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HETEROSIS AND INBREEDING DEPRESSION IN GRAIN SORGHUM HYBRIDS

Abstract – This study aimed to estimate the heterosis, heterobeltiosis, and inbreeding depression in grain sorghum hybrids. Twenty-five hybrids were evaluated in two seasons. The evaluated traits were days to flowering (FL), plant height (PH), grain yield (GY), and thousand grains mass (M1000). The contrast tested were F₁ hybrids vs. check cultivars, F₁ hybrids vs. parental lines, and F₁ hybrids vs. F₂ hybrids. The hybrids 1167048, 1099044, 1170017, and 1169054 had a five-day less flowering time than their parental lines. The hybrid 1170017 had a high grain yield (6.23 t ha⁻¹) with 43.55% of heterobeltiosis. The diversity between lines was narrow. However, hybrids with higher grain yield, heterosis, and heterobeltiosis showed higher genetic distances from their parental lines. The inbreeding depression between F₁ vs. F₂ was 30%, indicating that using F₁ hybrids seeds is worthwhile.

Keywords: *Sorghum bicolor*, single-cross hybrid, heterobeltiosis, sorghum breeding, plant breeding

HETEROSE E DEPRESSÃO ENDOGÂMICA EM HÍBRIDOS DE SORGO GRANÍFERO

Resumo - O objetivo do trabalho foi estimar a heterose, heterobeltiose e depressão endogâmica em híbridos de sorgo granífero. Vinte e cinco híbridos foram avaliados em duas safras. As características mensuradas foram: dias para florescimento (FL), altura de plantas (PH), produtividade de grãos (GY) e massa de mil grãos (M1000). Os contrastes testados foram; híbridos F₁ vs testemunhas, híbridos F₁ vs linhagens parentais e híbridos F₁ vs híbridos F₂. Os híbridos 1167048, 1099044, 1170017 e 1169054, foram em média, 5 dias mais precoces do que suas linhagens parentais. O híbrido 1170017 teve alta produtividade de grãos (6.23 t.ha⁻¹) com 43,55% de heterobeltiose. A diversidade entre linhagens foi baixa. Entretanto, os híbridos com maiores produtividades, valores de heterose e heterobeltiose, mostraram maiores distâncias genéticas em comparação a seus parentais. A depressão endogâmica de F₁ para F₂ foi de 30%, indicando que, compensa utilizar sementes de híbridos F₁.

Palavras-chave: *Sorghum bicolor*, híbridos simples, heterobeltiose, melhoramento de sorgo, melhoramento de plantas.

Sorghum [*Sorghum bicolor* (L.) Moench] is the world's fifth most important cereal crop because of its natural drought tolerance and versatile use as feed, food, and fuel. The sorghum crop is used for food in Africa and Asia and livestock feed in America (Menezes et al., 2021; Hossain et al., 2022).

In Brazil, grain sorghum production achieves 3.04 million tons in the 2021/22 harvest in 950 thousand hectares and yields an average of 3.2 t ha⁻¹ (Conab, 2022). Sorghum has a high yield potential, and its commercial value approaches 85% of the corn, with lower production costs and almost the same nutritional value for proteins and carbs (Menezes et al., 2021).

In grain sorghum breeding programs, parental line selection is one of the main decisions faced by the breeder. Only the parent's performance, called performance *per se*, is not enough to infer their potential to generate superior hybrids (Borém et al., 2014). The F₁ of a crossing may express a higher plant vigor than its parents, an effect named heterosis, a relevant genetic trait used in plant breeding.

Heterosis is the phenotypic and genotypic superiority of the hybrid compared to the mean of its two parental lines. While heterobeltiosis is the superiority of the hybrid compared to their best parental line, considering any trait. Both heterosis and heterobeltiosis are estimated in segregating and divergent populations (Boratar & Ninghot, 2015). The heterosis, combined with low inbreeding depression, indicates additive genetic variance, which can be fixed by segregating generations (Kumar et al., 2016).

Juárez et al. (2017) and Boratar & Ninghot (2015) studied heterosis and heterobeltiosis in grain sorghum hybrids. These researchers identified the negative performance of heterosis for flowering, with plant cycle reduction (-14.29%). For the other

characteristics, heterosis was positive for plant height (49.60%), panicle length (30.01%), and grain yield (72.09%). However, even with the presented studies showing the advantages of F₁ hybrids, the use of open-pollinated varieties is usual in Brazil. The reason is the lower cost of F₂ seeds from F₁ hybrids grown in the last season. Due to this, it is essential to prove that using F₁ hybrids can increase grain yield and expresses hybrid vigor and genetic diversity (Oliveira et al., 2021).

Genetic diversity studies in sorghum lines support breeders in making decisions and choosing lines with better specific combining abilities (Rocha et al., 2018). Genotyping techniques have been adopted through polymorphic molecular markers along the sorghum genome. In addition, some techniques, such as genotype by sequencing (GBS), can also assist the breeder in the genotype's characterization and genetic distance studies (Elshire et al., 2011). Moreover, the phenotype and genotype should be used simultaneously to improve the selection results and predict the line crosses results. It means that the heterosis could be estimated using the combining parameters. For that reason, the genetic distance and diversity among lines are essential tools for breeding plants.

The present study aimed to estimate the heterosis and heterobeltiosis of grain hybrids sorghum in the F₁ generation to determine inbreeding depression in the F₂ population. Moreover, the goal was to study the genetic diversity among parental lines to choose the best hybrids combinations regarding the phenotypic characteristics of the breeding program.

Material and Methods

Experimental design

The trials were carried out in the 2014/15 and 2015/16 seasons in Sete Lagoas, MG, Brazil, latitude 19° 27' 57" S, longitude 44° 14' 49" W, altitude 771 m. The experimental plot consisted of four rows with five m, with 0.5 m between rows, keeping ten plants per meter after thinning, considering the two central rows as the plot area, and three replicates. The interaction effect between years was insignificant; thus, the hybrids' average was made. The experimental design was completely randomized blocks with fixed effects for all variance components.

Seventeen lines were crossed to generate the experimental F_1 hybrids (Table 1). Among these are ten A lines (male sterile) and seven R lines (restorer). Twenty-five hybrids (fifteen from Embrapa Maize and Sorghum and ten from private companies) were evaluated. Those ten hybrids from private companies were used as check cultivars. These hybrids from Embrapa were grown in F_1 cycles, along with their parental lines and their F_2 generations, originated by saved seeds from the year before to study heterosis (H%) and heterobeltiosis (Hb%). All the hybrids were used to estimate inbreeding depression except for 1099044, 1170017, and 1169054, which did not have F_2 generations.

Phenotypic evaluations

The evaluated traits were days to flowering (FL), measured by counting days from sowing to flowering of 50% of the plants (days); plant height (PH) measured from the soil to the apex of the panicle (cm); grain yield (PROD), grain weight of the experimental unit, corrected for 13% of humidity and extrapolated to tons ha^{-1} ; a thousand grains mass

(M1000) weighing of 1000 grains, corrected for 13% humidity.

Genetic-statistical analyzes

Subsequently, degrees of freedom were decomposed for the effects of parentals, hybrid combinations F_1 and F_2 , and checks, in the following contrasts: 1) F_1 hybrids vs. check cultivars; 2) F_1 hybrids vs. parentals; 3) F_1 hybrids vs. F_2 hybrids.

Estimation of heterosis, heterobeltiosis, and inbreeding depression

The following equation (Matzinger et al., 1962) set up the heterosis estimate (H%):

$$H (\%) = \left[\frac{\bar{F}_1 - \bar{P}}{\bar{P}} \right] \times 100$$

In which;

\bar{F}_1 = F_1 generation average

\bar{P} = parental average

To estimate the heterobeltiosis (Hb%) as a percentage, the equation used was (Fonseca & Patterson, 1968):

$$Hb (\%) = \left[\frac{[\bar{F}_1 - \overline{MP}]}{\overline{MP}} \right] \times 100$$

In which;

\overline{MP} = average of the best parental line.

\bar{F}_1 = F_1 generation average

To estimate inbreeding depression (I%) as a percentage, the equation used was (Matzinger et al., 1962):

Table 1. Coding of 25-grain sorghum hybrids and their parental lines, evaluated in Sete Lagoas, MG, Brazil, in the 2014/15 and 2015/2016 seasons.

Crosses	Genetic distance	Hybrids	Companies
L-10 (A) x L-11 (R)	0.4285	1167048	EMBRAPA
L-07 (A) x L-11 (R)	0.1684	1167093	EMBRAPA
L-07 (A) x L-12 (R)	0.2365	1168093	EMBRAPA
L-06 (A) x L-11 (R)	0.4266	1167092	EMBRAPA
L-01 (A) x L-11 (R)	0.2238	1167017	EMBRAPA
L-05 (A) x L-11 (R)	0.4266	1236020	EMBRAPA
L-04 (A) x L-16 (R)	0.2094	1105661	EMBRAPA
L-02 (A) x L-11 (R)	0.3819	1236043	EMBRAPA
L-04 (A) x L-17 (R)	0.3032	BRS 330	EMBRAPA
L-03 (A) x L-17 (R)	0.2691	BRS 332	EMBRAPA
L-04 (A) x L-11 (R)	0.2268	BRS 373	EMBRAPA
L-04 (A) x L-14 (R)	0.2052	BRS 380	EMBRAPA
L-09 (A) x L-11 (R)	0.4248	1099044	EMBRAPA
L-01 (A) x L-15 (R)	0.2033	1170017	EMBRAPA
L-08 (A) x L-13 (R)	0.3751	1169054	EMBRAPA
		1G100	BREVANT
		1G282	BREVANT
		50A50	Pioneer
		AG 1040	ISS
		AS 4625	ISS
		Jade	SEMEALI
		80G80	AGROMEN
		Buster	Nuseeds
		FOX	Nuseeds
		A 9735 R	NIDERA

Table 2. Analysis of variance for days to flowering (FL), in days; plants height (PH), in cm; grain yield (GY), in t ha⁻¹; and thousand-grain mass (M1000), in g, for 25 hybrids of sorghum, in the 2014/2015 and 2015/2016 seasons.

SV	DF	Mean Square			
		FL	PH	GY	M1000
Hybrids (F ₁ 's)	14	37.70**	203.90**	1.98**	16.11*
Checks	9	30.17**	342.26**	3.84**	14.87*
F ₁ 's vs Checks	1	5.78 ^{ns}	1161.62**	2.15 ^{ns}	148.10**
Error	48	2.59	32.11	0.63	6.78
General mean		62.51	116.21	5.40	20.73
h ² (%)		93.15	84.25	68.01	57.88
CV (%)		2.57	4.88	14.75	12.57

SV: Source of Variation. DF: Degree of freedom. CV: Coefficient of variation. h²; heritability. *, **, ns significant to 5%, 1%, and non-significant respectively.

Table 3. Summary of combined analysis of variance for contrast F₁'s versus Parental lines, for days to flowering (FL), in days; plants height (PH), in cm; grains yield (GY), in t ha⁻¹; and thousand-grain mass (M1000), in g, in the 2014/2015 and 2015/2016 seasons.

SV	DF	Mean Square			
		FL	PH	GY	M1000
Hybrids (F ₁ 's)	14	36.45**	733.59**	1.68**	2.65 ^{ns}
Parentals (P)	16	825.97**	842.13**	3.47**	4.32*
F ₁ 's vs P	1	147.16**	829.04**	51.68**	18.13**
Error	62	3.30	55.31	0.48	2.35
General mean		62.77	123.09	4.51	23.97
h ² (%)		90.95	92.46	71.38	11.18
CV (%)		2.89	6.04	15.38	6.40

SV: Source of Variation. DF: Degree of freedom. CV: Coefficient of variation. h²; heritability. *, **, ns significant to 5%, 1%, and non-significant respectively.

Table 4. Summary of combined analysis of variance for contrast F_1 's versus F_2 's, for flowering (FL), in days; plants height (PH), in cm; grains yield (GY), in t ha⁻¹; and thousand-grain mass (M1000), in g, in the 2014/2015 and 2015/2016 seasons.

SV	DF	FL	PH	GY	M1000
Mean Square					
Hybrids (F_1 's)	21	39.40**	554.01**	2.29**	12.93*
Hybrids (F_2 's)	21	45.27**	368.00**	1.44**	6.90 ^{ns}
F_1 's vs. F_2 's	1	34.18**	143.20 ^{ns}	104.20**	0.47 ^{ns}
Error	92	4.57	61.97	0.38	7.28
General mean		63.81	127.85	4.60	23.88
h ² (%)		88.39	88.81	83.24	43.66
CV (%)		3.35	6.16	13.47	11.30
ID (%)		0.56	-0.98	-30.33	5.41

SV: Source of Variation. DF: Degree of freedom. CV: Coefficient of variation. h²; heritability. ID: Inbreeding depression. *, **, ns significant to 5%, 1%, and non-significant respectively.

$$I (\%) = \left[\frac{[\bar{F}_1 - \bar{F}_2]}{\bar{F}_1} \right] \times 100$$

In which:

\bar{F}_1 = mean of the hybrids;

\bar{F}_2 = F_2 population average after self-pollination of the F_1 hybrid.

Estimation of genetic distance

The genetic distance between 17 parental lines was estimated based on the data of 148,395 SNPs markers using the state identification coefficient (IBS) (Powell et al., 2010). Samples of young leaves were collected from each line to extract the genomic DNA. After that, the leaves were lyophilized, and the DNA extraction procedure was performed. Genomic DNA was extracted by the CTAB (Cetyl Trimethylammonium Bromide) method (Porebski et

al., 1997). DNA quantification and qualification were performed on a triacetate gel. The sequencing method used was GBS (Genotyping by Sequencing), with restriction enzyme ApeKIe. The SNPs were called using the GBS pipeline, available in the TASSEL 5.0 software. Finally, the markers were filtered by the minor allele frequency (MAF > 5%) and missing data < 20%. The statistical program was TASSEL 5.0. Neighbor-Joining (Saitou & Nei, 1987) was the grouping method, plus the ape package and version R 3.2.5 (R Core Team, 2016).

Results and discussion

The effects of hybrids (F_1 's) and check cultivars were significant for all characteristics, meaning variability among the genotypes. On the other hand, the effect of the contrast F_1 's vs. check cultivars was significant for PH and M1000 ($p < 0.01$) and not significant for the other characteristics, showing a statistical difference between the average of the experimental F_1 's hybrids and the commercial

hybrids (check cultivars) for PH and M1000 (Table 2). In both traits, PH and M1000, the average for the check cultivars was higher than F_1 's average.

The effect of hybrids (F_1 's) was significant for FL, PH, and GY and not significant for M1000 ($p < 0.01$) (Table 3). In addition, the source of parental variation and the contrast between F_1 's vs. Parentals were significant for all characteristics.

Considering 22 hybrids, F_1 's and F_2 's effects were significant for all traits except for M1000 of the F_2 's hybrids (Table 4). The contrast F_1 's vs. F_2 's effect was significant for FL and GY ($p < 0.01$) and not significant for PH and M1000. These results mean differences between F_1 's and F_2 's responses, considering FL and PROD. The F_1 's hybrids averages for GY were higher than F_2 's, showing that it is more advantageous to use F_1 's hybrids in commercial crops than F_2 's. Even with the lowest investment in F_2 seeds

use, it is essential to study the cost of production to confirm the advantage.

The coefficients of variation of the traits were within the acceptable limits for sorghum field tests (Menezes et al., 2017). Heritability (h^2) was above 68% for FL, PH, and GY, proving a high contribution of genotypic variance and low environmental variance in the expression of the traits. Only for M1000, the h^2 was lower, varying from 11.18% to 57.88% between the effects showing low variability for this characteristic. Heritability is one of the most critical parameters for expressing the hybrid genetic potential. High h^2 expresses the low phenotypic variance, and it is the same to consider a short environmental effect. The genetic variance has a higher value on the h^2 equation, and genetic inheritance is the central part of the hybrid variation.

Inbreeding depression (Table 4) was

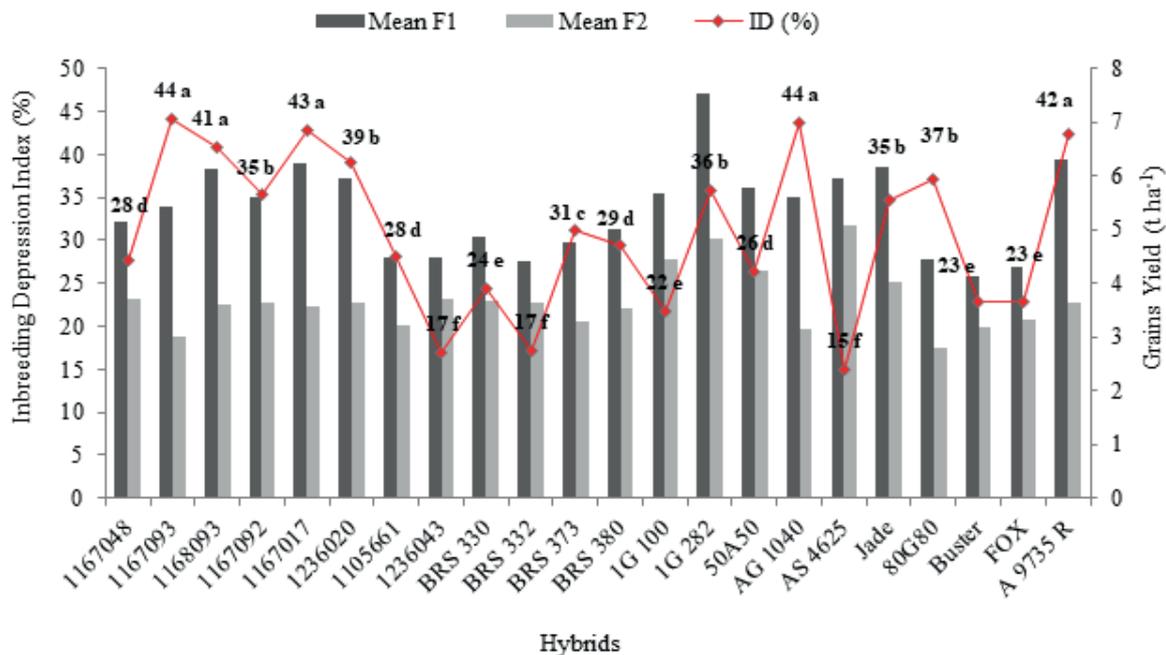


Figure 1. Inbreeding depression index (ID%) of experimental and commercial hybrids for grain yield (GY). Legend: The same letter means that the hybrids do not have statistical differences, according to the Scott Knott test, in 5% of significance.

estimated for the generation of F_2 hybrids from the self-pollination of F_1 hybrids (Figure 1). For FL, PH, and M1000, there was low inbreeding depression. However, the GY showed a high inbreeding depression (30.3%). The reduction in GY using F_2 seeds was first reported in the works of Quinby (1974), although with less than 10% of inbreeding depression. Other studies showed that 42% of grain yield decreased when using F_2 seeds (Geeta & Rana, 1987).

Production costs for grain sorghum grown in the second season, based on data from the Instituto de Fortalecimento da Agropecuária de Goiás (IFAG), showed that seeds represented 7.17% of costs, pre-planting herbicide 2.88%, other herbicides, insecticides and fungicides with 1.89%, 2.67%, and 1.54%, respectively. According to IFAG (2021), with an expectation of 3.6 ton ha^{-1} and an average price of \$ 5.84 sc, the expected gross revenue would be \$ 350.33 per hectare.

The advantage of using F_1 seeds is apparent when comparing income versus inputs. For example, using F_1 seeds, the hybrid AG1040 produced 5.6 t ha^{-1} (Figure 1), with gross profitability of \$543.96 ha. When F_2 seeds were used, the productivity reached 3.2 t ha^{-1} (Figure 1) and profitability of \$ 306.74 ha^{-1} , with a reduction of 43.6 % in gross crop revenue. This hybrid showed the most significant inbreeding depression among all the commercial hybrids evaluated in the present work, and maybe the F_1 seed's acquisition costs are worth it. Kumar et al. (2016) worked with forage sorghum and obtained similar results for inbreeding depression. In that case, all traits, such as plant weight and brix sucrose, presented significant inbred depression.

Figure 1 shows the yield of the F_1 and F_2 hybrids and the inbreeding depression (ID%). The hybrids with the lowest ID% were 1236043, BRS330, BRS332, 1G100, AS 4625, Buster, and Fox, with an

index below 25%. The hybrid AS 4625 had the lowest ID% among all the evaluated hybrids, with 14.8% of inbreeding depression, and it was classified in the group with the highest grain yield (5.9 t ha^{-1}).

Among the commercial hybrids of Embrapa Maize and Sorghum, BRS332 had the lowest ID%, with 17.2%, while BRS330, BRS373, and BRS380 had 24.4%, 31.1%, 29.4%, respectively. Considering the experimental hybrids, 1236043 stood out, which presented 16.9% of inbreeding depression, and it was the second with the lowest ID%. On average, Embrapa's commercial hybrids presented a lower ID% (25.5%) than the experimental hybrids (34.3%).

The hybrids 1168093, 1167017, 1236020, 1G282, JADE, and A9735 R presented the highest grain yields, above 6.0 t ha^{-1} , and the highest ID%. The 1G282 hybrid had the highest grain yield (7.52 t ha^{-1}), and a 35.8% depression rate, expressing the disadvantages of using seeds in F_2 generation. This case was repeated with the hybrids A 9735 R (6.3 t ha^{-1}) and 1167017 (6.2 t ha^{-1}), which presented the second and third highest yields, and ID% of 42.4% and 42.8%, respectively.

Meena et al. (2017), working with sorghum, used ten lines, three testers, 30 commercial hybrids, and three experimental hybrids and presented convergent results to them found in this work. For these authors, heterosis had a lower limit of -26.71% and an upper limit of 16.06% in flowering. The results show the possibility of selecting hybrids earlier than their parentals, which is especially important for sorghum planted in the late second season.

The plant height showed high values of heterobeltiosis. However, the purpose is to reduce the height of the plants to the standard of approximately 1.50 m. The average heterobeltiosis for this trait was 24%. However, the hybrids with the highest Hb% were 1168048 (34.7%) and 1099044 (38.8%), with

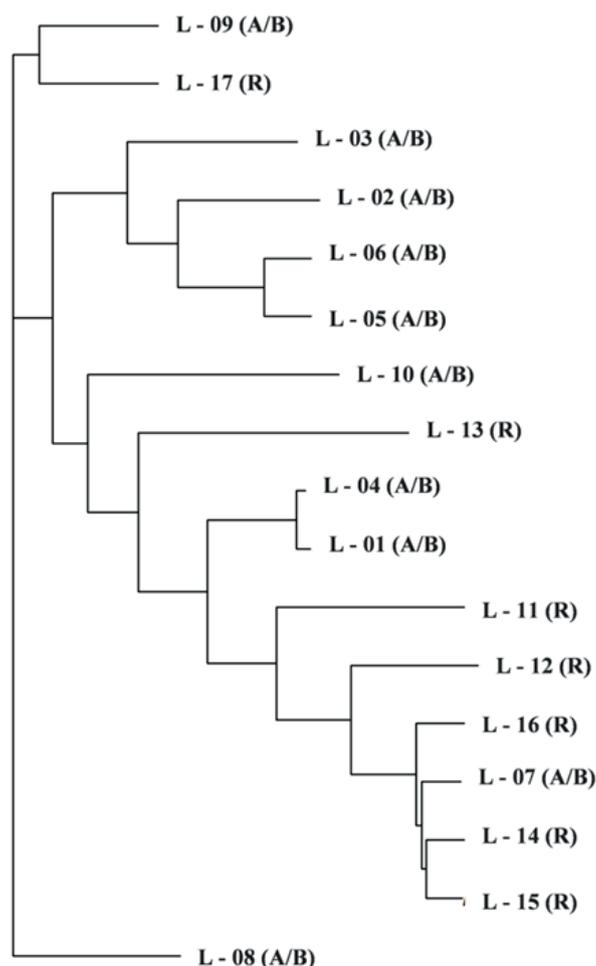


Figure 2. Dendrogram of 17 lines according to *Neighbor-Joining* method, considering dates of 148.395 *SNPs* markers. The genetic distances among sorghum lines were calculated using the state identification coefficient (IBS).

an average height of 123 cm and 127 cm, respectively. That is, the height of these hybrids is consistent with the selection standards for grain sorghum genotypes. In addition, it indicates that the average of the parentals for plant height is low and that the best of the parentals also has a small height. Lombardi et al. (2018) and Singh & Shrotria (2008) reported heterosis and heterobeltiosis positive for plant height, with results of 3% to 52% heterosis for hybrids. The behavior of H% and Hb% of hybrids for plant height converge between works,

indicating that, even in selecting shorter parentals, the heterotic gains must be considered to predict an increase in hybrids' height.

For GY, the individual results determine hybrids with high potentials, such as BRS330, which presented Hb of 55.3%, with a productivity of 4.8 t ha⁻¹. The hybrids with the second highest Hb value (53.5%) were 1236020 (6.1 t ha⁻¹) and 1099044 (5.5 t ha⁻¹), with higher grain yields. L-11 was their best reciprocal parent (Table 1). The

hybrid 1167017 is derived from L-11 and presented the second highest productivity (6.2 t ha⁻¹) among the hybrids of Embrapa.

Thousand-grain mass is an essential trait and a significant component of grain productivity. However, in this experiment, heterosis and heterobeltiosis for these traits were not representative, even with negative values. In Wagaw & Tadesse (2020), the thousand-grain mass does not have significant heterosis, indicating the ability of the crosses to produce hybrids having increased performance of these traits failed, or the variability for genotypes was narrow.

A dendrogram was performed using the Neighbor-Jointed method to understand the relationship among Embrapa's lines (Figure 2). Most of the lines are derived from mixing between races. Only lines L-12 and L-17 are pure lines originating from *Caudatum*. These lines were improved in Brazil and originated from Africa or the United States of America.

In the dendrogram (Figure 2), the first group formed is lines L-09 and L-17. After that, the other lines fell into group 2, and the L-08 line was separated from the others in group 3. The R (restorer) lines generally are in different groups, presenting greater genetic distance. On the other hand, line A was closer, showing low variability, explained by the reduced number of existing male-sterility lines. These results corroborate those found by Jaikishan et al. (2018), Silva et al. (2021), and Menezes et al. (2017).

Silva et al. (2021), studying the genetic distance between parental lines of Embrapa's grain sorghum hybrids, showed correlations between genetic distance and heterosis. However, the works converge in that the most productive hybrids also had the most significant genetic distance between parentals. In both studies, it is possible to notice that there is low genetic diversity between hybrids

and between lines and that increasing this genetic variability would be an alternative to generating hybrids with higher grain yields.

The hybrid F₁ 1236020 (GY= 5.95 t ha⁻¹; d = 0.4303) presented superior performance and the most significant genetic distance between parent lines observed in this work. Hybrids 1167048 (H% = 78.06; d = 0.4285) and 1099044 (H% = 61.48; d = 0.4248) showed the highest heterosis results and the most extended distances between parental lines. An important fact to explain these results is that hybrids with higher productivity and higher heterosis values have one of the reciprocal parentals (L-11).

L-11 was used as a male parent of 11 hybrids. Among these hybrids, seven were classified as those with higher grain yields or higher values of heterosis and heterobeltiosis. They are 1167048, 1167093, 1167092, 1167017, 1236020, BRS 373, and 1099044. The hybrid 1167017 (GY= 6.23 t ha⁻¹, H% = 56.19), which was the second most productive one, 1236020 (GY=5.95 t ha⁻¹, H%=59.54), and 1099044 (GY=5.50 t ha⁻¹, H% = 61.48), from crosses with L-11, presented higher GY averages and the highest H% values. In addition, the hybrids 1236020 and 1099044 had the highest values for Hb%, both with 53.5%, surpassing their best father, L-11. In Wagaw & Tadesse (2020), the highest heterosis obtained was 162%, an average of 52.4. That information shows that simple sorghum hybrids have a high potential to increase yield grains.

The female line L-01 was the parent of hybrids with higher grain yields (1170017 and 1167017). This line presented a high performance per se (4.39 t ha⁻¹). Therefore, it is essential that the starting point for choosing parentals is to consider the performance per se of the line. Furthermore, these lines must have good combining ability, resulting in promising hybrids with a high specific ability to express heterobeltiosis. The female lines L-01 (4.39 t

ha⁻¹), L-06 (4.61 t ha⁻¹), and L-07 (4.20 t ha⁻¹) obtained the best performance *per se* and originated superior hybrids. Consequently, they culminated in heterosis and were the most productive in this study. A similar result was observed by Wagaw & Tadesse (2020) and Kumar et al., 2016, when the best female line was the same more contributed to producing the hybrids with the best yield grain.

Conclusions

The loss of F₂ grain yield is higher than the cost of the F₁ seeds. Therefore, it is advantageous for the farmer to use F₁ seeds every season to guarantee higher grain yields.

The lines group showed low genetic diversity, mainly between A/B lines, justified by the short number of lines and the long process to obtain these lines. Therefore, extending the diversity of parental lines is crucial to obtain significant genetic gains in F₁ hybrids.

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