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Genetics/ Original Article

Genetic potential of maize full-sib progenies subjected to a reciprocal recurrent selection

Abstract – The objective of this work was to quantify the genetic potential of full-sib maize progenies subjected to a reciprocal recurrent selection, in order to obtain high-yielding hybrids. The experiment was carried out in the alpha lattice design, with three replicates and 24 blocks. One hundred and two full-sib maize progenies, from the crossing of two populations and two checks, were evaluated for the following traits: grain yield, seed mass, number of ears per plant, days to maturity, days to anthesis, days to silking, anthesis-silking interval, ear height, plant height, ear position, and stem lodging. Genetic parameters were estimated through REML/BLUP and multivariate analyses (correlation and similarity network, cluster heat map, and genetic gains). There are genetic variability and divergent clusters among the studied full-sib maize progenies. Seed mass, number of ears per plant, and anthesis-silking interval are the traits that most contribute to the improvement of grain yield and divergence among the full-sib maize progenies. Genetic potential should be exploited through the selection and recombination in reciprocal recurrent selection to obtain high-yielding hybrids.

Index terms: *Zea mays*, genetic variability, REML/BLUP.

Potencial genético de progênies de irmãos germanos de milho em seleção recorrente recíproca

Resumo – O objetivo deste trabalho foi quantificar o potencial genético de progênies de irmãos germanos de milho, em uma seleção recorrente recíproca, para obtenção de híbridos com alto rendimento. O experimento foi realizado em delineamento alfa látice, com três repetições e 24 blocos. Foram avaliadas 102 progênies de irmãos germanos de milho, do cruzamento de duas populações e duas testemunhas, quanto às seguintes características: produtividade de grão, massa de sementes, número de espigas por planta, dias para a maturação, dias para o florescimento masculino, dias para o florescimento feminino, intervalo de florescimento, altura da espiga, altura da planta, posição da espiga e acamamento do caule. Os parâmetros genéticos foram estimados via REML/BLUP e análises multivariadas (rede de correlações e similaridade, agrupamento de mapa de calor e ganhos genéticos). Há variabilidade genética e agrupamentos divergentes entre as progênies de irmãos germanos de milho estudadas. A massa de sementes, o número de espigas por planta e o intervalo de florescimento são as características que mais contribuem para o melhoramento da produtividade e a divergência entre progênies de irmãos germanos de milho. O potencial genético deve ser explorado por meio de seleção e recombinação, na seleção recorrente recíproca, para a obtenção de híbridos de alto rendimento.

Termos para indexação: *Zea mays*, variabilidade genética, REML/BLUP.

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Introduction

Producing countries of maize amount to 117 in the world; among them, Brazil ranks 33rd for the average grain yield (5,550 kg ha^{-1}), which is very low in comparison with that of the USA (11,110 kg ha^{-1}) (USDA, 2022). This fact reinforces the need for more research to develop high-yielding hybrids, which is one of the main objectives of the reciprocal full-sib recurrent selection program of maize, for simultaneously improving two genetically diverse populations and their cross (Zagatto Paterniani et al., 2019).

The recurrent selection maximizes heterosis, especially for quantitatively inherited traits (Hallauer & Carena, 2012) either S1 or S2 inbred progenies, and a combination of S1 and S2 inbred progenies. The inter-population reciprocal RS programs were restricted to either half-sib or full-sib family selection. Grain yield was the primary trait considered in selection, but selection indices that include grain moisture at harvest and resistance to root and stalk lodging also were considered in making the selections that were intermated to form the next cycle population. Approximately, 10 to 20 selections were intermated for each cycle. Estimates of the genetic variation among progenies tested (σ^2_g), such as grain yield, whose direct selection is generally not efficient, requiring indirect selection of associated traits with higher direct effect, genetic gain, and easily measurable and high heritability (Cruz et al., 2014). However, the genetic improvement of grain yield and its associated traits depend on the nature and magnitude of genetic variability, agronomic potential, and genetic divergence present in reciprocal selection of full-sib maize progenies.

Several authors have been studying the genetic variability and associations of traits of maize highlighting the most important traits for crop improvement (Laude & Carena, 2015; Roy et al., 2018; Naveenkumar et al., 2020; Nelimor et al., 2020; Kanna et al., 2021; Faria et al. 2022). When studying the genetic divergence, they showed the importance of the correct selection of parents whose crossings result in a high heterotic effect in the progenies, maximizing the chances for obtaining high-yielding progenies in segregating generations (Cruz et al., 2014). Thus, the application of this knowledge in the maize breeding program is essential to identify critical traits and establish heterotic clusters which could be the source of heterosis to obtain high-yielding hybrids.

The objective of this work was to quantify the genetic potential of full-sib maize progenies in the reciprocal recurrent selection for the attainment of high-yielding hybrids.

Materials and Methods

The experiment was carried out between November 2021 and March 2022, in the experimental area of Muquém farm (21°12'S, 45°59'W, at 918.84 m altitude), at the Centro de Desenvolvimento Científico e Tecnológico para a Agricultura of the Universidade Federal de Lavras, located in the municipality of Lavras, in the state of Minas Gerais (MG), Brazil. The soil is a Latossolo Vermelho-Amarelo with smooth wavy relief that belongs to the class of Ferralsols, according to the international taxonomic classification (IUSS Working Group WRB, 2015). The climate is rainy temperate (Cwa), according to the Köppen-Geiger's classification, with temperature and precipitation during the trial of 23.74°C and 232.56 mm, respectively (Lavras meteorological station: 21°13'34.0"S, 44°58'47.0"W).

A total of 102 full-sib maize progenies was obtained by the crossing of two populations on the eighth cycle of reciprocal recurrent selection (RRS), in the maize program of Universidade Federal de Lavras. The RRS program started in 2003, and the two base populations (A and B) derived initially from two commercial single cross hybrids (A: DKB 333B and B: DOW 657). Each population was obtained by random intercrossing of 3000 F_1 plants of each simple hybrid, which generated two populations in Hardy-Weinberg equilibrium.

The 102 full-sib progenies and two commercial double hybrids (checks) (Table 1) were installed in an alpha lattice design, with three replicates and 24 blocks per replicate. Sowing was carried out on 11/16/2021, with a density of 4 seed per linear meter, in 4 m length plots, spaced at 0.6 m apart. Fertilization was applied at planting with 250 kg ha^{-1} fertilizer corresponding to 8% N + 28% P_2O_5 + 16% K_2O. Topdressing fertilization with 200 kg ha^{-1} of urea-N (45% N) granules was carried out 25 days after sowing. The other crop managements were performed in accordance with the recommendations for the region (Borém et al., 2017).

The evaluated traits were grain yield (GY, kg ha^{-1}), seed mass (SM, g), number of ears per plant (EN), days to maturity (DM), days to anthesis (DA), days to silking (DS), anthesis-silking interval (ASI), ear height (EH, cm), plant height (PH, cm), ear position (EP), and stem lodging (SL, %).

Data analyses were carried out using the restricted maximum likelihood (REML) and the best linear unbiased predictor (BLUP) methods. The analysis of deviance was performed considering the following mixed model (Resende, 2016): $y = X_r + Z_g + W_b + \varepsilon$, where: y is the vector of observations, y is the vector of the fixed effects of replication, g, b, and ε are vectors of the random effects of full-sib maize progenies, blocks, and errors, respectively. X, Z, and W represent the incidence matrices for r, g, and b, respectively. The significance of effects of random progenies from the analysis of deviance was verified by the likelihood ratio test (LRT) at 0.1, 1.0, and 5.0% probability. The genetic parameters heritability (h^2) and genetic selection accuracy (Ac) were estimated by the following equations:

$$h^2 = \frac{\hat{\sigma}_g^2}{\hat{\sigma}_g^2 + \hat{\sigma}_e^2},$$

were: $\hat{\sigma}_g^2$ is the genotypic variance, and $\hat{\sigma}_e^2$ is the residual variance; and

$$Ac = \sqrt{1 - \frac{PEV}{\hat{\sigma}_g^2}},$$

where: PEV is the prediction error variance of BLUP values. The heritability was classified as low <30%, moderate (30–60%) and high >60% (Johnson, et al., 1955).

The BLUP values were used for the estimation of the Pearson's correlation coefficients, which were applied to construct the similarity network according to Epskamp et al. (2012), considering correlations with magnitude above 0.18 to identify trait clusters significantly correlated with each other and grain yield. For a better visualization and interpretation,

Table 1. Full-sib maize (*Zea mays*) progenies from the crossing of two populations (A and B), and two checks.

Progeny[1]	Identification	Progeny	Identification	Progeny	Identification	Progeny	Identification
226Ax42B	1	232Ax8B	27	259AX13B	53	307Bx80A	79
5Ax50B	2	35Ax46B	28	66Ax80B	54	33Bx81A	80
80Ax111B	3	49Ax87B	29	47Ax89B	55	202Bx10A	81
227Ax54B	4	301Ax52B	30	208Ax109B	56	302Bx89A	82
229Ax110B	5	243Ax10B	31	304Bx83A	57	235Bx48A	83
2Ax21B	6	34Ax46B	32	225Bx28A	58	311Bx37A	84
78Ax84B	7	241Ax37B	33	301Bx5A	59	7Bx7A	85
261Ax108B	8	40Ax50B	34	306Bx49A	60	312Bx31A	86
54Ax80B	9	39Ax21B	35	23Bx31A	61	68Bx85A	87
74Ax79B	10	263Ax27B	36	87Bx88A	62	231Bx38A	88
225Ax42B	11	28Ax51B	37	303Bx5A	63	232Bx38A	89
336Ax29B	12	304Ax88B	38	305Bx49A	64	241Bx40A	90
44Ax72B	13	215Ax44B	39	51Bx10A	65	314Bx20A	91
202Ax27B	14	305Ax86B	40	223Bx9A	66	105Bx83A	92
307Ax3B	15	58Ax81B	41	10Bx10A	67	310Bx23A	93
53Ax80B	16	36Ax46B	42	63Bx86A	68	205Bx13A	94
26Ax53B	17	242Ax10B	43	239Bx46A	69	219Bx12A	95
235Ax78B	18	76Ax87B	44	200Bx89A	70	315Bx43A	96
20Ax79B	19	56Ax82B	45	238Bx46A	71	38Bx10A	97
213Ax35B	20	10Ax10B	46	309Bx82A	72	85Bx89A	98
236Ax107B	21	300Ax85B	47	208Bx41A	73	37Bx11A	99
303Ax82B	22	210Ax40B	48	35Bx19A	74	64Bx85A	100
212Ax44B	23	228Ax112B	49	9Bx9A	75	216Bx45A	101
59Ax80B	24	4Ax54B	50	308Bx44A	76	316Bx17A	102
302Ax84B	25	68Ax81B	51	203Bx19A	77	Check1-Ufla JM 100	103
209Ax43B	26	7Ax34B	52	17Bx22A	78	Check2-Pioneer 3707	104

(1)Number of progenies and population A or B. The two base populations (A and B) derived from two commercial single cross hybrids (A: DKB 333B and B: DOW 657).

traits were partitioned into growth, reproduction, production traits, and their relationship with grain yield. Red lines represent negative correlations, and green lines represent positive correlations; the line thickness is proportional to the magnitude of the correlation. The lines showed a correlation in modulus higher than 0.1 (cutoff point: 0.1). The diagnosis of multicollinearity in the matrix of Pearson's correlation coefficients was made by the method of Montgomery et al. (2012) to perform the path analysis, which consists of standardized multiple linear regression, considering a casual chain model. The correlations were decomposed into a set of coefficients that indicate the direct and indirect effect of the explanatory traits on grain yield (Wright, 1921).

For clustering analysis, Euclidean distances between pairwise progenies were estimated and used in Ward.D method. The ggtree heatmap clusterings were used to visualize the heterotic clusters of progenies and their standardized means of the traits (Yu, 2020). This representation is advantageous in the quick visual analysis of the agronomic potential of the progenies among and within the clusterings, which allows of a higher efficiency in the identification and selection of divergent progenies and the best performance of one or several traits

The analysis of the means and variation of clusters was performed using boxplots. The Trait contribution to the genetic divergence and selection intensity of 15% for each population (A x B and B x A) from the 102 full-sib progenies and the genetic gains were estimated (Cruz et al., 2014). The desired selection directions were high gain for GY, SM, and EN, moderate gain for DM and PH, and low gain for EP, DS, ASI, and SL. Statistical analysis of the data were performed using the R Core Team software (2022).

Results and Discussion

There were significant differences ($p<0.001$, 0.01, and 0.05) by the likelihood ratio test (LRT) among the 102 full-sib maize progenies for the traits, indicating a high genetic variability present in the populations. However, the means of progenies were similar to those of the checks ($p>0.05$) for all traits (Table 2). This is interesting because the checks are commercial double hybrids, which shows the excellent performance of the progenies. High heritability was observed for DS, DA, SM, EH, and DM, and moderate heritability, for GY, ASI, PH, EP, and SL.

A high heritability indicates a higher correlation between phenotype and genotype, and it is associated with the additive effect of genes (Cruz et al., 2014; Magar et al., 2021). The accuracy results for DS, SM, EN, DM, DA, EH, PH, and EP were high to very high, supporting the criteria set by Resende and Duarte (2007), indicating high correlation between predicted and true genotypic values of the progenies for this trait. The high heritability results for SM, EN, DS, DA, and EH are in accordance with those reported by Kanna et al. (2021); these authors also observed high heritability for GY, ASI, and PH conversely to the moderate heritability observed in the present study. Magar et al. (2021) reported high heritability for SM and ASI, while contrasting results were found for GY and DA, with high and low heritability observed, respectively. Silveira et al. (2022) corroborate the results of the present study by reporting comparable findings regarding high and moderate heritability estimates for GY, SM, DA, EH, PH, and DS. However, their observations diverged in the case of EN and EP, as they observed low heritability for these traits. High heritability, similar to the findings of this study, was also observed by Faria et al. (2022) for traits such as DA, DS, PH, EH, and SM, whereas moderate heritability was reported for GY and EN.

A high to moderate heritability indicates less effect of the environment on the traits of the progenies and possibilities of success in selection activities (Cruz et al., 2014; Kanna et al., 2021). However, it is expected to observe discrepancies in heritability estimates for the same traits, as demonstrated by Magar et al. (2021) and Silveira et al. (2022), given their quantitative nature. This fact suggests that an effective selection should be practiced in the evaluation environments themselves, in order to obtain genetic gains. Heritability is not only a peculiarity of the trait but also of the population and of the environment to which individuals are subjected (Olivoto et al., 2017). Regarding the variation in the means of the progenies from this study, significant improvements were observed in terms of higher GY and EN, as well as lower DS and ASI, indicating favorable advancements in several important traits. These results align with the observations made by Kanna et al. (2021), Magar et al. (2021), Faria et al. (2022), and Valadares et al. (2022), who also reported a wide range of means for the same traits across different genotypes and evaluation environments. Thus, high means associated with high variability indicate the possibility of selecting and developing high-yielding hybrids in the reciprocal recurrent selection program.

The correlations were significant at 0.1, 1, and 5% probability by the t-test (Figure 1). The GY showed a significant positive correlation with EN, SM, DM, EH, and a significant negative correlation with ASI. Nonsignificant positive correlations were observed for PH and EP, and negative with DA, DS and SL (Figure 1 A). However, significant positive correlations were observed between SM and DM, between DM, DA, DS, EH, PH, and EP. A significant positive correlations was observed for SL with DA, DS, and EH. Significant negative correlations were observed between SM and SL, DA and ASI, ASI and EP, and for EN with DS and DA. Indirect selection of progenies with higher SM and EN and shorter ASI should be preferred to improve grain yield. However, higher SL and DS decrease GY due to their strong negative correlation with the SM and EN traits, which are positively correlated with GY. Additionally, higher PH has a positive impact on GY through DM, which is significantly and positively correlated with GY. Hence, it is crucial not to overlook these traits in the selection program.

These findings align with the results reported by Roy et al. (2018), who identified a significant positive correlation between GY and SM, PH and EH, DM and DA. However, a discrepancy arises in terms of the negative correlation observed between DM, PH, and EH in their study. Faria et al. (2022) observed a significant, positive correlation between GY and EN, PH and EH, DA and DS. Silveira et al. (2022) observed a significant, positive correlation between GY and EN, PH and EH, DA and DS, EH and EP, and a negative correlation between GY and DA, and between DS and ASI. For Pandey et al. (2017), the correlation between DM and GY was negative. Kanna et al. (2021) observed a positive correlation between GY with DA, and between DS and ASI, while observing a negative correlation between GY and SM conversely

Table 2. Deviance analysis of 102 full-sib maize (*Zea mays*) progenies for their genetic and statistical parameters.

Trait	M	logLik	Dev	X^2	h^2	Ac	Mean	Min	Max	MeanCk1	MeanCk2	F: p>0.05
GY (kg ha^{-1})	M2	-2,780.29	5,560.57	12.93	0.46	0.68	9,433.09	7,484.26	10,956.29	7,333.17	10,856.15	1.44
	M1	-2,773.82	5,547.64									
SM (g)	M2	-786.63	1,573.25	62.54	0.74	0.86	32.45	28.75	37.10	30.52	33.23	0.35
	M1	-755.35	1,510.71									
EN	M2	-116.71	233.41	18.68	0.51	0.71	1.14	1.07	1.58	1.00	1.00	0.32
	M1	-107.37	214.73									
DM	M2	-955.31	1,910.63	36.23	0.65	0.81	129.13	129.13	135.16	128.88	134.28	0.84
	M1	-937.20	1,874.39									
DA	M2	-649.51	1,299.02	88.33	0.80	0.89	67.72	64.92	70.51	69.04	67.95	0.32
	M1	-605.34	1,210.69									
DS	M2	-649.09	1,298.18	95.03	0.81	0.90	68.84	66.07	72.86	70.60	69.22	0.57
	M1	-601.58	1,203.16									
ASI	M2	-482.33	964.65	8.61	0.39	0.62	1.12	0.67	1.87	1.65	1.34	0.27
	M1	-478.02	956.05									
EH (cm)	M2	-1,257.11	2,514.22	38.83	0.66	0.81	152.08	132.40	167.10	155.68	139.52	0.71
	M1	-1,237.70	2,475.40									
PH (cm)	M2	-1,303.68	2,607.37	26.06	0.59	0.77	235.59	256.60	270.81	254.71	231.70	2.00
	M1	-1,290.66	2,581.31									
EP	M2	525.24	-1,050.48	20.65	0.54	0.73	0.59	0.55	0.66	0.61	0.60	0.26
	M1	535.57	-1,071.13									
SL (%)	M2	-1,050.01	2,100.02	5.62	0.34	0.58	3.06	1.71	9.69	0.63	0.38	0.27
	M1	-1,047.20	2,094.40									

Genetic parameters: GY, grain yield; SM, seed mass; EN, number of ears per plant; DM, days to maturity; DA, days to anthesis; DS, days to silking; ASI, anthesis-silking interval; EH, ear height; PH, plant height; EP, ear position; and SL, stem lodging. Significant by chi-square test (X^2) at 0.001 (>6.63), 0.01 (>3.84 = 6.63), and 0.05 (= 3.84). M1, complete model; M2, reduced model; h^2, heritability, Ac, accuracy; Min, minimum; Max, maximum; CK, checks; F, F- test for checks.

to the results of the present study. These contrasts can be explained by differences of genetic material and growing environments, indicating that an effective selection should be practiced considering the genetic particularities of the population and the evaluation environment.

The first cluster (SM and DM traits) and the second one (DM, EH, and PH traits) are significantly and positively correlated with each other and with GY, respectively (Figure 1 B). Some authors also observed a highly positive correlation between PH and EH, which suggests that the assessment of PH dispenses with EH (Roy et al., 2018; Kanna et al., 2021; Magar et al., 2021; Faria et al., 2022). Therefore, it reduces the need to measure a higher number of explanatory traits, providing higher efficiency for the selection and time savings in future evaluations. However, the correlation results between SM and DM in this study reveal a strong positive correlation, contrasting with the findings of Pandey et al. (2017), who observed a significant negative correlation between these traits.

After the multicollinearity analysis of the yield traits, EH and DA were excluded from the path analysis model because they presented variance inflation factors [(VIFs > 10) and condition numbers (CN > 1,000) indicating that they are the cause of the multicollinearity, besides being redundant and more represented by other traits, according to Cruz et al. (2014). The path analysis for traits with lower VIFs and (NC) (Table 3) showed that the coefficients of determination were lower than the residual effects, which is indicative that the set of traits included in the model does not explains satisfactorily the variations in the GY trait, and that there are other essential traits which can play a critical role in the genetic improvement of the studied genetic progenies. All traits had direct effects higher than the indirect ones, which suggests a simultaneous selection in the favorable and unfavorable direction for the traits positively and negatively correlated with grain

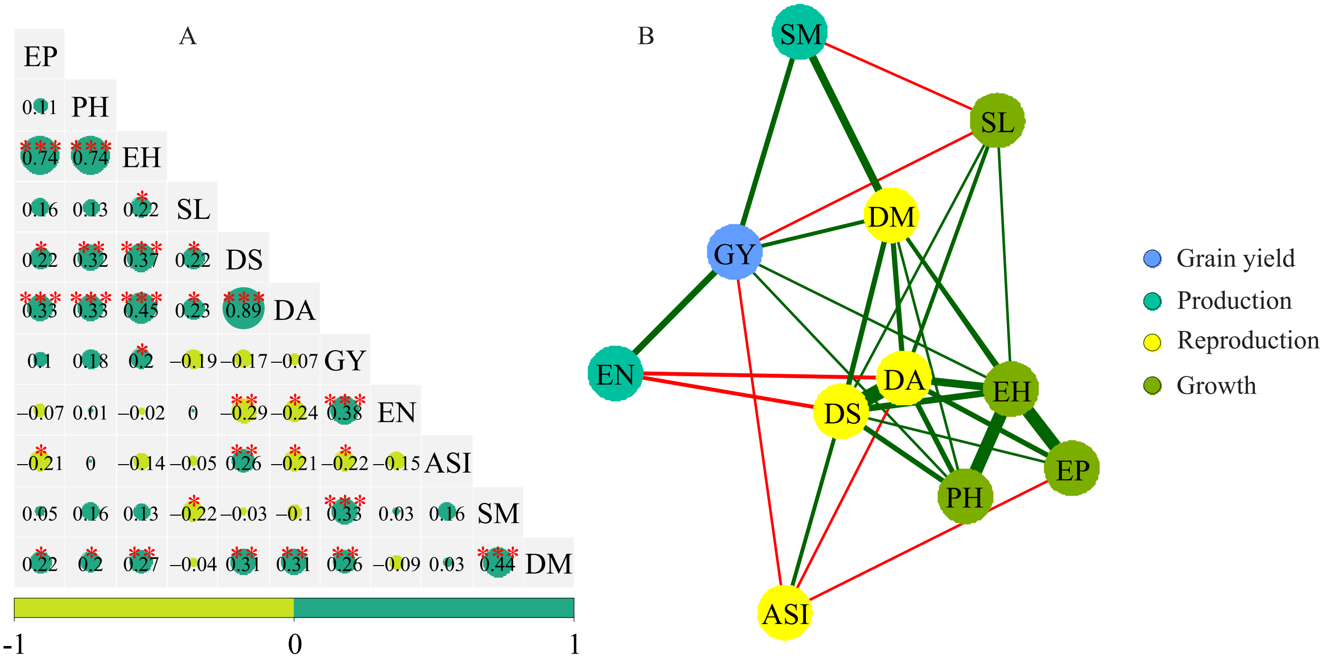

Figure 1. Person's correlation (r) based on BLUP values: A, the size of the circles is proportional to the magnitude and significance of the correlation coefficients; B, similarity network of correlations between grain yield traits. Red and green lines represent negative and positive correlations, respectively. The width of the line is proportional to the strength of the correlation. The thickness of the lines was controlled by applying 0.1cutoff value. Cluster of positive correlated traits in 102 full-sib maize (*Zea mays*) progenies. Traits: GY, grain yield; SM, seed mass; EN, number of ears per plant; DM, days to maturity; DA, days to anthesis; DS, days to silking; ASO, anthesis-silking interval; EH, ear height; PH, plant height; EP, ear position; and SL, stem lodging.

yield, respectively, Cruz et al. (2014), to obtain high-yielding hybrids with multiple traits. However, EN and SM showed the highest positive, direct effect on GY, followed by DM and PH. ASI and SL had the high direct, negative effect on GY, followed by DS. Similar results were reported by Ram Reddy & Jabeen (2016), who observed a higher negative, direct effect of ASI on GY. Roy et al. (2018) observed a higher direct, positive effect of SM, PH, and DM, and a negative, direct effect of SL on GY. Kanna et al. (2021) observed a higher direct, positive effect of EN on GY and high negative, direct effect of PH on GY, which is in contrast to the results found in the present study. Furthermore, Pandey et al. (2017) also observed contrary results to this study, when reporting a higher direct, negative effect of PH on GY.

In the present study, the selection for higher SM and EN and lower ASI is promising for the attaining of high-yielding maize progenies, as these traits simultaneously showed a higher direct effect and significant correlation with GY, associated with high and moderate heritability. Progenies showing low ASI are more drought tolerant, according to Zagatto Paterniani et al. (2019). ASI is an important trait in the synchronization of pollen with silking, for which positive and shortest values are desired to ensure a higher fertilization, filling, and grain yield.

The selection progress for these traits will be better through the recurrent selection that seeks to exploit the overall combining ability; however, for the exploitation of the specific combining ability, genetically divergent progenies are necessary (Kanna et al., 2021). The heat map clustering showed six genetically divergent clusters among the 102 full-sib maize progenies and the agronomic potential of each of them (Figure 2). These divergent cluster are heterotic and can be exploited in the selection and recombination activities of the reciprocal recurrent selection of full-sib maize for the obtention of high-yielding hybrids. The SM, EN, and ASI traits were more important in the cluster formation and divergence between full-sib progenies (Figure 3 A), confirming these traits as the main determinants of higher variability among interpopulation full-sib maize progenies. Several authors who have studied the genetic divergence in maize, such as Nelimor et al. (2020), classified five divergent clusters of 72 extra-early maize accessions, showing EN as the most important trait for differentiation. Naveenkumar et al. (2020) observed three clusters of 111 maize lines and showed the divergence relationship with the traits PH, EH, GY, and ASI. Faria et al. (2022) found 22 clusters of 187 maize lines, identifying the EN, GY, and DS traits as the most related ones to genetic divergence. In the present study, the clusters I and II were shown as close and genetically more divergent than clusters III, IV, V and VI, through the rootpoint separator, which indicates that the recombination among progenies of more divergent clusters will allow of a higher heterosis and variability of the populations.

Table 3. Direct (bolded diagonal) and indirect (off-diagonal) effects of traits on the grain yield of 102 full-sib maize (*Zea mays*) progenies.

Trait	SM	EN	DM	DS	ASI	PH	EP	SL	r
SM	**0.21**	0.01	0.08	0.00	-0.03	0.02	0.00	0.03	0.33
EN	0.01	**0.34**	-0.02	0.03	0.03	0.00	-0.01	0.00	0.38
DM	0.09	-0.03	**0.19**	-0.03	-0.01	0.03	0.02	0.01	0.26
DS	-0.01	-0.1	0.06	**-0.11**	-0.04	0.05	0.02	-0.03	-0.17
ASI	0.03	-0.05	0.01	-0.03	**-0.17**	0.00	-0.02	0.01	-0.22
PH	0.03	0.00	0.04	-0.03	0.00	**0.16**	0.01	-0.02	0.18
EP	0.01	-0.03	0.04	-0.02	0.04	0.02	**0.07**	-0.02	0.10
SL	-0.04	0.00	-0.01	-0.02	0.01	0.02	0.01	**-0.15**	-0.19
NC	1.93	1.45	1.29	1.00	0.76	0.63	0.58	0.35	-
VIF	1.44	1.12	1.48	1.62	1.25	1.19	1.19	1.14	-

Traits: SM, seed mass; EN, number of ears per plant; DM, days to maturity; DS, days to silking; ASI, anthesis-silking interval; PH; plant height; EP, ear position, and SL, stem lodging. Residual effect, 0.7950; coefficient of determination, 0.368; r, correlation coefficients; NC, condition number; and VIF, variance inflation factors; (-), absent.

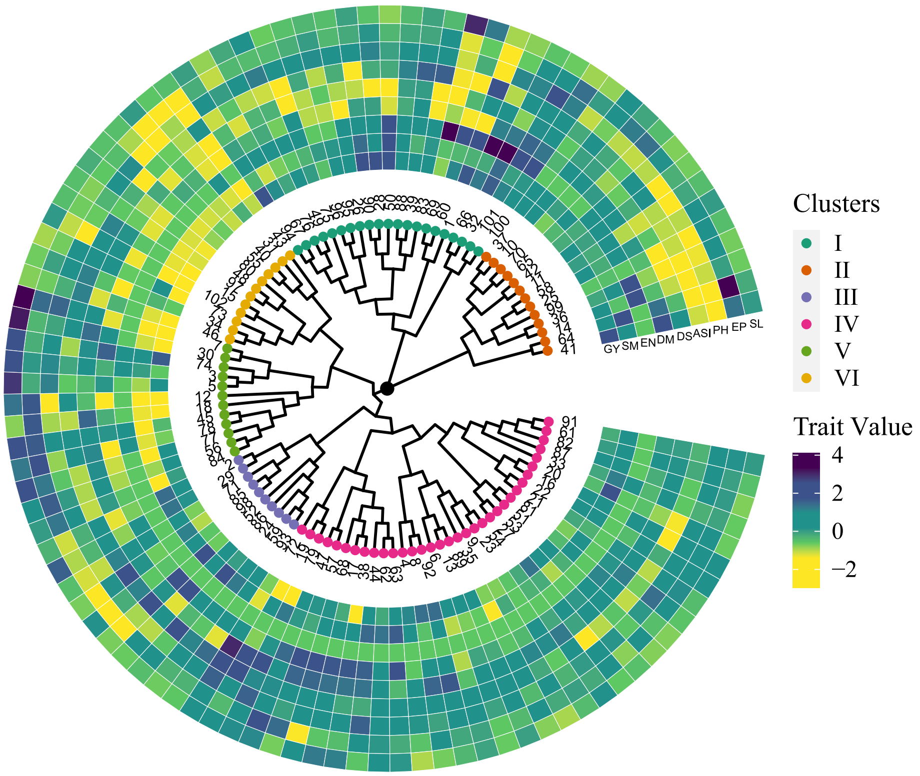

Figure 2. Cluster heat map of 102 full-sib maize (*Zea mays*) progenies. Clusters (I to VI). GY, grain yield; SM, seed mass; EN, number of ears per plant; DM, days to maturity; DS, days to silking; ASI, anthesis-silking interval; PH, plant height. EP, ear position; and SL, stem lodging. The yellow to darkblue viridis color gradients of trait values (value of standardized traits) show from the lowest to the highest means. The black point in the center of the circular dendrogram is the rootpoint.

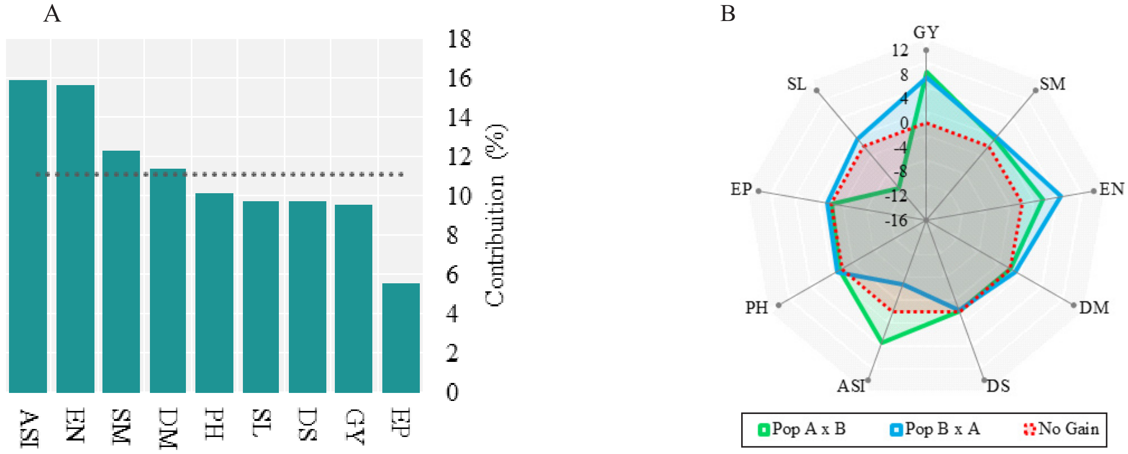

Figure 3. Contribution of traits to the genetic divergence (A), and genetic gains (%) (B) of 15 full-sib maize (*Zea mays*) progenies derived from populations A x B and B x A. The two base populations (A and B) were derived from two commercial single cross hybrids (A: DKB 333B and B: DOW 657). Traits: GY, grain yield; SM, seed mass; EN, number of ears per plant; DM, days to maturity; DS, days to silking; ASI, anthesis-silking interval; PH, plant height; EP, ear position; and SL, stem lodging (SL).

For the selection of progenies for recombination, the agronomic potential of the traits associated with genetic divergence should be considered, according to Cruz et al. (2014), so that they can present complementary genes that provide higher heterosis in F_1, and transgressive individuals in segregating generations. Associated with these criteria, the heat map clustering (Figure 2) and the mean variations of clusters (Figure 4) allow of the characterization of clusters with higher, moderate and lower agronomic potential of the traits.

Cluster I (21 progenies) were characterized by high means for GY, EN, and PH, moderate ones for SM and EP, and low means for DM, DS, ASI, and SL.

Cluster II (13 progenies) had a high mean for EP, moderate means for GY, SM, EN, and DM, low ones for DS, ASI, PH, and SL.

Cluster III (10 progenies) had a high mean for SM and ASI, moderate GY, DM, and PH, and the lowest mean for EN, DS, EP, and SL.

Cluster IV (34 progenies) showed a high mean for DS and PH, a moderate one for GY, DM, ASI, and EP, and a low mean for EN and SL.

Cluster V (12 progenies) had a high mean for EP and SL, a moderate mean for EN and PH, and low means for GY, SM, DM, and ASI.

Cluster VI (12 progenies) showed a moderate mean for ASI, and PH, and low means for the other traits.

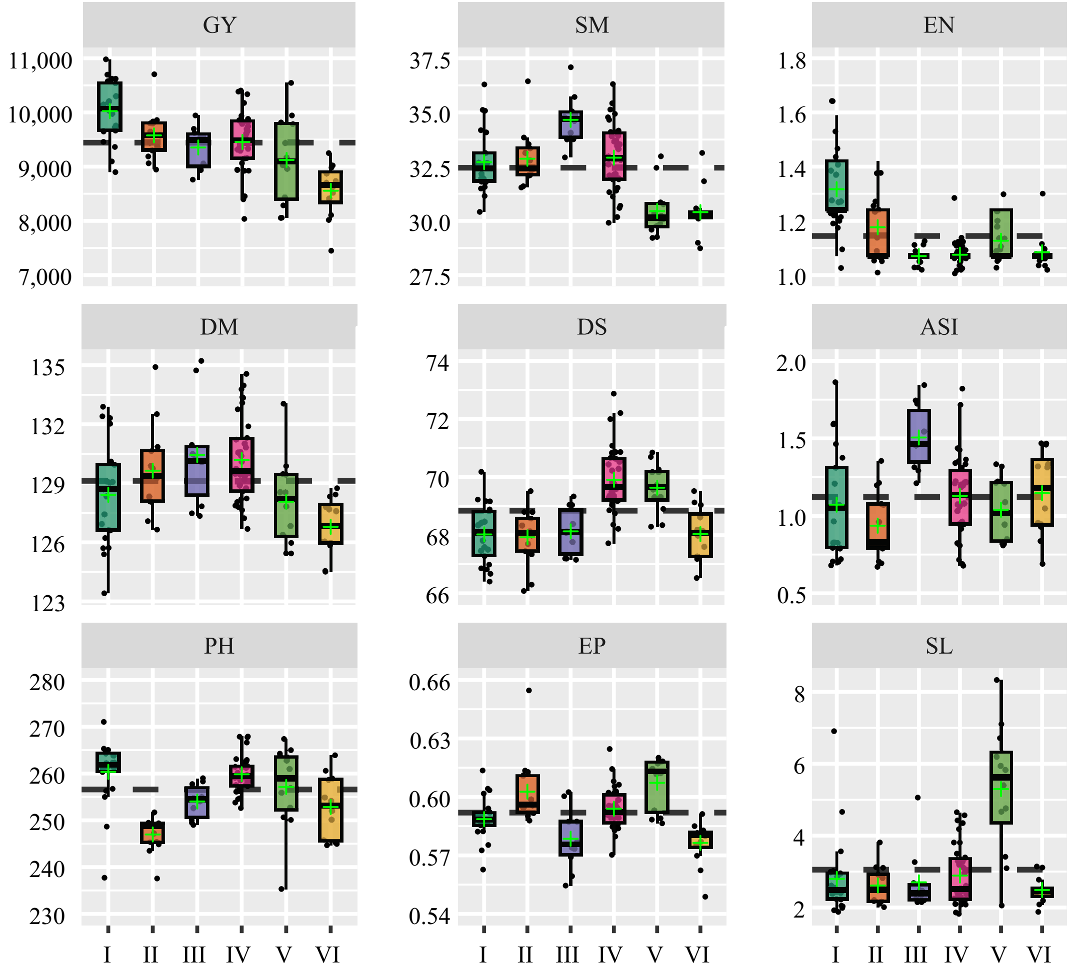

Figure 4. Means and variation of clusters (I to VI). The continuous black line that cuts through the boxplots is the general mean. A, mean of the clusters represented by the green point shape in the middle of the boxplots. Traits: GY, grain yield; SM, seed mass; EN, number of ears per plant; DM, days to maturity; DS, days to silking; ASI, anthesis-silking interval (ASI); PH, plant height; EP, ear position; and SL, stem lodging. The red point shape in the middle of the boxplots.

In general, the most high-yielding progenies were related to the following mean levels: higher EN and PH; moderate to high SM; low to moderate DM and EP; and to low DS, ASI, and SL. These results can allow of the attainment of heterotic clusters of superior progenies, as well as they can guide more efficient selection strategies aiming at desired gains in multitraits.

Thus, 15 progenies from population A x B were selected, with the following progenies: 1, 26, 28, 32, 39, and 50 from cluster I; 10 and 41 from cluster II; and 4, 6, 8, 13, 27, 44, and 53 from cluster IV.

Another 15 progenies, from the B x A population, were the following ones: 60, 66, 67, 83, 88, 90, 94, and 101 from cluster I; 64 from cluster II; 86 and 93, from cluster III; and 63 and 92, from cluster IV.

A more strategic breeding plan is to classify genotypes based on heterotic clusters, since inbred lines are often developed from crosses within heterotic clusters (Laude & Carena, 2015). The less divergent progenies with good performance within each cluster may be crossed in pairs, to produce biparental populations for the development of inbred lines, according to Faria et al. (2022). Conversely, part of interpopulation progenies that belong to the same cluster can result in good hybrids from crosses because it presents higher means associated with moderate divergence in its subclusters. Prasad & Singh (1986) found higher heterosis for maize grain yield that resulted from the crossing of parents with moderate genetic diversity than the heterosis resulting from the crossing of parents with extreme diversity.

For the selection gains of the 15 progenies from each population, desired genetic gains are expected for SM, EN, and GY, associated with high to moderate heritability (Figure 3 B), but in population A x B, gains associated with heritability are expected for SL (highly desired) and ASI (unwanted). In population B x A, gains associated with moderate heritability are expected for SL (unwanted) and ASI (desired). The differences indicate the existence of genetic complementarity between the populations, which is advantageous for the development of high-yielding hybrids with performance in their associated secondary traits. A lower gain close to zero associated with high heritability was observed for PH, EP, DS, and DM.

Contrary results to this study were reported by Kanna et al. (2021), who found low gains in SM and EN; these authors and Magar et al. (2021) also observed high gain for ASI associated with high heritability. The results of this study are consistent with those of Pandey et al. (2017) and Magar et al. (2021), who reported a higher gain for SM associated with high heritability. However, there are discrepancies regarding the results of this study, which showed a higher gain for ASI and GY. According Kanna et al. (2021) the selection progress for traits that show a higher gain associated with high to moderate heritability will be better through the recurrent selection seeking to exploit the overall combining ability. Traits showing a low genetic gain associated with high and moderate heritability are under nonadditive genetic action; therefore, a breeding method that aims to exploit the specific combining ability is recommended.

Conclusions

1. Seed mass, number of ears per plant and anthesis-silking interval are the most contributing traits to the improvement of grain yield and divergence among full-sib maize (*Zea mays*) progenies.
2. There is genetic potential to be exploited through the selection and recombination in the reciprocal recurrent selection targeting high-yielding maize hybrids.

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