliar a eficiência da seleção direta e indireta sobre a seleção genômica ampla (GWS) e comparar estratégias multivariadas aplicadas à GWS via índices de seleção. Dez populações F2 com 800 indivíduos foram simuladas, tendo-se considerando quatro características com herdabilidades diferentes. Os dados simulados foram submetidos a análises de seleção genômica. As cinco seguintes estratégias de índices de seleção foram desenvolvidas e aplicadas à GWS: ponderação dos efeitos dos marcadores pela variância residual; codificação e padronização dos efeitos dos marcadores; aplicação da média aos efeitos dos marcadores; aplicação do índice de Mulamba & Mock aos valores genéticos genômicos; e codificação e padronização dos valores fenotípicos antes das análises de GWS. Os métodos de GWS foram mais eficientes do que a seleção fenotípica. As estratégias multivariadas avaliadas proporcionam maior eficiência de seleção do que a seleção fenotípica direta e indireta e do que a seleção direta e indireta baseada em valores genéticos genômicos e no índice de seleção fenotípica.

Termos para indexação: herdabilidade, análise multivariada, genética quantitativa, índice de seleção.

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Introduction

The goal of genome-wide selection (GWS) methods (Meuwissen et al., 2001) is the early phenotype selection, which relies on the effect predictions (on phenotype) of a large number of molecular markers. The main purposes of breeding programs are to maximize the gains with selection and to reduce the selection time (early selection). For that, GWS has been aroused more interest among breeders. The advantage of GWS is an early direct selection based on genotypic information correlated to the desired phenotype (Crossa et al., 2017; Voss-Fels et al., 2019; Budhlakoti et al., 2022; Gidamo et al., 2023).

In addition, in plant breeding programs it is of paramount importance to apply multivariate strategies, to simultaneously obtain gains from the selection of several important traits. In this context, the theory of selection indices stands out, for allowing of the formation of an additional trait established by the optimal linear combination of traits of economic interest (Cruz et al., 2012). Some studies show the efficiency of applying selection indices in plant breeding (França et al., 2016; Junqueira et al., 2016; Kumar et al., 2016; Silva et al., 2016, 2017; Vieira et al., 2016).

The implementation of the selection index theory in GWS will be a promising proposal for plant breeding programs, to enable the direct early selection of superior individuals in a set of economic important traits in a reduced time. Currently, there are some studies describing the efficiency of applying this theory in GWS, to obtain genetic gains in plant breeding (Ceron-Rojas et al., 2015; Fernandes et al., 2018; Silva et al., 2021).

Different selection indices result in different selection alternatives and, when considering the same index, there are different selection scenarios and different ways of statistically treating the data (Cruz et al., 2012). Thus, the application of indices in GWS requires further investigation, to adjust better strategies that allow the breeder to quick and efficiently identify promising, more suited genotypes to the purposes of plant breeding programs (Ceron-Rojas et al., 2015).

Random regression best linear unbiased predictor (RRBLUP) and multivariate partial least square (MPLS) methods were used in different selection scenarios in the present work, whose objective was to evaluate the efficiency of direct and indirect selections in GWS and to compare multivariate strategies applied to GWS via selection indices.

Materials and Methods

Data were simulated by considering a diploid species with 2n = 2x = 20 chromosomes as reference. Ten linkage groups were estimated, and each one was simulated for 100 cM size, with 100 codominant molecular marks spaced by 1cM per linkage group, totaling 1000 markers. Parental line genomes were designated as one dominant homozygote (A_1A_1) and one recessive homozygote (A_2A_2). Thus, the crossing between the parentals generated the F1 population with all marks in heterozygosis (A_1A_2).

From the self-fertilization of individuals in the F1 population, ten F2 mapping populations were simulated, with 800 individuals each. Each individual formation of the F2 populations was carried out, so that each individual of the F1 population produced 5000 gametes which were randomly recombined. The simulated F2 populations were coded for a given locus as 0 (representing A_1A_1 individuals), 1 (representing A_1A_2 individuals), and 2 (representing A_2A_2 individuals).

The quantitative traits were simulated considering a binomial distribution $(a+b)^s$, for which a = b = 0.5, and s = 19. The additive model (additive gene action and absence of dominance between the alleles) was considered for the simulation. Four quantitative traits were simulated (C1, C2, C3, and C4), each one controlled by 100 loci which were randomly distributed at each trait. The broad-sense heritabilities (H^2) of each simulated trait were 0.2, 0.4, 0.6, and 0.8, for C1, C2, C3, and C4 traits, respectively.

In addition, two alleles per locus were considered, without quantitative trait loci (QTL) of greater effects. The effect of each QTL was defined by: $A_1A_1 = \mu + a$; $A_1A_2 = \mu$; $A_2A_2 = \mu - a$, representing the additive effect of each gene in the F2 population. Therefore, the phenotypes of the individuals (Y_i) were generated according to the following model:

$$Y_i = \mu + \sum_{j=1}^{100} \alpha_j + \varepsilon_i,$$

where: μ is the general mean of the trait; α_j is the genetic effect at each locus; and ε_i is the environmental effect.

To proceed with the GWS analyses, it was necessary to define the training and validation of populations.

For all GWS evaluated methodologies, the cross-validation was performed 5-fold with 10 replicates. That way, each F2 population with 800 individuals was divided into 5 equal groups containing 160 individuals each. Thus, the training populations were composed of 640 individuals and used to estimate the effects of the markers, while the agreement between the genetic values, which were predicted via estimates from the training population, were validated in each group of 160 individuals, considered as the validation population.

The RRBLUP (Meuwissen et al., 2001) uses the best linear unbiased prediction (BLUP), considering that all markers have the same variance (absence of major effect genes). The RRBLUP was analyzed using the mixed.solve function of the RRBLUP package (Endelman, 2011).

Five different strategies were considered to investigate the efficiency of applying indices in the GWS, as well as to identify and select genetically superior individuals. The proposed indices are defined by the following the equations:

$$Ef_m = \sum_{i=1}^{4} \frac{M_{mi}}{\sigma_i^2} = \frac{M_{m1}}{\sigma_1^2} + \frac{M_{m2}}{\sigma_2^2} + \frac{M_{m3}}{\sigma_3^2} + \frac{M_{m4}}{\sigma_4^2},$$

$$Ef_m = \sum_{i=1}^{4} \frac{(M_{mi} - \overline{M_{mi}})}{\sigma_i} =$$

$$\frac{(M_{m1} - \overline{M_{m1}})}{\sigma_1} + \frac{(M_{m2} - \overline{M_{m2}})}{\sigma_2} + \frac{(M_{m3} - \overline{M_{m3}})}{\sigma_3} + \frac{(M_{m4} - \overline{M_{m4}})}{\sigma_4},$$

$$\text{and } Ef_m = \frac{\sum_{i=1}^{4} M_{mi}}{t} = \frac{(M_{m1} + M_{m2} + M_{m3} + M_{m4})}{4},$$

where: Ef_m is the final effect of the marker m weighted by the four evaluated traits, considering m = 1, 2, ..., 1000 markers; M_{mi} is the estimated effect for marker m for trait i (i = 1, 2, 3, 4); σ^2_i is the residual variance obtained for trait i.

In addition, the index of Mulamba & Mock was applied to the matrix of genomic estimated breeding values (GEBVs) of the four traits estimated by the RRBLUP and MPLS genomic selection methods. The index determined by the sum of the coded (or centered on the mean) and standardized phenotypic values was also applied, before applying the GWS methods. Thus, after applying the index to the phenotypic values, the data were subjected to GWS analysis by the RRBLUP and MPLS methods.

Individuals with higher phenotypic, true genetic, and GEBVs values were selected for the four evaluated traits. For selection purposes, the desirable individuals with high values for the traits C1, C3, and C4, and individuals with lower values for the trait C2 were considered.

Eighty individuals (10%) with the best performance were selected according to each scenario, taking into consideration the phenotypic values and true genetic values. In possession of the selected individuals, the selection gains (SG) were estimated by the direct and indirect selection method, using the following equation:

$$SG\,(\%) = \frac{\left(\bar{X}_s - \bar{X}_o\right) \times h^2 \times 100}{\bar{X}_o},$$

where: $\bar{X}_s$ is the average of the selected individuals; and $\bar{X}_o$ is the average of the initial population.

To compare the efficiency of the different multivariate methods and strategies, in the identification and selection of genetically superior individuals, the selection coincidence coefficients (CC) were estimated among the 80 individuals selected from the phenotypic, true genetic, and GEBV values, as follows:

$$CC\,(\%) = \left(\frac{NS}{TN}\right) \times 100$$

where: NS is the number of individuals selected on the basis of the phenotypic value or true genetic value, which were the same selected on the basis of the GEBV; and TN is the total number of selected individuals.

In addition, to compare the different multivariate strategies, the index of the sum of ranks (Mulamba & Mock, 1978) was applied in the matrices of phenotypic values (MMp) and true genetic values (MMg) considering the four traits. All calculations used for comparison between the different evaluated methodologies were estimated considering the average of the 10 simulated populations, for the four traits with different heritabilities.

Results and Discussion

The results showed that the total gains, when performing the phenotypic selection, are lower than the maximum possible gains to be achieved considering the true genetic values, being even smaller for traits with lower heritabilities (Table 1). When selecting individuals with the lowest true genetic values, it was possible to achieve high negative direct gain with the selection for C2; however, the indirect selection was impaired, which resulted in indirect negative gains for the other traits as well.

The results suggest the superiority of the GWS methods (Table 2), in comparison with the phenotypic selection (Table 1), since the direct and total gains – obtained when selecting the 80 individuals with the highest GEBVs – were higher than those obtained with the phenotypic selection and close to the maximum possible genetic gains to be achieved with the selection. However, these results indicate that the MPLS method is efficient only for traits with the highest heritability, since the direct and total gains obtained for the lowest heritability trait (C1) are close to the selection based on the phenotypic value of the individuals (Table 1), which does not justify its application in these cases.

Hence, this highlights the importance of searching for accurate tools to maximize selection gains in breeding programs. In this sense, GWS stands out for its recognized efficiency in the selection of low heritability traits, and for allowing of more selection cycles per unit of time, resulting in greater genetic gains than that by phenotypic selection (Crossa et al., 2017; Fernandes et al., 2018; Voss-Fels et al., 2019; Budhlakoti et al., 2022).

In the GWS, GEBVs are used to classify and select genetically superior individuals. In the present study, the superiority of the GWS methods was observed in comparison to the direct and indirect gains provided by the phenotypic selection. Fernandes et al. (2018) compared the efficiency of several GWS strategies to increase the prediction accuracy of a main trait, using information from correlated traits; these authors verified the higher efficiency of indirect GWS in comparison with the phenotypic selection, and they concluded that by using an easy-to-measure trait in the early stage of the plant, with high heritability and correlated to a main trait, it is possible to obtain a reduction of the time per cycle and, consequently, the reduction of production costs, corroborating what is recommended by Meuwinssen et al. (2001) and Anilkumar et al. (2022).

Considering a different direction of selection for trait C2 (Table 2), it was possible to verify that the results for selection gains showed the same pattern observed with direct and indirect selection based on

Table 1. Direct and indirect selection gains estimates based on individuals' phenotypic values and true genetic values.

Direct selection	Indirect selection				Total
	C1	C2	C3	C4	
		Phenotypic value(1)			
C1	6.84	2.29	2.15	3.96	15.24
C2	1.35	11.15	3.15	3.00	18.65
C3	1.14	2.72	13.50	5.04	22.39
C4	1.91	2.72	5.09	13.66	23.37
		Genetic value(1)			
C1	15.29	11.01	7.19	10.26	43.75
C2	9.88	17.57	8.65	6.09	42.19
C3	6.39	8.86	17.32	7.39	39.96
C4	10.37	6.88	8.50	15.26	41.01
		Phenotypic value(2)			
C1	6.84	2.29	2.15	3.96	15.24
C2	-1.23	-10.91	-2.99	-2.53	17.65
C3	1.14	2.72	13.50	5.04	22.39
C4	1.91	2.72	5.09	13.66	23.37
		Genetic value(2)			
C1	15.29	11.01	7.19	10.26	43.75
C2	-9.54	-17.29	-8.48	-5.96	41.27
C3	6.39	8.86	17.32	7.39	39.96
C4	10.37	6.88	8.50	15.26	41.01

(1)Individuals selected from the highest value for the four traits with different heritabilities (C1, C2, C3, and C4). (2)Gains based on individuals selected from the highest value for traits C1, C3, and C4, and lowest values for trait C2.

true genetic values, which made the indirect selection unfeasible, as it would result in negative indirect gains. According to Cruz et al. (2012), the direct selection for certain traits can cause undesirable changes in others, when there are unfavorable correlations that can lead to low performance in secondary traits, so that the improved population may present serious problems and, consequently, the rejection by producers.

The RRBLUP method provided results closer to the maximum possible genetic gains to be achieved, with the selection of the 80 individuals with the lowest GEBVs for the C2 trait, since it is possibly a medium heritability trait. The MPLS method was less efficient and resulted in lower total gains. The MPLS approached the phenotypic selection when considering low heritability traits, suggesting that its application in GWS is justified only for heritability traits greater than 60%. Azevedo et al. (2013) found that the MPLS method was 75% less efficient, on average, than the RRBLUP for estimating GEBVs and the effects of markers in the evaluation of pig carcass traits, with different heritabilities.

The strategies to apply the mean to the effects of the markers (IRbmed), the coding and standardization of the phenotypic values, before performing the genomic selection analyses (IndRb), and the application of the index Mulamba & Mock in the GEBVs (MMRb), through the RRBLUP method, provided the highest total gains 51.28% (IRbmed), 50.93% (IndRb), and 50.80% (index of Mulamba & Mock) (Table 3). These results were similar to those obtained by the index of Mulamba & Mock applied to true genetic values (MMg), which provided 51.80% of the total genetic gain.

The strategy of coding and standardizing the effects of the markers (IRbcp and Iplcp) provided the lowest total genetic gains (20.20% and 14.76%, respectively), in comparison with other proposed multivariate strategies. In addition, this strategy applied to the MPLS method resulted in negative gains for traits with lower heritabilities (-0.08% and -1.27%). Observing the results provided by the strategy of weighting the effects of the markers by the residual variance, considering the same sense of selection for all characteristics, the

Table 2. Direct and indirect selection gains estimated in true genetic values, which were based on individuals ranked in decreasing order of genomic breeding values (GEBVs) obtained by the random regression best linear unbiased predictor (RRBLUP) and multivariate partial least square (MPLS) methods.

Direct selection	Indirect selection				Total
	C1	C2	C3	C4	
			RRBLUP[1]		
C1	13.85	10.48	6.82	10.46	41.61
C2	10.22	16.54	8.79	5.94	41.49
C3	6.54	8.75	16.73	7.58	39.60
C4	10.53	7.03	8.81	14.93	41.29
			RRBLUP[2]		
C1	13.85	10.48	6.82	10.46	41.61
C2	-9.82	-16.06	-8.45	-6.01	40.34
C3	6.54	8.75	16.73	7.58	39.60
C4	10.53	7.03	8.81	14.93	41.29
			MPLS[1]		
C1	8.59	6.82	3.78	5.68	24.87
C2	8.46	14.43	7.02	5.03	34.94
C3	6.50	8.83	16.45	7.61	39.39
C4	10.56	7.08	8.82	14.73	41.18
			MPLS[2]		
C1	8.59	6.82	3.78	5.68	24.87
C2	-7.86	-14.02	-6.34	-4.61	32.83
C3	6.50	8.83	16.45	7.61	39.39
C4	10.56	7.08	8.82	14.73	41.18

(1)Individuals ranked in decreasing order of GEBVs for all traits (C1, C2, C3, and C4). (2)Individuals ranked in decreasing order of GEBVs for C1, C3, and C4 traits and, in ascending order for C2 trait.

IRRBLUP and IMPLS indices had a little difference for the selection gain obtained (Table 3). In addition, these indices provided higher gains for the C4 trait (high heritability).

The coding and standardizing of the effects of the markers was the only strategy that provided negative gains in the desired trait (C2). However, it provided low gains for the other traits and the lowest total genetic gains, in comparison to the other selection strategies. Like the first scenario, the effect of the markers via the MPLS was negative (-0.77), in the selection gain obtained for the trait of lower heritability, through the selection of individuals by the GEBVs estimated by the coding and standardizing strategy. In general, none of the selection index strategies were efficient to maximize the gains with the selection in all traits, when considering the scenario with different sense of selection for C2 (Table 3).

Table 3. Estimated selection gains in true genetic values, which were based on individuals ranked in the decreasing order of genomic breeding values (GEBVs) obtained by the selection indices for all traits (same selection direction) ranked in decreasing order of GEBVs for traits C1, C3, and C4, and in ascending order for C2 trait (different selection direction).

Index(1)	Trait				Total
	C1	C2	C3	C4	
		Same selection direction			
MMg	12.75	13.73	13.27	12.05	51.80
IRRBLUP	11.21	9.57	12.04	14.33	47.15
IMPLS	11.34	9.89	12.24	13.96	47.43
IRbcp	5.27	6.71	5.53	2.69	20.20
Iplcp	-0.08	-1.27	7.13	6.28	14.76
IRbmed	12.58	13.65	13.29	11.76	51.28
IPlmed	11.66	12.38	11.49	10.53	46.06
MMRb	12.58	13.29	12.99	11.94	50.80
MMPl	11.56	12.23	12.59	11.05	47.43
IndRb	12.29	12.90	13.38	12.36	50.93
IndPl	10.80	11.13	11.71	11.22	44.86
		Different selection direction			
MMg	10.28	2.71	11.56	12.47	37.02
IRRBLUP	10.28	6.94	11.41	14.49	43.12
IMPLS	10.21	6.87	11.69	14.11	42.88
IRbcp	2.42	-6.22	3.97	6.31	18.92
Iplcp	-0.77	-4.97	6.29	6.84	18.87
IRbmed	9.62	4.15	11.92	12.86	38.55
IPlmed	7.85	3.29	9.05	9.74	29.93
MMRb	10.69	2.48	11.61	12.82	37.60
MMPl	15.26	0.22	10.55	10.54	36.57
IndRb	9.76	4.91	12.27	13.26	40.20
IndPl	7.34	3.06	9.58	10.58	30.56

(1)MMg, Mulamba & Mock index applied to true genetic values; IRRBLUP, index weighted by the residual variance through the random regression best linear unbiased predictor (RRBLUP); IMPLS, index weighted by the residual variance through the multivariate partial least square (MPLS) method; IRBCP, index effects of coded and standardized markers through RRBLUP; Iplcp, index effects of coded and standardized markers through MPLS; IRbmed, average index of marker effects through RRBLUP; IPlmed, average index of marker effects through MPLS; MMRb, Mulamba & Mock index applied to GEBVs through RRBLUP; MMPl, Mulamba & Mock index applied to GEBVs through MPLS; IndRb, index of phenotypic values coded and standardized through RRBLUP; and IndPl, index of phenotypic values coded and standardized through MPLS.

According to the theory of genomic selection index defined by Ceron-Rojas et al. (2015), the strategy of coding and standardizing phenotypic values (IndRb and IndPl) before applying the GWS methods does not apply to the concept, since the genomic selection index is applied to GEBVs. However, to estimate the values of GEBVs, this strategy considered the linear combination of all traits and provided high gains and coincidences in the selection of genetically superior individuals, mainly for the RRBLUP method. According to Fernandes et al. (2018), when using phenotypic data of correlated traits used in the validation, to estimate the effects of markers and GEBVs, it is possible to achieve substantial increases in genetic accuracy and gain with selection.

The smallest selection coincidences with the individuals selected by the true genetic values (Table 4) were verified for the methods through the strategy of coding and standardizing the effects of the markers (IRbcp and Iplcp), regardless of the trait. These results were lower than the coincidences obtained for the MMp index, suggesting that this strategy is not efficient for the selection of genetically superior individuals, considering the same sense of selection for all evaluated traits.

Table 4. Selection coincidence analysis of the selected individuals, in decreasing order of estimated genomic breeding values by each selection index, and the individuals selected by the highest true genetic values for the simulated traits C1, C2, C3, and C4.

Index(1)	Trait			
	C1	C2	C3	C4
MMg	57.88	52.88	50.00	53.63
MMp	43.75	39.13	39.00	43.38
IRRblup	49.13	35.63	44.25	76.75
IMPLS	50.00	36.75	46.13	72.13
IRbcp	22.75	23.75	23.63	16.75
Iplcp	10.63	7.00	26.25	27.63
IRbmed	58.13	54.38	51.88	53.75
IPlmed	52.13	47.25	43.75	45.75
MMRb	56.75	50.63	48.75	52.75
MMPl	50.88	46.50	46.13	46.75
IndRb	55.75	49.50	52.00	57.63
IndPl	47.63	41.50	43.63	49.50

(1)MMg, Mulamba & Mock index applied to true genetic values; MMp, Mulamba & Mock index applied to phenotypic values; IRRblup, index weighted by the residual variance through the random regression best linear unbiased predictor (RRblup); IMPLS, index weighted by the residual variance through MPLS; IRbcp, index effects of coded and standardized markers through RRblup; Iplcp, index effects of coded and standardized markers through MPLS; IRbmed, average index of marker effects through RRblup; IPlmed, average index of marker effects through MPLS; MMRb, Mulamba & Mock index applied to GEBVs through RRblup; MMPl, Mulamba & Mock index applied to GEBVs through MPLS; IndRb, index of phenotypic values coded and standardized through RRblup; IndPl, index of phenotypic values coded and standardized through MPLS.

The strategy of applying the means of marker effects estimated through the RRBLUP (IRbmed) provided the selection of individuals with higher coincidence coefficients with the genetically superior individuals than those obtained by the MMg, for all evaluated traits. The strategies to weight the marker effects by the residual variance (IRRBLUP and IMPLS) showed the greatest coincidences in the selection of genetically superior individuals, when considering the C4 trait (higher heritability), providing 76.75% and 72.13% coincidence coefficients, respectively. However, the coincidence obtained for C2, by the IRRBLUP and IMPLS strategies, were smaller than the coincidences obtained for the MMp index, considering the same trait.

In general, none of the strategies were efficient to select the genetically superior individuals that had the lowest true genetic values for the C2 trait, evidenced by the low coincidences observed for this trait (Table 5). In this scenario, higher coincidences obtained with the individuals selected by the lowest true genetic values (C2) were obtained by the strategy of coding and standardizing the effects of the markers by RRBLUP and MPLS, resulting in 22.13% and 18.88% for the indices IRRBLUP and IMPLS, respectively.

The strategy of weighting the effects of the markers, by the residual variance through RRBLUP and MPLS methods (IRRBLUP and IMPLS), showed the least coincidences in the selection of genetically superior individuals, when considering the C2 trait (Table 5). In this selection scenario, this strategy provided the greatest coincidences when considering the other traits, mainly for the trait of higher heritability (C4). In general, the results provided by the strategy of weighting the effects of the markers by the residual variance, regardless of the GWS method used (IRRBLUP and IMPLS), were little influenced by the change in the selection scenario (Table 4 and Table 5).

Regardless of the scenario, the coincidences of all the proposed indices with the MMg index were greater than its coincidence with the MMp, except

Table 5. Coincidence of the selected individuals in decreasing order of genomic breeding values for C1, C3, and C4 traits and, in ascending order for C2 trait, estimated by each selection index, and the individuals selected by true genetic values, following the same criteria.

Index[(1)]	C1	C2	C3	C4
MMg	43.00	3.38	41.13	56.13
MMf	26.13	3.75	32.13	36.75
IRRblup	44.13	0.63	41.75	79.00
IMPLS	43.25	0.88	43.75	74.00
IRbcp	16.38	22.13	17.00	27.25
Iplcp	8.75	18.88	22.63	29.13
IRbmed	40.63	2.75	43.63	59.25
IPlmed	32.75	4.63	33.13	42.13
MMRb	39.13	2.13	38.75	56.75
MMPl	30.25	3.63	35.38	43.75
IndRb	41.50	1.88	45.75	64.13
IndPl	29.38	3.88	35.00	45.50

(1)MMg, Mulamba & Mock index applied to true genetic values; MMp, Mulamba & Mock index applied to phenotypic values; IRRblup, index weighted by the residual variance through the random regression best linear unbiased predictor (RRblup); IMPLS, index weighted by the residual variance through MPLS; IRbcp, index effects of coded and standardized markers through RRblup; Iplcp, index effects of coded and standardized markers through MPLS; IRbmed, average index of marker effects through RRblup; IPlmed, average index of marker effects through MPLS; MMRb, Mulamba & Mock index applied to GEBVs through RRblup; MMPl, Mulamba & Mock index applied to GEBVs through MPLS; IndRb, index of phenotypic values coded and standardized through RRblup; and IndPl, index of phenotypic values coded and standardized through MPLS.

when considering the indices based on the coding and standardization of the effects of markers (IRbcp and Iplcp) (Table 6). In general, the lowest coincidences observed among all strategies were for the IRbcp and Iplcp indices. The higher coincidences with the individuals selected by the MMg index were provided by three methods: MMRb, IRbmed, and IndRb. In addition, the coincidence coefficients found between these three strategies (MMRb, IRbmed, and IndRb) were of high magnitude, ranging from 83.13% to 92.38%.

In general, regardless of the scenario evaluated, the coincidences of most of the proposed indices were greater in relation to the MMg index than in relation to the MMp index. This fact indicates a greater efficiency of the indices applied to GWS, in the selection of genetically superior individuals in comparison with the index based only on phenotypic values. Heffner et al. (2011) also indicated success in the application of selection indices in GWS, in comparison with the selection indices applied to phenotypic data, and concluded that more research on the application of multivariate strategies in GWS is necessary, since one of the main objectives of breeders is the maximization of the total genetic gains with the selection for several traits, simultaneously.

Table 6. Comparison between the different multivariate strategies, through coincidence analysis, for two selection scenarios[(1)].

Indices[(2)]	MMg	MMp	IRRBLUP	IMPLS	IRbcp	Iplcp	IRbmed	IPlmed	MMRb	MMPl	IndRb	IndPl
MMg		56.88	69.50	70.13	25.75	17.88	84.38	66.00	86.00	71.38	82.50	62.88
MMp	43.25		54.50	55.75	27.13	22.13	58.13	61.63	59.38	63.00	60.38	68.38
IRRBLUP	65.38	42.88		87.75	21.50	27.75	70.63	56.25	70.00	60.38	75.75	61.13
IMPLS	64.75	45.25	85.75		22.38	30.63	71.00	60.25	70.38	65.25	75.75	61.63
IRbcp	38.50	33.63	31.88	31.38		33.25	28.75	29.50	29.00	27.75	28.13	27.38
Iplcp	32.88	30.63	33.63	36.88	53.88		18.63	21.38	18.13	22.75	21.25	22.13
IRbmed	72.25	47.50	74.00	73.13	45.25	37.63		68.13	90.13	72.13	92.38	64.63
IPlmed	46.50	51.00	47.00	53.00	35.88	34.13	54.00		67.50	85.38	68.88	68.13
MMRb	73.13	47.25	69.00	67.88	47.88	35.88	86.63	53.00		73.75	88.88	64.13
MMPl	54.25	52.00	51.13	57.63	38.50	37.75	60.63	80.88	61.38		73.63	68.13
IndRb	71.88	48.00	79.25	79.00	42.00	37.63	90.75	55.13	83.13	61.25		66.75
IndPl	49.63	61.88	50.75	52.63	34.38	32.25	54.50	53.88	53.63	54.63	54.88	

(1)Scenario 1 (above the main diagonal), selection in decreasing order of individuals for all evaluated traits; and scenario 2 (below the main diagonal), selection in decreasing order for all evaluated traits. (2)MMg, Mulamba & Mock index applied to true genetic values; MMp, Mulamba & Mock index applied to phenotypic values; IRRBLUP, index weighted by the residual variance through the random regression best linear unbiased predictor (RRBLUP); IMPLS, index weighted by the residual variance through MPLS; IRbcp, index effects of coded and standardized markers through RRBLUP; Iplcp, index effects of coded and standardized markers through MPLS; IRbmed, average index of marker effects through RRBLUP; IPlmed, average index of marker effects through MPLS; MMRb, Mulamba & Mock index applied to GEBVs through RRBLUP; MMPl, Mulamba & Mock index applied to GEBVs through MPLS; IndRb, index of phenotypic values coded and standardized through RRBLUP; IndPl, index of phenotypic values coded and standardized through MPLS.

Conclusions

1. The application of indices in genomic-wide selection (GWS) methods is an efficient proposal to obtain genetic gains in several traits, simultaneously, and it is promising for the application in plant breeding programs.
2. Direct and indirect selection using GWS methods is more efficient than phenotypic selection, especially for traits with lower heritabilities; however, in general, the use of genomic selection indices provides a greater total genetic gains than the direct and indirect selection.
3. The coding and standardizing strategy (IRbcp and Iplcp) results in lower total gains and lower selection coincidences than the other proposed indices.
4. The indices based on the strategy of weighting the effects of the markers by the residual variance (IRRBLUP and IMPLS) tend to maximize the gains in traits with higher heritabilities.
5. The IndRb, IRbmed, and IMMR indices show the highest total genetic gains with the selection and are the ones that came closest to the MMg index.

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