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COMBINING ABILITY AND HETEROSIS IN SORGHUM (*Sorghum bicolor* L.)

MAFTUCHAH[1,2*], H. WIDYANINGRUM[1], A. ZAINUDIN[1], SULISTYAWATI[3], H.A. RESWARI[2], and H. SULISTIYANTO[2]

[1]Department of Agrotechnology, University of Muhammadyah Malang, Malang, East Java, Indonesia
[2]Center for Biotechnology, University of Muhammadyah Malang, Malang, East Java, Indonesia
[3]Faculty of Agriculture, Merdeka 'Pasuruan' University, 'Pasuruan' City, East Java, Indonesia
*Corresponding author email: maftuchah@umm.ac.id
Email addresses of co-authors: halimahwidya9797@gmail.com, aguszainudinumm@gmail.com, mommyandri@gmail.com, helvi_ardana@umm.ac.id, hendrysulistiyanto21@gmail.com

SUMMARY

For the sustainable improvement of sorghum (*Sorghum bicolor* L.), local genotypes were conventionally crossed in East Java, Indonesia to determine a) the crossing success of different genotypes, b) germination percentage and seed setting traits, and c) the combining ability and heterotic effect of sorghum parental genotypes and their F_1 diallel hybrids. Three sorghum genotypes ('Lamongan-1', 'Tulungagung-2', and 'Jombang') from the local germplasm were collected from various regions in East Java, Indonesia, and were crossed in a complete diallel design. The experiment was carried out in a randomized complete block design with four replications during 2018–2019 at the Agrotechnology Laboratory, Faculty of Agriculture, University of Muhammadiyah, Malang, Indonesia. Results showed that the parental genotypes and their F_1 hybrids exhibited significant differences in seed weight and seed diameter and nonsignificant differences in germination percentage and seed setting. The parental genotype 'Tulungagung-2' and its hybrids 'Jombang' × 'Tulungagung-2', 'Tulungagung-2' × 'Lamongan-1', and 'Jombang' × 'Tulungagung-2' presented the highest germination percentages, seed setting, seed weights, and seed diameters. The genotype 'Tulungagung-2' had the highest general combining ability and was identified as a good general paternal and maternal parent for the production of promising F_1 hybrids. The hybrid 'Jombang' × 'Lamongan-1' had the highest specific combining ability for all of the characters and was recognized as a promising F_1 hybrid for improving sorghum yield. Cluster analysis divided all of the parental genotypes and their F_1 hybrids into two large groups with a similarity of 13.13%.

Keywords: Conventional breeding, parental genotypes, F_1 diallel hybrids, crossing success, germination percentage, heterosis, heterobeltiosis, combining ability

Key findings: 'Tulungagung-2' was identified as a good general paternal and maternal parent for the production of promising F_1 hybrids with the highest germination percentage, seed setting, seed weight, and seed diameter. The F_1 hybrid 'Jombang' × 'Lamongan-1' was identified as the best specific combiner. The genotype 'Tulungagung-2' can be recommended for the assembly of superior sorghum cultivars with high productivity.

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INTRODUCTION

Sorghum (*Sorghum bicolor* L.) belongs to the family Gramineae; it is widely adapted and can be grown on marginal lands, such as dry, alkaline, acidic, or even infertile lands (Sembiring and Subekti, 2010). Sorghum is not only limited to use as food and feed ingredients, it can also be used as a processed material; moreover, given that its seeds contain ash (1.6%), fat (3.1%), protein (10.4%), carbohydrates (70.7%), crude fiber (2.0%), and energy (329 kcal), it can serve as a multipurpose crop (Suarni, 2012; Reddy *et al*., 2014; Jimoh and Abdullahi, 2017). It is a versatile crop that is useful as a food, feed, and industrial ingredient. As a food ingredient, sorghum is not considerably different from other cereals (ICRISAT, 2004). In general, the protein content of sorghum is higher than that of corn, brown rice, and barley but lower than that of wheat. The fat content of sorghum is higher than that of brown rice, wheat, and millet but lower than that of corn.

Sorghum is suitable for cultivation in Indonesia because this country has a tropical climate. It is relatively drought-tolerant and could be grown in areas with low soil fertility (Panjaitan *et al*., 2015). In Indonesia, the past research on the development of sorghum is very limited compared with that on other cereal crops, such as rice, maize, and wheat (Boonlertnirun *et al*., 2012). In Indonesia, the level of production and quality of sorghum remain low, and many regions still rely on the cultivation of local genotypes.

In Indonesia, the lack of superior cultivars is the main problem in sorghum development because little work has been conducted on their identification, development, and characterization (Susilowati and Saliem, 2013; Rao *et al*., 2016). Therefore, collecting and developing the local germplasm through different breeding programs is necessary to obtain wide genetic diversity in sorghum. The sorghum breeding program in East Java, Indonesia, is under development, and several local genotypes have been crossed to obtain superior genotypes. On the basis of the initial characterization of the local germplasm in East Java, eight sorghum genotypes ('Pasuruan', 'Lamongan-1', 'Lamongan-2', 'Tuban', 'Sampang-2', 'Tulungagung-1', 'Tulungagung-2', and 'Jombang') have been developed with increased potential and desirable agronomic characters and can be used as parental genotypes for the development of superior cultivars in future breeding programs (Sulistyawati *et al*., 2019a).

The sorghum genotype 'Lamongan-1' meets the specific criterion of maturation within 77 days (Sulistyawati *et al*., 2019b). The selection criteria for the development of superior sorghum cultivars include early maturity, medium plant height, and desirable protein and tannin contents (Subagio and Aqil, 2013). The sorghum genotype 'Lamongan-1' also has the highest leaf length and width, the highest number of seeds per panicle, and the second heaviest seed weight per panicle after the genotype 'Tulungangung-2'. The genotype 'Tulungagung' has the second highest plant height after the genotype 'Jombang', the highest fresh and dry 1000-seed weight with the second-highest number of seeds per panicle after the genotype 'Lamongan-1', but earlier flowering and harvesting than 'Lamongan-1' and 'Jombang'. Maftuchah *et al*. (2020, 2021) revealed that genotype 'Tulungagung-2' has more chances for development than other genotypes because it has the highest fresh and dry seed weights. The sorghum genotype 'Jombang' has the advantage of the highest plant height, leaf number, and reducing sugar content (Sulistyawati *et al*., 2019a, b).

The crossing success rate and seed germination of F_1 hybrids must to be determined to validate whether the F_1 derivatives can produce vigorous seeds such that selection can be made on the basis of the availability of the seeds of different cross combinations. Genetic parameters, such as heterosis and heterobeltiosis, are used to assess F_1 hybrids quantitatively (Boonlertnirun *et al*., 2012). Heterosis and heterobeltiosis can be used to improve plant characters by identifying parental combinations that can produce high-yielding F_1 strains. In sorghum, the selection of promising parental genotypes to produce a superior hybrid is dependent on heterotic effects F_1 populations (Ringo *et al*., 2015; Jaikishan *et al*., 2019)

Poehlman (1983) reported that not all pure-line combinations will produce superior hybrids. Therefore, pure lines must be tested for their cohesiveness to determine the best combination for hybrid seed production. Welsh (1981) stated that the population with the highest general combining ability (GCA) effects has high chances to produce F_1 hybrids with the highest specific combining ability (SCA) values. The first step in determining the yield between the lines is to evaluate GCA and SCA. GCA is a general concept for classifying relatively pure strains in accordance with their hybrid's appearance (Hallauer and Miranda, 1988; Rini *et al*., 2017). This information is needed to obtain the results of parental combinations that will produce offspring with high potential from which high yields can be achieved if their offspring from their cross combinations have positive heterosis and high combining ability. Given the above considerations, the present study was planned to determine a) the crossing success of different sorghum genotypes, b) germination percentage and seed setting traits, and c) the combining ability and heterotic effects of sorghum parental genotypes and their F_1 diallel hybrids at East Java, Indonesia.

MATERIALS AND METHODS

Breeding material

The present research on sorghum was carried out during 2018–2019 at the Agrotechnology Laboratory, Faculty of Agriculture, University of Muhammadiyah Malang, Indonesia. Three sorghum genotypes ('Lamongan-1', 'Tulungagung-2', and 'Jombang') belonging to the local germplasm were collected from various regions in East Java, Indonesia. All of the sorghum genotypes were crossed in a complete diallel fashion at Purutrejo Village, Purworejo Subdistrict, Pasuruan City, Indonesia (−7°39'53.39" latitude, 112°54'17.38" east longitude).

Crossing program

Sorghum seeds were sown in polybags with dimensions of 4 cm × 3 cm and containing a mixture of soil + compost + rice husk. After emergence and 20 days of planting, the sorghum seedlings were transferred to the field, where each hill contained a single plant.

Emasculation

The initial step was to prepare the equipment to be used in the crossing program of sorghum. Then, the sorghum flowers to be emasculated were selected. Flower selection was carried out as follows: two repetitions were used in one panicle, wherein for one repetition 3–4 secondary stalks were taken. Emasculation was started from the base to the tip of the secondary stalk and carried out by opening the husks (glume) of the sorghum flowers on one side by using tweezers. Then, the tweezers were inserted into the husks to remove slowly the three stamens (anthers) in the sorghum flowers. Finally, the emasculated sorghum flowers were covered with paper envelopes. The sorghum flowers were covered per repeat of the secondary flower stalk that has been emasculated. A large number of flowers were crossed. Specifically, 90 flowers for 'Lamongan-1' × 'Tulungagung-2', 91 flowers for 'Lamongan-1' × 'Jombang', 91 flowers for 'Tulungagung-2' × 'Lamongan-1', 84 flowers for 'Tulungagung-2' × 'Jombang', 81 flowers for 'Jombang' × 'Lamongan-1', and 84 flowers for 'Jombang' × 'Tulungagung-2' were crossed.

Pollination

The first step was to prepare the equipment for pollination. Then, the pollen grains of the selected genotypes were taken from stamens for use as male parents ('Lamongan-1', 'Tulungagung-2', and 'Jombang') by shaking the sorghum flower panicles slowly. Furthermore, pollination was carried out by opening the husks (glume) of sorghum flowers on one side of the husk by using tweezers and holding one side of the husk with fingers and then inserting the stamens vertically by using the tweezers into the husk and removing the other side of the chaff that was held with a finger to close the sorghum flower again. Then, the sorghum flowers were covered with paper bags. The secondary stalk of the pollinated sorghum flowers was also covered. The final stage was labeling information, i.e., the names of the parental genotypes used in the cross (female × male), replication, and the date of the cross.

Harvesting of the crosses seeds

The different crosses were harvested in accordance with the maturity and age of the sorghum genotypes. Harvest time was decided by looking at the visual characteristics of the stems, leaves, and panicles of ready-to-harvest sorghum. These visual characteristics included the yellowing of the leaves and stems, the formation of perfect panicles, and the hardening of the seeds. After harvesting, the sorghum was dried in the sun.

Sowing of parental genotypes and F_1 hybrid seeds

The different types of equipment and material used in the germination test were first prepared. The seeds of the parental genotypes and their crosses were soaked in warm water (40 °C) for 2 h, after which they were soaked in a fungicide solution for 15 min and then dried. Furthermore, the germination test was carried out by using the interpaper test method by soaking three sheets of jaw paper and placing them in a plastic box, after which the tissue was placed on top of the jaw paper. The treated seeds of the sorghum genotypes were arranged on tissue paper, then covered with three sheets of moistened bamboo paper. The plastic boxes were closed and labeled with the date and genotype information and then placed at room temperature (28 °C).

Planting seeds

After the sprouting of the sorghum seeds and the appearance of the radicle, the candidate genotypes were immediately planted in 4 cm × 3 cm polybags containing a mixture of soil + compost + husk. At 20 days after sowing (DAS), the plants of the different sorghum genotypes were transferred to the planting area in the field, where each hole contained one sorghum seed at the depth of 5 cm. The said experiment was carried out in a randomized complete block design with six treatments and four replications.

Data recorded

The data on the different quantitative characters of sorghum parental genotypes and F_1 hybrids were recorded. These data included germination percentage (normal, abnormal, and dead seeds), seed setting, seed weight, and seed diameter. The germination percentage of the normal sprouts was observed and recorded from days 1 to 14. Kamil (1979) and Juliantisa (2017) stated that the criteria for normal sprouts are the presence of primary and secondary roots, long and short hypocotyls, and one primary leaf. Abnormal sprouts are those that do not meet the requirements for normal sprouts (DG-TPH, 2000). Data on abnormal sprouts were recorded from observations on the germination of a seed in which one or both essential elements (plumule and radicle) did not grow properly until the last day of observation. Dead seeds were those that at the end of the test were no longer hard or fresh and were usually moldy, completely rotted, and lacking the main elements for emergence. Data on dead seeds were recorded by counting the number of moldy and rotten seeds that did not germinate until the last day of observation.

Sprouts (%) = Number of live sprouts/number of seedlings × 100%

Germination power (%) = Number of sprouts/number of seeds grown × 100

In accordance with Juliantisa (2017), the sorghum germination percentage was calculated by using the following formula:

$$\text{DB}(\%) = \frac{\text{Normal sprouts}}{\text{Number of seeds}} \text{ x } 100$$

The seeds (%) were those seeds that formed after sorghum was harvested and dried. The formula for seed setting was as follows (Xie *et al*., 2016):

$$\text{Seed set} = \frac{\text{Seeds formed}}{\text{Flowers crossed}} \text{ x } 100$$

Average seeds formed (#): Number of seeds formed in each cross/number of crosses

The average sorghum seed weight was recorded as follows:

Average seed weight = Total seed weight/number of seeds

Statistical analysis

All the obtained data were analyzed by using analysis of variance (ANOVA) to determine whether significant differences existed among the treatments or not (Steel *et al*., 1997). Differences between treatments were revealed through the honestly significant difference (BNJ) test at the 5% level. Germination data were tested by analysis of means at the 5% level.

Heterosis and heterobeltiosis

After obtaining the data on the mean performance of the parental genotypes and their F_1 hybrids for various traits in sorghum, the heterotic effects over mid- and high-parents were calculated in accordance with Fehr (1987) as follows:

$$hMP (\%) = [(\mu F1 - \mu MP)/\mu MP] \times 100$$

$$hHP (\%) = [(\mu F1 - \mu HP)/\mu HP] \times 100$$

where
hMP = Average heterosis of parents (heterosis)
μMP = Mean value of both parents
hHP = Average heterosis of the highest parent (heterobeltiosis)

μHP = Mean value of the highest parent (high parent)
μFmean = Value of the results of the study

Combining ability analysis

After significant differences were found among the parental inbred lines and their F_1 hybrids for various traits, the data were further subjected to combining ability analysis in accordance with Griffing (1956) Method-I based on Eisenhart's Model-II (Singh and Chaudhary, 1985) as follows

General combining ability

$$g_i = \frac{1}{2n}(Y_i. + Y_.i) - \frac{1}{n^2}Y..$$

where
gi = GCA effects for line i
n = Number of parents/varieties
Yi. = Total of mean values of F_1s resulting from crossing jth lines with ith lines
Y.i = Total of mean values of F_1s resulting from crossing ith lines with jth lines
Y.. = Grand total of all the mean values in the table

Specific combining ability

$$s_{ij} = \frac{1}{2}(Y_{ij}+Y_{ji}) - \frac{1}{2n}(Y_i.+Y_.i+Y_j.+Y_.j) + \frac{1}{n^2}Y..$$

where
Sij = SCA between the ith and jth lines
Yij = Mean value of the F_1 resulting from crossing the ith and jth lines
Yji = Mean value for F_1 resulting from crossing the jth and ith varieties
Yi. = Total of mean values of F_1's resulting from crossing jth line with ith varieties
Y.i = Reciprocal values of Yi
Y.j = Total values for F_1s resulting from crossing the ith line with jth line
Yj. = Values of reciprocal F_1s of Y.j
Y. = Grand total of the observations

Reciprocal effects

$$r_{ij} = \frac{1}{2}(Y_{ij} - Y_{ji})$$

where
Yij = Reciprocal effects of ith and jth varieties/lines
Yij = Mean values for the F_1 resulting from crossing the ith and jth lines
Yji = Reciprocal values of F_1 resulting from Yij

Cluster analysis

Cluster analysis was also performed to determine the kinship relationship through the level of similarity between the crosses of three sorghum parental genotypes. The quantitative and qualitative data obtained from these sorghum parental genotypes and their crosses were analyzed.

RESULTS

Germination percentage

The germination percentages of the sorghum parental genotypes and their F_1 hybrids ranged from 76.00% to 92.00% and from 0.00% to 100%, respectively (Table 1). The parental genotypes showed higher germination percentages (86.67%) than their F_1 hybrids (68.85%). Among the parental genotypes, 'Tulungagung-2' and 'Jombang' showed the highest and the same germination (92.00%) rates. The lowest germination rate was shown by 'Lamongan-1' (76.00%). Among the F_1 hybrids, 'Lamongan-1' × 'Jombang', 'Tulungagung-2' × 'Lamongan-1', and 'Jombang' × 'Tulungagung-2' showed the highest germination percentages of 100%, 88.09%, and 83.33%, respectively. However, the F_1 hybrid 'Lamongan-1' × 'Tulungagung-2' exhibited zero germination percentage. The F_1 hybrids 'Jombang' × 'Lamongan-1' (75.00%) and 'Tulungagung-2' × 'Jombang' presented moderate germination percentage (66.67%).

Seed setting

Seed setting is an important and final output of every crop plant. The average seed setting of the sorghum F_1 hybrids ranged from 0.75 to 9.00 with percentages of 3.57% and 37.50%, respectively (Table 2). On average, the F_1 hybrid 'Tulungagung-2' × 'Lamongan-1' showed the maximum number of seeds (9.00) with a percentage of 37.50%, followed by the F1 hybrid 'Jombang' × 'Tulungagung-2' (4.25 and 18.97%). The four F_1 hybrids 'Lamongan-1' × 'Jombang', 'Lamongan-1' × 'Tulungagung-2', 'Tulungagung-2' × 'Jombang', and 'Jombang' × 'Lamongan-1' presented the lowest number and percentage of seed setting with ranges of 0.75–1.50 and 3.57%–7.26%, respectively.

Table 1. Mean performance of sorghum parental genotypes and their F_1 hybrids for germination percentage.

Genotypes	Average					
	Seedling (#)	Live sprouts	Normal sprouts	Abnormal sprouts	Succumb sprouts	Germination (%)
Parental genotypes						
Lamongan-1	25	21	19	2	4.00	76.00
Tulungagung-2	25	24	23	1	1.00	92.00
Jombang	25	24	23	1	1.00	92.00
Mean	-	-	-	-	-	86.67
F_1 hybrids						
Lamongan-1 × Tulungagung-2	2	0	0	0	2.00	0.00
Lamongan-1 × Jombang	2	2	2	0	0.00	100
Tulungagung-2 × Lamongan-1	12	11	10	1	0.67	88.09
Tulungagung-2 × Jombang	2	2	1	0	0.50	66.67
Jombang × Lamongan-1	3	3	3	0	0.50	75.00
Jombang × Tulungagung-2	9	9	8	1	0.00	83.33
Mean	-	-	-	-	-	68.85

Table 2. Mean performance of sorghum F_1 diallel hybrids for seed setting.

F_1 hybrids	Replications	Flowers crossed (#)	Seeds formed (#)	Seeds formed (%)	Average seeds formed (#)	Average seeds formed (%)
Lamongan-1 × Tulungagung-2	1	20	0	0.00	1.00	4.38
	2	20	1	5.00		
	3	24	3	12.50		
	4	26	0	0.00		
Lamongan-1 × Jombang	1	25	0	0.00	0.75	3.57
	2	21	2	9.52		
	3	21	1	4.76		
	4	24	0	0.00		
Tulungagung-2 × Lamongan-1	1	25	9	36.00	9.00	37.50
	2	21	0	0.00		
	3	25	21	84.00		
	4	20	6	30.00		
Tulungagung-2 × Jombang	1	22	1	4.55	1.00	4.89
	2	22	0	0.00		
	3	20	0	0.00		
	4	20	3	15.00		
Jombang × Lamongan-1	1	21	4	19.05	1.50	7.26
	2	20	0	0.00		
	3	20	2	10.00		
	4	20	0	0.00		
Jombang × Tulungagung-2	1	23	14	60.87	4.25	18.97
	2	21	0	0.00		
	3	20	3	15.00		
	4	20	0	0.00		

Seed weight

The seed weight of the sorghum parental genotypes ranged from 0.023 g to 0.028 g and that of F_1 hybrids ranged from 0.008 g to 0.028 g (Table 3). Overall, the parental genotypes exhibited bolder seeds and higher seed weight (0.025 g) than their F_1 hybrids (0.019 g). Among the parental genotypes, 'Tulungagung-2' (0.028 g) presented the maximum seed weight, followed by 'Lamongan-1' (0.025 g) and 'Jombang' (0.023 g). Among the F_1 hybrids, the highest seed weight was shown by the two F_1 hybrids

Table 3. Mean performance of sorghum parental genotypes and their F_1 hybrids for seed weight.

Genotypes	Seed weight (g)
Parental genotypes	
Lamongan-1	0.025
Tulungagung-2	0.028
Jombang	0.023
Mean	0.025
F_1 Hybrids	
Lamongan- 1 × Tulungagung-2	0.008
Lamongan-1 × Jombang	0.019
Tulungagung-2 × Lamongan-1	0.017
Tulungagung-2 × Jombang	0.019
Jombang × Lamongan-1	0.020
Jombang × Tulungagung-2	0.028
Mean	0.019

'Jombang' × 'Tulungagung-2' (0.028 g) and 'Jombang' × 'Lamongan-1' (0.020 g). However, the F_1 hybrid 'Lamongan-1' × 'Tulungagung-2' (0.008 g) showed shrunken seeds and the lowest seed weight among all F_1 hybrids and parental genotypes. All other F_1 hybrids showed moderate values for seed weight.

Seed diameter

The seed vertical and horizontal dimensions of the sorghum parental genotypes ranged from 0.20 cm to 0.28 cm and 0.15 cm to 0.18 cm, respectively (Table 4). The seed vertical and horizontal dimensions of the F_1 hybrids varied from 0.11 cm to 0.27 cm and from 0.08 cm to 0.18 cm, respectively. On average, the parental genotypes had larger seeds in terms of vertical and horizontal dimensions (0.26 and 0.16 cm) than F_1 hybrids (0.18 and 0.12 cm). Among parental genotypes, 'Tulungagung-2' showed the maximum values for seed vertical and horizontal dimensions (0.31 and 0.18 cm), followed by 'Lamongan-1' (0.28 and 0.15 cm), whereas the lowest seed vertical and horizontal dimensions were presented by 'Jombang' (0.20 and 0.15 cm). Among F_1 hybrids, 'Tulungagung-2' × 'Lamongan-1' exhibited the highest values for seed vertical and horizontal dimensions (0.27 and 0.18 am) and 'Jombang' × 'Tulungagung-2' (0.25 and 0.15 cm). The F_1 hybrids 'Lamongan-1' × 'Tulungagung-2' (0.12 and 0.08 cm) and 'Lamongan-1' × 'Jombang' (0.11 and 0.08 cm) had close and the lowest seed vertical and horizontal dimensions. All other F_1 hybrids presented moderate values for seed vertical and horizontal dimensions. In sorghum, seed diameter is thought to be more influenced by genetic factors than by other factors.

Heterosis and heterobeltiosis

For germination percentage, the sorghum F_1 hybrid 'Lamongan-1' × 'Jombang' showed the highest positive heterotic effects over the mid- (0.19%) and better-parents (0.09%), followed by the F_1 hybrid 'Tulungagung-2' × 'Lamongan-1' (Table 5). However, all other F_1 hybrids exhibited negative heterosis and heterobeltiosis for germination percentage. The F_1 hybrid 'Jombang' × 'Tulungagung-2' exhibited the highest positive heterosis (0.10%) and heterobeltiosis (0.00%) for seed weight. However, all other F_1 hybrids revealed negative heterotic effects over their mid- and better-parents for seed weight. For seed vertical and horizontal dimensions, almost all of the F_1 hybrids, except for the F_1 hybrid 'Tulungagung-2' × 'Lamongan-1' with positive heterotic effects over its mid-parent (0.09%) and zero heterotic effect over its better parent for the said trait, exhibited negative heterotic effects over its mid- and high-parents.

Combining ability analysis

ANOVA showed that crosses ($P \leq 0.05$) and SCA ($P \leq 0.01$) mean squares were significant for seed vertical diameter (Table 6). The SCA mean squares were significant ($P \leq 0.05$) for seed horizontal diameter. However, all other mean squares for crosses, GCA, and SCA were nonsignificant for other traits. The sorghum genotype 'Tulungagung-2' had the highest positive GCA effects for seed weight and seed vertical and horizontal diameters, i.e., 0.0001, 0.0262, and 0.0164, respectively (Table 7). 'Lamongan-1' and 'Jombang' had the highest positive GCA effects for vertical diameter and seed weight, i.e., 0.0055 and 0.0002.

However, all the parental genotypes presented negative GCA effects for other traits. In the case of SCA effects in F_1 hybrids, the parental genotypes with the highest positive GCA effects were also unable to produce hybrids with positive SCA effects for the said traits, and all the F_1 hybrids revealed negative SCA effects for the studied traits (Table 8).

Table 4. Mean performance of sorghum parental genotypes and their F_1 hybrids for seed diameter.

Genotypes	Seed diameter (cm)	
	Vertical	Horizontal
Parental genotypes		
Lamongan-1	0.28	0.15
Tulungagung-2	0.31	0.18
Jombang	0.20	0.15
Means	0.26	0.16
F_1 Hybrids		
Lamongan-1 × Tulungagung-2	0.12	0.08
Lamongan-1 × Jombang	0.11	0.08
Tulungagung-2 × Lamongan-1	0.27	0.18
Tulungagung-2 × Jombang	0.14	0.10
Jombang × Lamongan-1	0.16	0.11
Jombang × Tulungagung-2	0.25	0.15
Means	0.18	0.12

Table 5. Sorghum F_1 hybrids with heterotic effects over their mid- and better-parents for germination percentage, seed weight, and seed diameter (vertical and horizontal).

F_1 Populations	Germination		Seed weight		Seed diameter (%)			
					Vertical		Horizontal	
	MP (%)	HP (%)	MP (%)	HP (%)	MP (%)	HP (%)	MP (%)	HP (%)
Lamongan-1 × Tulungagung-2	−1.00	−1.00	−0.70	−0.71	−0.59	−0.61	−0.52	−0.56
Lamongan-1 × Jombang	0.19	0.09	−0.21	−0.24	−0.54	−0.61	−0.47	−0.47
Tulungagung-2 × Lamongan-1	0.05	−0.04	−0.36	−0.39	−0.08	−0.13	0.09	0.00
Tulungagung-2 × Jombang	−0.28	−0.28	−0.25	−0.32	−0.45	−0.55	−0.39	−0.44
Jombang × Lamongan-1	−0.11	−0.18	−0.17	−0.20	−0.33	−0.43	−0.27	−0.27
Jombang × Tulungagung-2	−0.09	−0.09	0.10	0.00	−0.02	−0.19	−0.09	−0.17

MP: Mid-parent heterosis, HP: High-parent heterosis

Table 6. Analysis of the variance for a 3 × 3 sorghum diallel cross.

Source of variation	d.f.	Mean squares		
		Weight per seed	DVB	DHB
Replications	3	0.0001^{NS}	0.0147^{NS}	0.0047^{NS}
Crosses	8	0.0002^{NS}	0.0322*	0.0118^{NS}
GCA	2	0.0000^{NS}	0.0206^{NS}	0.0055^{NS}
SCA	3	0.0004^{NS}	0.0561**	0.0207*
Reciprocals	3	0.0001^{NS}	0.0159^{NS}	0.0069^{NS}
Error	24	0.0019	0.0072	0.0034

*, ** significant at the 5% and 1% levels of probability, NS = Nonsignificant

Table 7. Value of the combining power of sorghum diallel crosses.

Female/Male	Lamongan 1	Tulungagung 2	'Jombang'
Seed weight			
Lamongan 1	−0.0003	−0.0053	−0.0042
Tulungagung 2	−0.0045	0.0001	−0.0027
Jombang	−0.0003	−0.0024	0.0002
Seed vertical diameter			
Lamongan 1	0.2575	0.0610	0.0550
Tulungagung 2	0.2042	0.2900	0.0700
Jombang	0.0782	0.1225	0.1825
Seed horizontal diameter			
Lamongan 1	−0.0028	−0.0201	−0.0326
Tulungagung 2	−0.0488	0.0164	−0.0343
Jombang	−0.0063	−0.0137	−0.0136

GCA effects: diagonal values, SCA effects: Values above the diagonal, Rec: Values below the diagonal

Table 8. Specific combining ability effects for seed weight and seed vertical and horizontal diameters in six F_1 diallel hybrids.

F_1 populations	Seed weight	Seed	
		Vertical diameter	Horizontal diameter
Lamongan-1 × Tulungagung-2	−0.0053	−0.0458	−0.0201
Lamongan-1 × Jombang	−0.0042	−0.0540	−0.0326
Tulungagung-2 × Lamongan-1	−0.0045	−0.0716	−0.0488
Tulungagung-2 × Jombang	−0.0027	−0.0451	−0.0343
Jombang × Lamongan-1	−0.0003	−0.0116	−0.0063
Jombang × Tulungagung-2	−0.0024	−0.0262	−0.0137

Cluster analysis

Cluster analysis for quantitative and qualitative characters was carried out by using Mini Tab software version-17. The results were presented in a dendrogram (Figure 1). In the cluster analysis, the sorghum parental genotypes were designated as G2 ('Lamongan-1'), G8 ('Tulungagung-2'), and G-9 ('Jombang'). Cluster analysis divided all of the parental genotypes and their F_1 hybrids into two large groups with a similarity of 13.13%. The first group consisted of five F_1 hybrids (G2 × G8, G8 × G2, G8 × G9, G9 × G2, and G9 × G8) and the three parental genotypes 'Lamongan-1', 'Tulungagung-2', and 'Jombang'. The second group comprised the F_1 hybrid G2 × G9. The first group consisted of two subgroups, which had a similarity of 42.28%. The first subgroup contained only one F_1 hybrid (G2 × G8), whereas the second subgroup consisted of four F_1 hybrids (G8 × G2, G8 × G9, G9 × G2, and G9 × G8) and the three parental sorghum cultivars 'Lamongan-1', 'Tulungagung-2', and 'Jombang'.

DISCUSSION

Seed setting is the result of seed formation at harvest after hybridization. The percentage of the success rate of crosses is measured as the number of seeds formed (seed set) divided by the number of flowers crossed multiplied by 100%. A cross is said to be successful if it is marked by the formation of ovules and unsuccessful if ovules are not formed as indicated by the drying of the husks. Syukur *et al*. (2010) opined that if the prospective fruit begins to enlarge and does not fall out, then fertilization has occurred. On the other hand, if the prospective fruit does not enlarge or fall out, then fertilization has failed.

The highest percentage of seed formation was observed in the F_1 hybrid 'Tulungagung-2' × 'Lamongan-1' (37.50%). The seed formation rates of the five other F_1 hybrids 'Lamongan-1' × 'Tulungagung-2', 'Lamongan-1' × 'Jombang', 'Tulungagung-2' × 'Jombang', 'Jombang' × 'Lamongan-1', and 'Jombang' × 'Tulungagung-2' were 4.38%, 3.57%, 4.89%, 7.26%, and 18.97%,

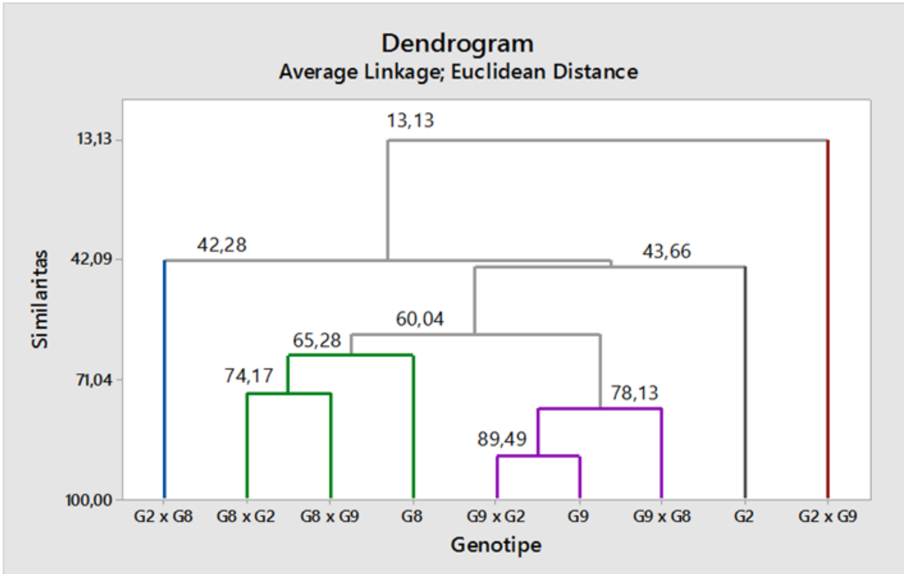

Figure 1. Dendrogram of the quantitative and qualitative traits of sorghum parental genotypes and their F_1 hybrids.

respectively. Many factors, including the condition of the pollen used, environmental factors, the receptive time of the female and male anthesis, and the level of the compatibility of the parental genotype used influence the success of crosses in sorghum. Pollen is highly susceptible to drought stress and thus quickly loses viability in accordance with the opinion of Lansac *et al*. (1994) and Andriani and Isnaini (2010), who stated that pollen cannot recover their viability even after rehydration under drought stress conditions and can be viable only for 3–6 h after blooming. Environmental factors, such as rainfall, sunlight, temperature, and humidity, can also affect the occurrence of fertilization. Syukur *et al*. (2010) stated that rainfall and high temperature cause the low success of hybridization in conventional crosses.

In sorghum, floral reception and anthesis is the period when flowers mature and become ready for pollination. In sorghum, female flowers are receptive for 3 days after blooming. The pistil (stigma) of sorghum flowers begins to enter the receptive period 2 days before the flowers bloom and is receptive for up to 8 to 16 days after the flowers bloom; however, it is optimally receptive for 3 days after the flowers bloom (Stephens, 1934; Pedersen *et al*., 1998; Bello, 2008). During pollination, when the female flowers have entered the receptive period, which is marked by the opening of husks in the morning, the husks on the flowers open for 20 min and close completely 2 h later. In sorghum, the time of the anthesis of male flowers occurs before 10 am. Field observations have shown that pollen could be obtained at 5 am. The past findings of Stephens (1934) showed that sorghum flowers generally bloom (anthesis) before 10 am. Hermaphrodite flowers bloom first, and single flowers bloom 2–4 days later.

Cross compatibility is the capability of the plants to form fruit (Syukur *et al*., 2010). Plant crosses that produce fruit are compatible, whereas those that do not produce fruit are incompatible. The level of the compatibility (matching) of the parental genotypes used is very distant. Kinship can affect the success of a cross, wherein the farther the kinship between the two parental genotypes used in the cross, the smaller the chance of obtaining F_1 plants. This phenomenon is in accordance with the opinion of Syukur *et al*. (2010), who stated that the implementation of crossing in distant relatives is difficult because of natural obstacles, such as weak hybrid seeds that cannot survive and sterile F_I plants. These barriers lead to the low success rates of distant relative crosses. The success of the cross (crossing ability) in some cross combinations is limited by the capability to form seeds (seed setting), which is dependent on the genomes of both parents. Differences in the parental genome cause inhibition during and after fertilization. Martin (1970) stated that a cross is classified as compatible if it can produce fruit at rates above 20%.

The maximum and at-par seed weight were shown by the F_1 hybrid 'Jombang' × 'Tulungagung-2' (0.028 g) and the parental genotype 'Tulungagung-2' (G8, 0.028 g), followed by 'Lamongan-1' (G2, 0.025 g) and 'Jombang' (G9, 0.023 g). The genetic influence of the two parents is suspected to play a role in the result of the cross. Kamil (1979) and Panjaitan *et al*. (2015) explained that plant genes affect the height and weight of seeds, seed shape, and seed size. The F_1 hybrid 'Lamongan-1' × 'Tulungagung-2' (0.008 g) had lower seed weight than the parental genotypes 'Lamongan-1' (G2 - 0.025 g) and 'Tulungagung-2' (G8 - 0.028 g) likely due to imperfect fertilization given that a successful distant relative cross has a low chance of forming a seed set in accordance with the opinion of Syukur *et al*. (2010) and Rao *et al*. (2016), who explained that the farther the kinship between the two parental genotypes used in a cross, the smaller the chance of obtaining normal F_I plants.

The analysis of seed vertical and horizontal diameter showed nonsignificant differences among sorghum genotypes likely as a result of the influence of the genetic makeup of the genotypes in accordance with the opinion of Lakitan (1995) and Supriono *et al*. (2017), who stated that in certain plants, seed size is generally not influenced by the environment but is more controlled by genetic factors. Genotypes showed nonsignificant differences for variables, i.e., live, normal, and abnormal sprouts. However, the normal and live sprouts were more pronounced in the F_1 hybrid 'Tulungagung-2' × 'Lamongan-1' than in other crosses, due to which the said hybrid provided a number of seeds. The germination of the seeds of parental genotypes and their F_1 hybrids is influenced by internal factors (seed moisture content and seed physical structure) and external factors (environmental factors, such as seed growth). Seed weight and seed size also affect seed germination. Large seeds have extensive food reserves with large embryo sizes such that the growth rate of germination is optimal. Satwiko (2013) explained that large and small seeds exhibit differences in the plant growth process and that compared with large seeds, small seeds have less optimal growth due to lower food reserves and smaller embryo size.

The germination percentage of the parental genotypes and their F_1 hybrids ranged from 66.67% to 100%. However, the parental genotypes and the F_1 hybrids 'Lamongan-1' × 'Tulungagung-2', 'Tulungagung-2' × 'Jombang', and 'Lamongan-1' showed a low percentage of germination likely due to their genetic makeup. Kartasapoetra (2003) and Juliantisa (2017) , stated that the genetic factors that affect seed vigor and the basic patterns of germination and growth are genetically inherited and differ from one species to another. Gardner (1991) and Juliantisa (2017) explained that seeds have low germination and vigor due to weakness; temperature fluctuations due to rain and sunlight that cause the chemical composition of seeds to change; and damage due to predator attacks that damage the crop and consequently reduce the quality and quality of the seeds.

Among genotypes, the F_1 hybrid 'Lamongan-1' × 'Jombang' had a higher plant height than its parental genotypes, i.e., 'Lamongan-1' and 'Jombang' likely as a result of the influence of genetic and environmental factors in accordance with the opinions of Gardner (1991) and Bunphan (2015), who stated that genetic and environmental factors affect plant growth. In addition to plant height, the leaves are a component of plant growth. The F_1 hybrids 'Lamongan-1' × 'Jombang' and 'Jombang' × 'Tulungagung-2' showed more leaves than all other sorghum genotypes. Tall genotypes are presumed to have a high number of leaves in line with the research of Siswanto (2015), who found that plant height is positively and significantly correlated with the number of leaves.

In different crop plants, heterosis and heterobeltiosis are widely used by the breeders to compare F_1 hybrids with their parental genotypes. Utomo *et al*. (2018) reported that the occurrence of heterosis is caused by the expression of genes that are passed down by both parental genotypes to their offspring. On the basis of these speculations, heterotic effects can be used to determine whether the parental genotype can be used in crosses or not. In this study, the F_1 hybrid 'Lamongan-1' × 'Jombang' showed the highest positive heterotic effects compared with its mid- and better parents, followed by the F_1 hybrid 'Tulungagung-2' × 'Lamongan-1' with midparent heterosis for germination percentage. For seed weight, the F_1 hybrid 'Jombang' × 'Tulungagung-2' presented the highest positive heterotic effects as compared with its mid-parent. For the vertical and horizontal dimensions of the seeds, the F_1 hybrid 'Tulungagung-2' × 'Lamongan-1' showed a positive heterotic effect over its mid-parent.

The estimation of combining ability values is very useful for breeders in identifying the best crossbreeding parents to obtain superior offspring. The difference in GCA and SCA values for each tested sorghum genotype could be attributed to the influence of several factors, i.e., the genotypes used in the cross, the observed characters, the model of the cross, and the combining ability method used (Rini *et al*., 2017; Izzah *et al*., 2019). The analysis of GCA, SCA, and reciprocal effects revealed that SCA effects were significantly different for the vertical and horizontal diameters of the seeds. The significant SCA variances indicated that the diversity of the cross combinations resulted in offspring that are better or worse than their parental genotypes (Budiyanti *et al*., 2016). The significantly different GCA and SCA for these three characters indicated the presence of additive and nonadditive gene action (Mishra *et al*., 2008). Another report showed that the significance of GCA and SCA implies that additive and dominance effects contribute to the genetic control for the character (Sahid *et al*., 2020).

In terms of GCA effects, the parental genotype 'Tulungagung-2' had a high positive GCA for seed weight and seed horizontal diameter, whereas the genotype 'Lamongan-1' had a high positive GCA for seed vertical diameter. These results indicated that the parental genotype 'Tulungagung-2' is the best general combiner for seed weight and seed horizontal diameter. Zare *et al*. (2011) reported that genotypes with positive GCA have good capability to combine with other genotypes for certain characters. In general, a cross between two parents with high GCA values produces hybrids with high SCA due to the interaction effect between positive × positive alleles (Hairmansis and Aswidinnoor, 2015). However, the present research showed that the parental genotype 'Tulungagung-2', despite being a good general combiner, did not produce F_1 hybrids with the highest positive SCA values, and all the hybrids revealed negative SCA effects for the studied traits.

Simamarta (2010) stated that the similarity distance is low if it ranges between 60% and 65%. Broadly speaking, the analysis of quantitative and qualitative character clusters revealed a similarity level of 13.13%. In the cluster analysis results presented in Figure 1, the F_1 hybrid 'Jombang' × 'Lamongan-1' had 89.49% similarity with the parental genotype 'Jombang' (G9), and the hybrid 'Jombang' × 'Tulungagung-2' had the similarity of 78.13% with the genotype 'Jombang' (G9) and the hybrid 'Jombang' × 'Lamongan-1'. The F_1 hybrids 'Tulungagung-2' × 'Lamongan-1' and 'Tulungagung-2' × 'Jombang' had 65.28% similarity with the female parental genotype 'Tulungagung-2' (G8) likely due to the genetic makeup of the genotypes. Anderson and Joseph (2016) and Siswanto *et al*. (2015) opined that genetic makeup and environmental and growing conditions can affect the potential yield of the sorghum genotypes. Mangoendidjojo (2003) stated that the highest diversity could be obtained in crosses between distantly related genotypes.

CONCLUSIONS

The parental genotypes and their F_1 hybrids revealed significant differences in seed weight and seed diameter and nonsignificant differences in germination percentage and seed setting. The parental genotype 'Tulungagung-2' and its F_1 hybrids 'Jombang' × 'Tulungagung-2', 'Tulungagung-2' × 'Lamongan-1', and 'Jombang' × 'Tulungagung-2' exhibited the highest germination percentage, seed setting, seed weight, and seed diameter. The F_1 hybrids 'Lamongan-1' × 'Jombang', 'Tulungagung-2' × 'Lamongan-1', 'Tulungagung-2' × 'Jombang', 'Jombang' × 'Lamongan-1', and 'Jombang' × 'Tulungagung-2' showed higher germination percentages of 100%, 88.00, 09%, 66.67%, 75.00%, and 83.33%, respectively, than the F_1 hybrid 'Lamongan-1' × 'Tulungagung-2', which had zero germination. The parental genotype 'Tulungagung-2' had the highest GCA effects and was identified as a good general paternal and maternal parent for the production of promising F_1 hybrids. The hybrid 'Jombang' × 'Lamongan-1' had the lowest negative SCA values for all the characters and is thus recommended for improving grain yield. Cluster analysis divided all of the sorghum genotypes into two large groups with 13.13% similarity. The F_1 hybrid 'Jombang' × 'Lamongan-1' had the greatest similarity with the parental genotype 'Jombang' (G9, 89.49%).

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