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Assessing the combining ability of grain sorghum hybrids using mixed models

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Abstract: The main objective of breeding programs for grain sorghum is to increase yield while simultaneously reducing the growth cycle length and plant height. In this study, we sought to identify promising lines of grain sorghum with these traits. The experiment was carried out in 2012 in the experimental area of Embrapa Agrossilvopastoril, in Sinop, Mato Grosso, Brazil. Using a partial diallel scheme, controlled crosses were performed between two groups of grain sorghum lines and we evaluated the following vegetative and productive traits: days to flowering (FL), plant height (PH), and grain yield (GY). Restricted maximum likelihood and best linear unbiased prediction analyses were performed to estimate variance components and predict genetic values, respectively. The general combining ability (GCA) and specific combining ability (SCA) of combination were estimated, with likelihood ratio test values revealing significant effects of the GCA of both parents for the traits FL, PH and GY, and, the predictive accuracy was greater than 0.90. The analyses have demonstrated that the hybrids H11, H22, H31, H32, H36, H51, H55, H56 and H71 have good combining capacity estimates. Their average flowering periods ranged from 57.06 to 60.44 days, with plant heights varying between 1.56 and 1.61 meters. The average grain yield ranged from 2419.08 to 3105.44 kg ha^{-1}. These traits hold significant importance within the context of sorghum breeding.

Keywords: Diallel, combining ability, REML/BLUP, selective accuracy, *Sorghum bicolor*.

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] is a cereal of African origin within the grass family Poaceae. Among the uses of this crop are the production of flour and biofuel, with the grains also being used for forage or soil coverage (Liu et al., 2020; Hao et al., 2021).

Breeding programs for sorghum hybrids exploit the phenomenon of genetic cytoplasmic male sterility and require three groups of lines, denominated A, B, and R (Klein et al., 2005; Praveen et al., 2015; Madugula et al., 2018). Lines A and B are isogenic, that is, they have the same alleles for nuclear genes and differ only with respect to cytoplasmic type. All A lines are characterized by cytoplasmic male sterility and are used as the female progenitor in hybrid seed production. Line B, isogenic to A, has normal cytoplasm (maintainer) and is used as a male progenitor in crossbreeding with line A genotypes to produce seeds of line A that will be sterile, as they contain recessive cytoplasmic genes (Parrella et al., 2011). The R line, characterized by dominant fertility restoring genes, is used in crosses with a male-sterile A line to produce fertile single-cross hybrids. Therefore, for the production of hybrid sorghum seeds, two generations are required, one for separate multiplication of the seeds of lines A and R, and the other to produce the hybrid seeds from the cross between A and R (Klein et al., 2005; Parrella et al., 2011; Praveen et al., 2015; Madugula et al., 2018).

Although for most crops, the main objective of breeding programs is to increase grain yield, other traits are also of importance and should be taken into account in the selection process, thereby ensuring the production of gains that are adequate with respect to all desirable traits (Ferreira et al., 2005). In the case of sorghum, the time taken to flower and even plant height are as important as grain yield, given that these traits directly influence the time that a plant will persist without rain and the type of mechanized harvest process, respectively (Tardin et al., 2013; Menezes et al., 2015; Olatoye et al., 2018; Faye et al., 2019).

The use of diallel crosses for the development of elite lines, as well as for examining their general combining ability (GCA) and specific combining ability (SCA), increases the probability of success in sorghum breeding programs (Oliveira et al., 2019; Gami et al., 2023; Talaviya et al., 2023) and others crop breeding such as sweet corn (Nadeem et al., 2023), cotton (Salem et al., 2020), and barley (Tokhetova et al., 2022). The GCA serves as the selection criterion for single parent and is associated with additive effects, whereas SCA functions as a selection index of parental cross combination and is relative with dominant effects (Baroni et al., 2020). In this regard, diallel crosses facilitate the selection of promising genitors based on estimates of combining ability, thereby enabling the production of segregating populations with selection potential for new improved elite lines. This type of analysis is accordingly considered fundamental for decision making, and can also be used to gain an understanding of the genetic effects associated with the evaluated traits (Cruz and Vencovsky, 1989; Islam et al., 2022), thereby representing an important tool in breeding programs (Cruz et al., 2012; Oliveira et al., 2019; Salem et al., 2020; Tokhetova et al., 2022; Gami et al., 2023; Nadeem et al., 2023; Talaviya et al., 2023;). Thus, the aim of the present study was to recommend promising lines that produce hybrids with ideal height for use in sorghum breeding programs, and to identify the best hybrids based on the performance and combining ability of the traits assessed.

Material and Methods

Experimental design

Controlled crosses were performed between two groups of grain sorghum lines using a partial diallel scheme. The R line group consisted of seven male plants, whereas the A lines consisted of six female plants, the crosses among which gave rise to 42 hybrids (Table 1). In 2012, growth trials of these hybrids were conducted in the experimental area of Embrapa Agrossilvipastoril, in Sinop municipality, Mato Grosso state (latitude 11°51′43″ and longitude 55°36′45″), which has an average altitude of 370 m. The 42 hybrids were evaluated under dryland conditions with sowing on March 10th, 2012 and the thinning of plants 15 days after emergence, leaving a population of 180.000 plants per hectare.

The experimental design adopted was a randomized complete block design with two repetitions. Each plot comprised two 5-m-long rows with a spacing of 0.50 m between rows. For the purposes of hybrid assessment, we evaluated the following three traits associated with the vegetative and productive components of sorghum: days to flowering (FL), which is the number of days elapsed from planting until 50% of plants in a plot are flowering; plant height (PH), which is the average height of two plants (m) within the useful area of the plot, measured from the soil surface to the apex of the panicle at harvest; and grain yield (GY), which is the weight of grain per plot extrapolated to kilograms per hectare (kg ha^{-1}), with subsequent measure of moisture content for correction to 13% moisture.

Table 1. Identification of the 42 sorghum hybrids and the 13 sorghum lines, assessed at Sinop municipality, Mato Grosso State.

Source	Identification				Source	Identification			
	Hybrid	Code	R line	A line		Hybrid	Code	R line	A line
1173-133	1	H_{11}	1	1	1173-1129	22	H_{44}	4	4
1173-127	2	H_{12}	1	2	1173-1131	23	H_{45}	4	5
1173-131	3	H_{13}	1	3	1173-1193	24	H_{46}	4	6
1173-169	4	H_{14}	1	4	1173-853	25	H_{51}	5	1
1173-171	5	H_{15}	1	5	1173-847	26	H_{52}	5	2
1173-229	6	H_{16}	1	6	1173-851	27	H_{53}	5	3
1173-253	7	H_{21}	2	1	1173-889	28	H_{54}	5	4
1173-247	8	H_{22}	2	2	1173-891	29	H_{55}	5	5
1173-251	9	H_{23}	2	3	1173-949	30	H_{56}	5	6
1173-289	10	H_{24}	2	4	1173-973	31	H_{61}	6	1
1173-291	11	H_{25}	2	5	1173-967	32	H_{62}	6	2
1173-353	12	H_{26}	2	6	1173-971	33	H_{63}	6	3
1173-373	13	H_{31}	3	1	1173-1009	34	H_{64}	6	4
1173-367	14	H_{32}	3	2	1173-1011	35	H_{65}	6	5
1173-371	15	H_{33}	3	3	1173-1075	36	H_{66}	6	6
1173-409	16	H_{34}	3	4	1173-613	37	H_{71}	7	1
1173-411	17	H_{35}	3	5	1173-607	38	H_{72}	7	2
1173-469	18	H_{36}	3	6	1173-611	39	H_{73}	7	3
1173-1093	19	H_{41}	4	1	1173-649	40	H_{74}	7	4
1173-1087	20	H_{42}	4	2	1173-651	41	H_{75}	7	5
1173-1091	21	H_{43}	4	3	1173-713	42	H_{76}	7	6

The experimental design adopted was a randomized complete block design with two repetitions. Each plot comprised two 5-m-long rows with a spacing of 0.50 m between rows. For the purposes of hybrid assessment, we evaluated the following three traits associated with the vegetative and productive components of sorghum: days to flowering (FL), which is the number of days elapsed from planting until 50% of plants in a plot are flowering; plant height (PH), which is the average height of two plants (m) within the useful area of the plot, measured from the soil surface to the apex of the panicle at harvest; and grain yield (GY), which is the weight of grain per plot extrapolated to kilograms per hectare (kg ha^{-1}), with subsequent measure of moisture content for correction to 13% moisture.

Statistical analyses

To estimate variance components and predict genotypic values, we used restricted maximum likelihood/best linear unbiased prediction (REML/BLUP) procedures respectively, according to Patterson and Thompson (1971) and Henderson (1975). The statistical model was determined based on the following equation:

$$y = Xr + Zm + Wf + Tc + e$$

where y is the vector of the data; r is the vector of the replication effects (assumed as fixed) added to the overall mean; m is the vector of the effects of genitors of line R (male) assumed as random $(m \sim N(0, \hat{\sigma}_m^2)$, where $\hat{\sigma}_m^2$ is the genotypic variance of the genitors of line R; f is the vector of the genitors effects of line A (female) assumed as random ($f \sim N(0, \hat{\sigma}_f^2)$, where $\hat{\sigma}_f^2$ is the genotypic variance of the genitors of line A; *c* is the vector of the specific combining ability (SCA) effects of the R lines with the A lines ($c \sim N(0, \hat{\sigma}_c^2)$, where $\hat{\sigma}_c^2$ is the genotypic variance of the hybrids resulting from the combination of the genitors of line R with line A; and *e* is the vector of errors or (random) residues ($e \sim N(0, \hat{\sigma}_{res}^2)$, where $\hat{\sigma}_{res}^2$ is the residual variance. The capital letters X, Z, W, and T represent the incidence matrices for the referred effects.

The phenotypic variance $\left(\hat{\sigma}_{phen}^2\right)$, total heritability of the genotypic effects (h_x^2), individual additive genetic coefficient of variation (CV_x), and mean selective accuracy of the additive values ($r_{\hat{g}g}$) were obtained using the following respective equations (Resende and Alves, 2020):

$$\hat{\sigma}_{phen}^2 = \hat{\sigma}_m^2 + \hat{\sigma}_f^2 + \hat{\sigma}_c^2 + \hat{\sigma}_{res}^2$$

$$h_x^2 = \frac{\hat{\sigma}_x^2}{\hat{\sigma}_{fen}^2},$$

$$CV_x = 100\sqrt{\frac{\hat{\sigma}_x^2}{\mu}}, \text{ and}$$

$$r_{\hat{g}g} = \sqrt{1 - \frac{PEV}{\hat{\sigma}_x^2}}$$

where $\hat{\sigma}_x^2$ represents the genotypic variance of line R, genotypic variance of line A, or genotypic variance of the combination of the genitors of line R and line A; μ is the overall mean of the genotypes of each treatment; and PEV is the predicted error variance.

The significance of the random effects of the model were assessed using the likelihood ratio test (LRT) (Rao, 1973) determined using the following equation:

$$LRT = -2(LogL_F - LogL_R),$$

where $LogL_F$ is the logarithm of the maximum likelihood function of the full model, and $LogL_R$ is the logarithm of the maximum likelihood function of the reduced model at the 5% probability level determined by the Chi-square test, considering one degree of freedom.

Analyses were performed using RBio (Bhering, 2017), Genes Portal (Cruz, 2013) and Selegen REML/BLUP (Resende, 2016) software.

Results and discussion

The likelihood ratio test (LRT) values revealed significant effects of the GCA of both parents with respect to the traits FL, PH, and GY (Table 2). These significant effects of GCA indicate the presence of favorable alleles and that the inheritance of these alleles is additive in nature. Moreover, these findings reveal that at least one of the parents of the line groups shows significant effects for the characteristics of interest, thereby ensuring the inheritance of these traits (Baroni et al., 2020; Cruz et al., 2012).

Table 2. Likelihood ratio test (LRT) for the general combining ability (GCA) and specific capacity ability (SCA) for the 42 sorghum hybrids from Sinop municipality, Mato Grosso State. FL = days to flowering, PH = plant height, and GY = grain yield.

Effects	FL	PH	GY
GCA I (R)	7.53*	7.12*	25.75*
GCA II (A)	13.64*	20.76*	12.85*
SCA	10.48*	9.04*	1.3
Mean	59.83	1.58	2722.86
Accuracy	0.93	0.93	0.90
	5.66	13.22	39.80

* significant at 5% of probability and 1 degree of freedom, by the LRT.

For most of the assessed traits, the GCA effects of the line groups were higher than those of SCA indicating the considerable importance of additive effects in controlling these traits. With respect to SCA effects, significant estimates were obtained only for the characteristics FL and PH.

Regarding GY trait, the non-significance of SCA effects, based LRT analysis, indicates that this trait did not differ significant from that expected based on the GCA of the genitors. This is consistent with the findings of Menezes et al. (2014), who evaluated lines of grain sorghum tolerant to aluminum. The predominance of additive gene action in the evaluated characteristics is conducive to genetic improvement through selection, given that an individual or group of superior individuals when selected will produce offspring that are also superior, whereas conversely, dominance interactions hinder the selection of superior individuals (Chudasama et al., 2022; Patel et al., 2022). Nevertheless, non-additive effects can also be exploited to obtain promising hybrid combinations, as dominance interactions favor the production of superior hybrids, particularly those derived from genitors with favorable GCA effects. Moreover, the presence of non-additive effects is important in that it enables the examination of hybrids (Soares et al., 2015; Chudasama et al., 2022; Patel et al., 2022; Talaviya et al., 2023).

Table 3 presents estimates of the GCA effects of the genitors of each line group, that is, how much each genitor contributes to the evaluated trait. In the case of R group lines. genitors 4, 5, and 3 were found to make the greatest contribution to the observed reduction in FL trait, whereas for the height-related trait PH, only genitor 6 in this group of lines showed true genotypic values (u + g) that are lower than those recommended, although genitors 1 and 7 showed notably small deviations from the maximum ideotype of 1.5 m. Notably, genitor 3 was also found to make the highest contribution to an increase yield, which was well above that of the second largest contributor, genitor 2, the genetic values of which are close to those of genitors 5 and 7.

With respect to the genitors of group A lines, those identified as contributing favorable alleles to their offspring to maintain a height within the range of the desired ideotype are the females 4 and 5, whereas the other genitors were found to contribute strongly to an increase in plant height. The contribution of A lines to GY, genitors 1 and 6 were identified as those contributing most to an increase in this trait, whereas except for genitors 4 and 5, the others were found contribute favorable alleles for a reduction in FL.

Table 3 – Estimates of the general combining ability (GCA) for the 42 sorghum hybrids, assessed in 2012 at Sinop municipality, Mato Grosso State. FL = days to flowering, PH = plant height, and GY = grain yield.

Genitors	R Lines		
	FL	PH	GY
1	61.6488	1.5184	2516.716
2	61.0004	1.7492	3090.345
3	59.3795	1.6274	4330.033
4	57.175	1.5889	1561.667
5	58.3421	1.5504	2878.373
6	60.4817	1.4991	1941.926
7	60.8059	1.5248	2740.989
	A Lines		
1	58.0455	1.6573	3217.461
2	59.4176	1.7163	2726.428
3	58.7315	1.7228	2028.713
4	63.3466	1.3821	2200.574
5	61.6627	1.3756	2690.208
6	57.796	1.6245	3473.801

The SCA effects can be characterized as deviations in the performance of a hybrid relative to that which is expected based on the GCA of its genitors. In this regard, it is of interest to note that, depending on the trait, at least one of the genitors of hybrids showing favorable SCA have either high or low overall combining ability, thereby showing promise for the transmission and control of traits (Chudasama et al., 2022; Talaviya et al., 2023). Several of the hybrids assessed in the present study were found to show desirable SCA estimates for some traits (Table 4), i.e., low values for flowering, close to zero for plant height, and high values for grain yield, the latter of which was shown to be non-significant based on LRT analysis (Table 2). Contrastingly, FL and PH were found to be significant with respect to both parental GCA and SCA. Accordingly, we thus identified H55, H51, H32, H23, H56, H33, H46, H41, H36, H71, H76, and H22 as those hybrids with genitors having a favorable GCA and that show SCA effects contributing to a reduction in the number of days to flowering. It is also worth noting that hybrids H21 and H31, the two genitors of which have favorable GCA estimates for FL, also have a SCA contributing to an increase of this characteristic, albeit of low magnitude. In addition to these hybrids, we identified hybrid H11 as the most productive, although the effect was not significant, and is characterized by an early growth cycle. Furthermore, with respect to PH, among those early hybrids identified as showing SCA values close to zero, that is, those with alleles that contribute to neither excessive increase or reductions in height, were H51, H36, H32, H16, H55, H11, H25, H26, H22, H31, H54, H71, H24, H56, and H34.

Table 4 – Estimates of the specific combing ability (SCA) for the 42 sorghum hybrids, assessed in 2012 at Sinop municipality, Mato Grosso State. FL = days to flowering, PH = plant height, and GY = grain yield.

Code	FL	PH	GY	Code	FL	PH	GY	Code	FL	PH	GY
H_{11}	60.26	1.58	3105.44	H_{33}	58.32	1.63	2536.42	H_{55}	57.06	1.58	2801.69
H_{12}	61.01	1.64	2948.96	H_{34}	61.90	1.62	2854.50	H_{56}	58.30	1.61	2861.71
H_{13}	59.14	1.73	2654.75	H_{35}	60.69	1.53	2578.41	H_{61}	61.04	1.63	2861.85
H_{14}	60.72	1.41	2549.89	H_{36}	59.27	1.57	2985.37	H_{62}	57.79	1.62	2679.21
H_{15}	59.52	1.48	2369.57	H_{41}	58.58	1.44	2527.79	H_{63}	59.25	1.55	2844.31
H_{16}	60.42	1.57	2678.39	H_{42}	58.66	1.63	2734.86	H_{64}	60.17	1.58	2556.36
H_{21}	60.36	1.66	2734.31	H_{43}	59.12	1.56	2605.81	H_{65}	61.29	1.46	2593.18
H_{22}	59.78	1.59	2746.83	H_{44}	59.04	1.49	2687.62	H_{66}	60.20	1.55	2687.90
H_{23}	57.90	1.65	2624.14	H_{45}	62.16	1.81	3013.53	H_{71}	59.49	1.61	2697.18
H_{24}	61.16	1.61	2491.06	H_{46}	58.41	1.56	2597.51	H_{72}	60.91	1.51	2439.69
H_{25}	59.95	1.58	2878.39	H_{51}	57.47	1.56	2419.08	H_{73}	62.36	1.47	2739.26
H_{26}	61.19	1.58	2916.28	H_{52}	62.55	1.56	2778.94	H_{74}	58.29	1.66	3057.68
H_{31}	60.44	1.61	2885.08	H_{53}	62.00	1.52	2815.83	H_{75}	59.41	1.53	2814.01
H_{32}	57.86	1.57	2732.79	H_{54}	59.93	1.61	2682.70	H_{76}	59.65	1.63	2592.03

H = Hybrids; ID = Identification;

In terms of the coefficient of genetic variation (CVg), we obtained a value of less than 10% for days to flowering (FL) and close to 10% for PH (Table 2), whereas CVg values close to 30% were obtained for the trait GY. The CVg values obtained for the traits FL and PH in the present study were also found to similar or lower than those reported in other studies on sorghum crops (Menezes et al., 2015, 2014; Tardin et al., 2013). The high CVg value obtained for GY is, however, in line with expectations, given that this trait is influenced to a considerable extent by environmental factors and values of similar large magnitude have been reported in the literature (Menezes et al., 2014; Tardin et al., 2013).

For all evaluated traits, we obtained a selective accuracy ($r_{\hat{g}g}$) value greater than 0.90 (Table 2). According to Resende and Alves (2020), experimental coefficient of variation values provide little indication as to the selective accuracy of an evaluation and, consequently, do not take into consideration the level of genotypic variation or the number of repetitions. In this respect, the use of the F statistic is an alternative approach that simultaneously takes into consideration all these aspects in experimental evaluations. Thus, even if high CVg values are obtained, this would not be indicative of poor conducted experiment, but rather an intrinsic value for a given characteristic, as, according to Resende and Alves (2020) a selective accuracy higher than 0.90 (as obtained found in the present study) indicates very high experimental accuracy.

The average grain yield estimated for the assessed hybrids was 2772.86 kg.ha^{-1}, which is below the average Brazilian national production of 3376 kg.ha^{-1} obtained in the 2022/2023 harvest, according to data from Conab (2023). However, among the population under study, it is notable that several hybrids produced extrapolated yields exceeding 4000 kg.ha^{-1}, and even 5000 kg.ha^{-1}, which surpasses the grain yield values reported in other studies (Mota et al., 2016; de Santana et al., 2017).

Values obtained for the average time to flowering indicated that the assessed hybrids are characterized by a precocious growth cycle, with 50% of plants flowering prior to 60 days (Baumhardt et al., 2005; Baumhardt and Howell, 2006). The time to flowering in most hybrids did not exceed 60 days and none took more than 70 days to flower, the latter period of which is generally observed in the hybrids planted in Brazil. The average height of the evaluated hybrids was 1.58 m, which is greater than the satisfactory height for mechanized harvesting (Tardin et al., 2013). However, although the average value exceeds that recommended, the height of some of the hybrids, for example, H14, H65, H15, H44, H75, H64, H35, H55, H54, H41, H74, H34, H66, and H73, was found to be within the recommended range. Such evaluations of the characteristics height and flowering are of relevance for breeding programs, in that these are traits are influenced to a lesser extent by environmental factors and thus facilitate early selection of the most promising lines, thereby saving time and reducing the area required for field trials (Menezes et al., 2015).

A difference in the flowing times of cultivars is of particular interest to farmers (Tardin et al., 2013), as this enables the diversification of genotypes to be sown, with late cultivars being sown at the beginning of the cropping cycle and earlier cultivars toward the end of the sowing period, which accordingly contributes to a staggered period of harvest. Among those hybrids flowering within 60 days, H35 and H34 are notable, in that they are productive genotypes characterized by a desired ideotype for height.

Hybrids taller than the recommended height tend to fluff up and thereby hinder mechanical harvesting (Silva et al., 2015). Conversely, given the correlation between plant height and productivity, hybrids with insufficient height growth tend to show lower productivity. Thus, those hybrids that grow to heights close to the maximum recommended should be preferentially selected, as these are likely to be more productive. In this regard, hybrids H71, H55, and H35 would be of particular interest, as these are characterized by productivities exceeding the national average and have an ideal ideotype for height. As one of the most productive hybrids, H34 is also worthy of mention, given that although its growth height is greater than that typically desired for mechanized harvesting, the difference does not generally exceed 2 cm.

Conclusions

Considering all traits, we recommend the genitors 3, 5, and 7 from the R lines and the genitors 1 and 6 from A lines. The hybrids H11, H22, H31, H32, H36, H51, H55, H56, and H71 are those with good combining abilities and that show the best performance with regarding the most important traits for sorghum breeding.

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