

Estimation of genetic parameters and heterosis through line \times tester crosses of national sorghum varieties and local Indonesian cultivars

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Abstract. *Rachman F, Trikoesoemaningtyas, Wirnas D, Reflinur. 2022. Estimation of genetic parameters and heterosis through line \times tester crosses of national sorghum varieties and local Indonesian cultivars. Biodiversitas 23: 1588-1597.* Diverse gene sources possessed by local sorghum cultivars are potentially useful for superior varieties development. This study aimed to determine the genetic parameters and heterosis of sorghum lines derived from national varieties and local cultivars crosses. A total of eight F1 hybrids derived from line \times tester mating design with four lines (PI-150-20A, Soraya 3 IPB, Kawali, Bioguma 1 Agritan) and two testers (Pulut 3 and Pulut 5) were used in the present study. This experiment was arranged in a randomized complete block design (RCBD) with three replications. Results showed that several agronomical important traits, such as plant height, leaf number, days to flowering, days to harvesting, panicle length, panicle diameter, and 1000-grain weight were significantly affected by additive gene action, while others by non-additive gene action. Based on field observation, three out of six parental lines showed the best performance of grain yields traits. Of these, Soraya 3 IPB \times Pulut 5 and Bioguma 1 Agritan \times Pulut 5 crosses were the best cross combination showing high values for both combining ability and heterosis parameters. These findings would help breeders to determine the selection methods for desirable traits and cross combinations to develop a new variety with high yield performance.

Keywords: Crossbreeding, inheritance, local germplasm, quantitative genetics

INTRODUCTION

Cereals and tuber crops are the primary sources of carbohydrates. Sorghum is one of the alternative cereal crops that can be used as carbohydrate sources, which is closely related to rice, corn, and wheat (Andriani and Isnaini 2013). Sorghum has higher nutritional content than rice in protein, vitamins, and essential minerals (Widowati 2010). In addition, Etuk et al. (2012) also stated that sorghum contains 8.90%-10.48% crude protein, 2.50%-3.70% fat, 1.40%-3.01% fiber, and 61.24%-76.60% sugar. Based on vitamin contents, FAO (1995) reported 100 g of sorghum seeds contained 0.13 mg of vitamin B2, 4.5 mg of vitamin B3, and 0.47 mg of vitamin B6.

Currently, the available genetic resources of sorghum consist of released national varieties, introduced accessions, collection genotypes from several research institutes, and local cultivars (Talanca and Andayani 2013). The local cultivars were developed in certain specific locations and mainly developed at the farmer level. Local Indonesian sorghum cultivars had several advantages, such as environmental stress tolerances (Lestari et al. 2014; Benggu and Nguru 2018), high ethanol yield (Agung et al. 2014), pathogen resistances (Sofiah 2021), and contain polyphenols, anthocyanins, and tannin (Mukkun et al. 2021). Eastern Indonesia dominates the sorghum development because such areas are suitable for agro-

climatic conditions for sorghum growth (Subagio and Aqil 2013). The diversity of local Indonesian sorghum cultivars is widely distributed in East Java (Sulistiyawati et al. 2019; Maftuchah et al. 2021), Yogyakarta (Martiwati et al. 2020), West Nusa Tenggara (Fitrahtunnisa et al. 2020), and East Nusa Tenggara (Mukkun et al. 2018; Tnunay et al. 2019).

Superior sorghum varieties generally have early maturity, medium height, and good cooking qualities (Tabri and Zubachtirodin 2013). These varieties can be developed by several breeding strategies, including crosses, mutation, and genetic methods transformation. However, crossing is considered to be one of the simplest methods for expanding genetic diversity (Syukur et al. 2012). Crossing with a particular mating design could also be used to estimate heterosis, combining ability, and gene action (Acquaah 2007; Syukur et al. 2012). Selection of the mating design method is important based on the amount of information on genetic parameters, combining ability, and heterosis.

Genetic parameters can be estimated using line \times tester mating design, where several lines will be crossed over testers. This method can be used to estimate the combining ability, heritability, and gene action that influenced traits (Singh and Chaudhary 1979). This mating design is the simplest method but provides complete genetic information because of the availability of full-sibs and half-sibs' information (Nduwumuremyi et al. 2013; Kose 2017;

Yehia and Elhashash 2019). In sorghum, several studies used line × tester mating design for estimating genetic parameters (Muturi et al. 2019; Sen et al. 2019), combining ability (Rini et al. 2017; SaadAbdel-Aty et al. 2018; Suguna et al. 2021), and heterosis values (Jarwar et al. 2017; Rehana et al. 2019; Abebe et al. 2020).

The yield potential of local Indonesian sorghum cultivars is 40% lower than that of national varieties (Hidayanti 2020), but may have various desirable traits that can be used in sorghum breeding programs. Although their yield potential is low, various desirable traits that exist in local cultivars would be potential benefit for other important traits improvements in sorghum breeding program. It is expected that new varieties with high production, good nutritional content, and tolerance to environmental stresses, etc. can be developed by utilization of local sorghum cultivars as donors in crossing. To date, there is no genetic information available for generating sorghum varieties using local Indonesian sorghum cultivars. For this reason, genetic studies related to estimation of genetic parameters through line × tester analysis are needed to provide basic information for breeders in sorghum improvement. Therefore, combining ability should be taken into consideration as an important basis for the crossbreeding parents' selection. This study aimed to determine the genetic parameters and heterosis of sorghum lines derived from national varieties and local cultivars crosses.

MATERIALS AND METHODS

Study area

The F₁ hybrids and their parental were evaluated from March to July 2021 at Cikarawang experimental field, IPB University, Bogor, West Java, Indonesia. The field site was located at an altitude of 165 m asl. with clay-loam latosol soil (Melati et al. 2021). The agro-climates condition of research sites were listed in Table 1. Post-harvest observation was conducted at Plant Breeding Laboratory, IPB University, Bogor, West Java, Indonesia.

Plant materials

The four sorghum lines (PI-150-20A, Soraya 3 IPB, Kawali, Bioguma 1 Agritan) and two testers (Pulut 3, Pulut 5) were crossed through line × tester mating design and resulted eight F₁ hybrids (Table 2). PI-150-20A was chosen to represent the introduced accessions, which have been widely used for short sorghum development (Trikoesoemaningtyas et al. 2017). Soraya 3 IPB represents the IPB University breeding lines, which has acid-dry land tolerance (Sitanggang 2013) and has ratoon ability (Ardiyanti et al. 2019), while Kawali and Bioguma 1 Agritan are representatives of national released variety. Pulut 3 and Pulut 5 were local cultivars collected from West Nusa Tenggara and West Java, respectively. These cultivars were chosen because they have the advantage of pests resistance and are claimed by farmers to have waxy properties (Sofiah 2021).

Table 1. The agro-climates condition of research sites

Months	T _{min} (°C)	T _{max} (°C)	T _{avg} (°C)	RH (%)	RR (mm)	SS (hours)
March 2021 ¹⁾	22.6	31.9	26.2	87.4	91.1	51.9
April 2021	22.3	31.9	26.2	84.9	213.5	128.3
May 2021	23.0	32.4	26.8	84.4	406.0	176.3
June 2021	22.0	31.7	25.9	86.1	281.0	171.6
July 2021 ²⁾	21.6	31.9	25.9	81.5	3.5	42.4

Note: ¹⁾20-31 March 2021, ²⁾1-6 July 2021, T_{min}: minimum temperature, T_{max}: maximum temperature, T_{avg}: average temperature, RH: relative humidity, RR: rainfall, SS: sunshine duration (Source: BMKG 2021)

Table 2. Sorghum genotypes used in this study

Genotypes	Notes	Source
PI-150-20A × Pulut 3	F ₁ Hybrids	IPB University
PI-150-20A × Pulut 5	F ₁ Hybrids	IPB University
Soraya 3 IPB × Pulut 3	F ₁ Hybrids	IPB University
Soraya 3 IPB × Pulut 5	F ₁ Hybrids	IPB University
Kawali × Pulut 3	F ₁ Hybrids	IPB University
Kawali × Pulut 5	F ₁ Hybrids	IPB University
Bioguma 1 Agritan × Pulut 3	F ₁ Hybrids	IPB University
Bioguma 1 Agritan × Pulut 5	F ₁ Hybrids	IPB University
PI-150-20A	Introduction accession	ICRISAT
Soraya 3 IPB	Breeding lines	IPB University
Kawali	National variety	ICERI, IAARD
Bioguma 1 Agritan	National variety	ICABIOGRAD, IAARD
Pulut 3	Local cultivar	West Nusa Tenggara
Pulut 5	Local cultivar	West Java

Procedures

A total of 14 genotypes were arranged in a randomized complete block design (RCBD) with three replications. The 2.25×1.20 m plot was planted with 3 rows, where the evaluated genotype rows were planted between the border rows with a plant spacing of 75×15 cm. Fertilizer application was conducted with 46 kg N ha⁻¹, 36 kg P₂O₅ ha⁻¹, and 60 kg K₂O ha⁻¹ as basal dose, and 23 kg N ha⁻¹ were applied 4 weeks after planting. The crop pests were controlled mechanically and chemically. The panicles were harvested when a black layer in the grains appeared. This standard cultivation for optimum sorghum production was carried out according to Wirnas et al. (2021) with modification. Each plot consisted of 8 samples for agronomic observation. A total of ten sorghum agronomical traits of which three traits (plant height, leaf number, and stem diameter) and seven traits (days to flowering, days to harvesting, panicle length, panicle diameter, dry panicle weight at 15% moisture content, 1000-grain weight, and grain yield per panicle) were observed at vegetative and generative stage, respectively. All the traits were recorded according to the guidelines recommended by UPOV (2014).

Data analysis

The data were analyzed with analysis of variance (ANOVA) and a line \times tester analysis for estimating the genetic variance, degree of dominance, broad-sense heritability, and narrow-sense heritability. The line \times tester analysis, general combining ability (GCA) and specific combining ability (SCA) effects were calculated based on Kempthorne (1957) and Singh and Chaudhary (1979) using R with Agricolae package (de Mendiburu and Simon 2015; de Mendiburu 2021). The t-student test was conducted to test the general combining ability and specific combining ability to zero value (Kenga et al. 2004). These analyzes were conducted using Microsoft Excel.

Mid-parent heterosis (MPH) and best-parent heterosis (BPH) were analyzed using AGD-R (Rodríguez et al. 2015) then visualized in heatmap using R with ggplot2 package (Wickham 2016). Pearson's correlation for MPH values and BPH values between several agronomic traits were conducted according to Su et al. (2017) using R with Agricolae package (de Mendiburu and Simon 2015; de Mendiburu 2021).

RESULTS AND DISCUSSION

Estimation of genetic parameters

The results of ANOVA showed differences between the parents of the cross and the hybrids (P vs F₁) for all traits, except for days to flowering, days to harvesting, panicle length, panicle diameter, and 1000-grain weight. This result shows that the data used was suitable for combining ability study. It also indicates that these traits had a good inheritance for heterotic effects from parents to hybrids (Mondal et al. 2009; Sanghera and Hussain 2012). The 1% level of significant differences among hybrids was shown in plant height, leaf number, stem diameter, days to flowering, days to harvesting, and 1000-grain weight. In the line component, the 1% significant difference was shown in plant height, leaf number, days to flowering, days to harvesting, and panicle length. The 5% level of significant difference was shown in 1000-grain weight. The tester component showed a significant difference in plant height and panicle length traits (Table 3). The significant line and tester components related to a large general combining ability (GCA) variance in controlling related traits, and additives gene effect affected these traits (Panwar 2005). The line \times tester interaction component significantly affected the stem diameter (Table 3). The significance of line tester interaction would be related to specific combining ability (SCA) (Suguna et al. 2021). In this case, SCA will significantly affect the expression of the traits, which is strongly influenced by non-additive variance. The SCA is associated with heterosis value (Krystkowiak et al. 2009; Huang et al. 2015), so heterosis breeding for these traits might be conducted.

Based on the contribution of lines, testers, and their interactions to the total hybrid variance, the line component largely contributed to all traits, except stem diameter, dry panicle weight, and 1000-grain weight. The large proportion of lines predicting the selection of line parents

requires more significant consideration than tester parents. The larger contribution of the tester component was shown on stem diameter, so the selection of tester parents for manipulating this trait needs to be considered than the selection of line parents. A large proportion of the line \times tester interaction components was found on dry panicle weight and grain yield per panicle (Table 3). A large proportion of the line \times tester interaction components predict an SCA effect and non-additive variance effect. Therefore, variety development for yield components could be directed to hybrid varieties. These results were also in line with Rini et al. (2017) and Khadi et al. (2018).

Greater GCA variances than SCA variances found on plant height, leaf number, days to flowering, days to harvesting, panicle length, panicle diameter, and 1000-grain weight. It caused the ratio of the GCA variance to the SCA variance to be more than one, while the degree of dominance was less than one (Table 4). It explains that additive gene strongly influences these traits, so parental selection becomes more critical for improving these traits. A similar result was also found in Prabhakar et al. (2013) and Ingle et al. (2018). Meanwhile, stem diameter, dry panicle weight, and grain yield per panicle had a smaller GCA/SCA variance ratio, so the dominance degree is more than one (Table 4). Based on this result, the action of non-additive genes had a more significant role in controlling these traits. It should be considered when developing hybrids variety for yield components. Ni et al. (2012) reported that non-additive genes influenced 1000-grain weight and the number of grains per panicle.

The broad-sense heritability of all traits except panicle length and panicle diameter was relatively high (ranged between 63-98%) (Table 4). It shows that there was a considerable genetic influence in controlling these traits. A high value of broad-sense heritability indicates that the population has high genetic variability and that selection can be carried out effectively. If the broad-sense heritability value was relatively low, the population's genetic variability was also quite low (Usman et al. 2017). The formation of new populations for increasing genetic diversity for related traits needs to be done. Moreover, low broad-sense heritability indicates a large environmental influence on the observed phenotype, so selection based on related traits will be ineffective due to masking effect from environment (Devesh et al. 2018).

The narrow-sense heritability for stem diameter, dry panicle weight, and grain yield per panicle was very low compared to the broad-sense heritability (Table 4). A very large non-additive affected these traits was found, so it can be manipulated for utilizing hybrid breeding. In contrast, other traits had a large narrow-sense heritability indicating the significant role of additive genes action. Selection for these traits improvement would give a higher genetic gain as Mohammed et al. (2015) stated. In early generations, traits with low narrow-sense heritability were highly affected by dominant genes, so selection at this condition will become inefficient. Therefore, selection for the related traits through the bulk selection method must be conducted in advance generation (F₆ or F₇) (Acquaah 2007) because fixation of additive genes occurred in later generations

making it possible to efficiently produce a good selection response and genetic gain (Acquaah 2007; Dubey and Rangaiah 2019).

Estimation of combining ability

Genotype PI-150-20A was a significantly good general combiner for short plants and early maturity among the lines, such as days to flowering and days to harvesting. In addition, Kawali was a significantly good general combiner for increasing leaf number. Furthermore, Soraya 3 IPB was a good combiner for increasing stem diameter and panicle length. Moreover, Bioguma 1 Agritan was a good combiner for panicle diameter, dry panicle weight, 1000-grain weight, and grain yield per panicle. The result showed that Bioguma 1 Agritan can be used as female parents for high-yielding varieties, whereas PI-150-20A can be used as a female parent to produce short plants and early maturity. Besides that, Pulut 3 was a good combiner for increasing stem diameter and early maturity traits, such as days to

flowering and days to harvesting (Table 5). Estimation of parents' GCA could assist in identifying superior parents for the formation of superior genotypes based on the number of favorable alleles that have additive gene action (Narasimhamurthy and Gowda 2013).

Specific combining ability (SCA) is one of the genetic parameters that reflects the influence of non-additive genes towards traits. It can be used to determine the best cross combination for achieving plant breeding program objectives. The SCA effect is more considered in hybrid development than the GCA effect (Rini et al. 2017). There were variations on the SCA effect for all traits (Table 5). Soraya 3 IPB × Pulut 5 and Kawali × Pulut 3 had higher SCA effects for stem diameter and leaf number, respectively. These combinations might be the best for improving vegetative traits, such as forage yield. The high SCA for the vegetative trait is in line with Mohammed (2009) for sorghum forage development, especially for ethanol production and animal feed.

Table 3. Analysis of variance and contribution from each component to hybrid variance for various agronomic traits in sorghum

Source of variation	df	PH	LN	SD	DTF	DTH	PL	PD	DPW	1000-GW	GYP
Replication	2	226.65**	0.05 ^{ns}	0.10**	0.64 ^{ns}	0.60 ^{ns}	6.85 ^{ns}	1.15 ^{ns}	290.67 ^{ns}	15.80**	233.43 ^{ns}
Genotype	13	7138.67**	10.54**	0.07**	90.45**	151.03**	8.27 ^{ns}	0.29 ^{ns}	430.28**	42.94**	244.74**
Parent (P)	5	8258.38**	10.38**	0.07**	75.87**	137.60**	15.48 ^{ns}	0.32 ^{ns}	507.88**	51.57**	296.09*
P vs F ₁	1	4249.50**	4.77**	0.14**	8.65 ^{ns}	14.00 ^{ns}	0.15 ^{ns}	0.56 ^{ns}	1095.93**	2.90 ^{ns}	414.38**
F ₁	7	6751.61**	11.48**	0.06**	112.55**	180.20**	4.29 ^{ns}	0.23 ^{ns}	279.76 ^{ns}	42.50**	183.82 ^{ns}
Line (L)	3	15533.07**	26.02**	0.03 ^{ns}	260.50**	417.67**	8.94**	0.29 ^{ns}	105.14 ^{ns}	95.25*	66.85 ^{ns}
Tester (T)	1	583.42*	0.45 ^{ns}	0.20 ^{ns}	1.50 ^{ns}	1.50 ^{ns}	2.48*	0.47 ^{ns}	597.60 ^{ns}	0.31 ^{ns}	432.85 ^{ns}
L×T	3	26.22 ^{ns}	0.61 ^{ns}	0.02*	1.61 ^{ns}	2.28 ^{ns}	0.24 ^{ns}	0.09 ^{ns}	348.42 ^{ns}	3.82 ^{ns}	217.78 ^{ns}
Line (%)		98.60	97.17	17.44	99.20	99.34	89.37	54.55	16.11	96.05	15.59
Tester (%)		1.24	0.56	44.42	0.19	0.12	8.26	29.21	30.52	0.10	33.64
L × T (%)		0.17	2.28	38.14	0.61	0.54	2.37	16.25	53.38	3.85	50.78

Note: df: degree of freedom, **significant at level 1%, *significant at level 5%, ^{ns}: not significant at level 5%, PH: plant height, LN: leaf number, SD: stem diameter, DTF: days to flowering, DTH: days to harvesting, PL: panicle length PD: panicle diameter, DPW: dry panicle weight, 1000-GW: 1000-grain weight, GYP: grain yield per panicle

Table 4. Estimation of genetic components of variance, degree of dominance, and heritability for various agronomic traits in sorghum

Genetic components	PH	LN	SD	DTF	DTH	PL	PD	DPW	1000-GW	GYP
σ^2 lines	2584.48	4.23	-0.01	43.15	69.23	1.45	0.03	-40.55	15.24	-25.16
σ^2 testers	46.43	-0.01	0.01	-0.01	-0.07	0.19	0.03	20.77	-0.29	17.92
σ^2 GCA	392.32	0.63	0.00	6.47	10.38	0.24	0.01	-4.01	2.26	-1.98
σ^2 SCA	-7.89	0.10	0.01	-0.93	-0.56	-2.25	-0.17	74.71	0.40	45.73
σ^2 GCA/ σ^2 SCA	-49.70	6.14	0.03	-7.00	-18.57	-0.10	-0.05	-0.05	5.65	-0.04
σ^2 additive	784.64	1.27	0.00	12.94	20.76	0.47	0.02	-8.01	4.51	-3.96
σ^2 dominance	-7.89	0.10	0.01	-0.93	-0.56	-2.25	-0.17	74.71	0.40	45.73
Degree of dominance	0.00	0.29	4.09	0.00	0.00	0.00	0.00	NA	0.30	NA
h_{bs}^2	0.98	0.93	0.73	0.90	0.94	0.17	0.08	0.64	0.85	0.63
h_{ns}^2	0.98	0.86	0.04	0.90	0.94	0.17	0.08	0.00	0.78	0.00

Note: h_{bs}^2 : broad-sense heritability, h_{ns}^2 : narrow-sense heritability, NA: not applicable, PH: plant height, LN: leaf number, SD: stem diameter, DTF: days to flowering, DTH: days to harvesting, PL: panicle length, PD: panicle diameter, DPW: dry panicle weight, 1000-GW: 1000-grain weight, GYP: grain yield per panicle

Table 5. General combining ability (GCA) and specific combining ability (SCA) effect for various agronomic traits in sorghum

Genotypes	PH	LN	SD	DTF	DTH	PL	PD	DPW	1000-GW	GYP
Line										
PI-150-20A	-54.52**	-1.27**	0.00 ^{ns}	-6.58**	-8.17**	-0.34 ^{ns}	-0.19 ^{ns}	-0.89 ^{ns}	-3.04**	-0.98 ^{ns}
Soraya 3 IPB	-21.07**	-1.36**	0.06 ^{ns}	-4.58**	-6.17**	1.80 ^{ns}	-0.19 ^{ns}	1.48 ^{ns}	-0.80 ^{ns}	-0.51 ^{ns}
Kawali	10.47*	3.06**	0.03 ^{ns}	6.92**	8.00**	-0.54 ^{ns}	0.16 ^{ns}	-5.27 ^{ns}	-1.97*	-3.19 ^{ns}
Bioguma 1 Agritan	65.12**	-0.43 ^{ns}	-0.09 ^{ns}	4.25**	6.33**	-0.91 ^{ns}	0.22 ^{ns}	4.68 ^{ns}	5.82**	4.69 ^{ns}
S.E GCA	2.88	0.22	0.05	0.86	0.81	1.08	0.32	4.55	0.66	3.67
S.E (g _i – g _j)	4.08	0.32	0.07	1.21	1.15	1.53	0.45	6.44	0.93	5.18
Tester										
Pulut 3	4.93 ^{ns}	0.14 ^{ns}	-0.09 ^{ns}	-0.25 ^{ns}	-0.25 ^{ns}	-0.32 ^{ns}	-0.14 ^{ns}	-4.99 ^{ns}	-0.11 ^{ns}	-4.25 ^{ns}
Pulut 5	-4.93 ^{ns}	-0.14 ^{ns}	0.09 ^{ns}	0.25 ^{ns}	0.25 ^{ns}	0.32 ^{ns}	0.14 ^{ns}	4.99 ^{ns}	0.11 ^{ns}	4.25 ^{ns}
S.E GCA	2.04	0.16	0.04	0.61	0.57	0.76	0.22	3.22	0.47	2.59
S.E (g _i – g _j)	2.88	0.22	0.05	0.86	0.81	1.08	0.32	4.55	0.66	3.67
Cross combination										
PI-150-20A × Pulut 3	-0.14 ^{ns}	-0.09 ^{ns}	-0.05 ^{ns}	0.25 ^{ns}	0.25 ^{ns}	0.09 ^{ns}	-0.02 ^{ns}	4.96 ^{ns}	0.67 ^{ns}	4.52 ^{ns}
PI-150-20A × Pulut 5	0.14 ^{ns}	0.09 ^{ns}	0.05 ^{ns}	-0.25 ^{ns}	-0.25 ^{ns}	-0.09 ^{ns}	0.02 ^{ns}	-4.96 ^{ns}	-0.67 ^{ns}	-4.52 ^{ns}
Soraya 3 IPB × Pulut 3	-1.13 ^{ns}	-0.39 ^{ns}	-0.08 ^{ns}	-0.75 ^{ns}	-0.42 ^{ns}	0.14 ^{ns}	-0.04 ^{ns}	-7.97 ^{ns}	-1.13 ^{ns}	-6.33 ^{ns}
Soraya 3 IPB × Pulut 5	1.13 ^{ns}	0.39 ^{ns}	0.08 ^{ns}	0.75 ^{ns}	0.42 ^{ns}	-0.14 ^{ns}	0.04 ^{ns}	7.97 ^{ns}	1.13 ^{ns}	6.33 ^{ns}
Kawali × Pulut 3	-1.71 ^{ns}	0.35 ^{ns}	0.14 ^{ns}	0.42 ^{ns}	-0.58 ^{ns}	0.07 ^{ns}	0.17 ^{ns}	7.89 ^{ns}	0.43 ^{ns}	5.74 ^{ns}
Kawali × Pulut 5	1.71 ^{ns}	-0.35 ^{ns}	-0.14 ^{ns}	-0.42 ^{ns}	0.58 ^{ns}	-0.07 ^{ns}	-0.17 ^{ns}	-7.89 ^{ns}	-0.43 ^{ns}	-5.74 ^{ns}
Bioguma 1 Agritan × Pulut 3	2.98 ^{ns}	0.13 ^{ns}	-0.00 ^{ns}	0.08 ^{ns}	0.75 ^{ns}	-0.29 ^{ns}	-0.11 ^{ns}	-4.88 ^{ns}	0.03 ^{ns}	-3.94 ^{ns}
Bioguma 1 Agritan × Pulut 5	-2.98 ^{ns}	-0.13 ^{ns}	0.00 ^{ns}	-0.08 ^{ns}	-0.75 ^{ns}	0.29 ^{ns}	0.11 ^{ns}	4.88 ^{ns}	-0.03 ^{ns}	3.94 ^{ns}
S.E. SCA	4.08	0.32	0.07	1.21	1.15	1.53	0.45	6.44	0.93	5.18
S.E (S _{ij} – S _{kl})	5.77	0.45	0.10	1.71	1.62	2.16	0.63	9.10	1.32	7.33

Note: SE: standard error, **significant at level 1% based on t-student test, *significant at level 5% based on t-student test, ^{ns}: not significant at level 5%, PH: plant height, LN: leaf number, SD: stem diameter, DTF: days to flowering, DTH: days to harvesting, PL: panicle length, PD: panicle diameter, DPW: dry panicle weight, 1000-GW: 1000-grain weight, GYP: grain yield per panicle

Bioguma 1 Agritan × Pulut 5 was the combination with the lowest SCA effect for plant height and days to harvesting, while Soraya 3 IPB × Pulut 3 for days to flowering. It shows that the combination of these crosses can be used for hybrids with short plants and early maturity. Mengistu et al. (2020) also found the presence of early maturity in hybrids compared to their parents. At the same time, sorghum with early maturity traits would potentially produce more grain and increase harvest index as stated by Derese et al. (2018). The best combination for high-yielding hybrids development based on the SCA effect was found. Kawali × Pulut 3 was the best combination for panicle length and panicle diameter, respectively. Soraya 3 IPB × Pulut 5 had the highest SCA effect for dry panicle weight, 1000-grain weight, and grain yield per panicle. A similar result was also found in other studies (Kenga et al. 2004; Prabhakar et al. 2013; Amelework et al. 2017)

Cross combination with the best SCA did not originate from good general combiner parents for enhancing all attributes except plant height. On leaf number and dry panicle weight, poor × poor general combiner produced the highest SCA. In contrast, poor × good general combiner produced the highest SCA on panicle length. Cross combination with strong SCA effects was categorized as good general combiners if they were inherited from one or both parents. However, due to the lack of higher-order additive interaction, this does not always occur (Kenga et al. 2004). Epistasis generated by additive-dominant interactions gene was assumed to cause the poor × good general combiner with the highest SCA, while non-additive gene interactions for a poor × poor general combiner

(Kumar et al. 2011). As a result, choosing the best hybrid combination cannot be explained solely based on GCA values but must also consider SCA values. The number of beneficial alleles increase in hybrids formed from the pairing of parents with the best GCA values and good SCA values (Kamara et al. 2021).

Estimation of heterosis among progenies

The mid-parent heterosis (MPH) and best-parent heterosis (BPH) of plant height were generally ranged negative to zero value in all combinations of crosses, except for Bioguma 1 Agritan × Pulut 3 (Figure 1). The lowest heterosis for plant height was found in PI-150-20A × Pulut 5. It implies that the hybrids produced sorghum with a shorter plant height, allowing farmers to easily maintain and harvest the crop (Hashimoto et al. 2021). Gaddameedi et al. (2020) also reported a similar result for plant height heterosis in sorghum. Wirnas et al. (2021) stated that sorghum with short to medium plant height was recommended for sorghum cultivation for food purposes. Farmers also preferred it because it also has early maturity.

The MPH and BPH values for stem diameter ranged from -10.1% to 32.03% and -16.41% to 22.14%, respectively. This kind of similar result was also found by Prakash et al. (2010) and Paliwal et al. (2016). The highest value of heterosis is found on Soraya 3 × Pulut 5 and PI-150-20-A × Pulut 5 (Figure 1), so these hybrids might produce a larger stem diameter. The thicker stem was a desired trait, as it allowed sorghum to perform better and be resistant to lodging (Wirnas et al. 2021). Shah et al. (2016) also stated that plant height, stem diameter, and stem wall thickness contribute toward lodging resistance in cereal. At the same

time, Rivera-Burgos et al. (2019) discovered that a larger stem diameter produced more ethanol.

The MPH values ranged from -5.38% to 16.37% for leaf number traits, while the BPH values ranged from -9.04% to 7.58%. The low value of heterosis, both negative and positive is not in line with Sheunda et al. (2019). Heterosis is influenced by dominance gene action (Hashimoto et al. 2021) and dominance-dominance epistasis (Boeven et al. 2020). Based on this study, leaf number is highly affected by the additive effect. Other than that, the best positive heterosis was found in Soraya 3 IPB × Pulut 5 and PI-150-20A × Pulut 5 (Figure 1), so these hybrids would produce a higher number of leaves than their parents. An increase in the number of leaves was a desirable trait and it is expected to increase grain yield through a high photosynthetic rate (Fang et al. 2018). A large number of leaves is also associated with high biomass yield (Abubakar and Bubuche 2013; Makanda 2017).

The MPH and BPH values for days to flowering traits ranged from -7.49% to 8.85% and -12.82% to 5.18%, respectively. Also, the MPH and BPH values for days to harvesting ranged from -9.21% to 4.41% and -15.18% to 1.65%, respectively. In this study, four hybrids had negative MPH values, while five had negative BPH values for both traits (Figure 1). Significant and negative heterosis values in sorghum were also observed by Sheunda et al. (2019), Crozier et al. (2020), and Veldandi et al. (2021). Soraya 3 IPB × Pulut 3 and PI-150-20A × Pulut 3 were hybrids with the lowest MPH and BPH values for both traits. These hybrids might be developed for early maturity varieties. The influence of additive genes that control these two features caused sorghum progenies to mature early relative to their parents (Makanda et al. 2009).

The MPH and BPH values for panicle length ranged from -14.81% to 10.53% and -16.65% to -0.86%,

respectively. There are 75% and 100% hybrids with negative MPH and BPH values, respectively, and the development of this hybrid might decrease panicle length (undesired traits). This result was not in line with Sheunda et al. (2019) and Mengistu et al. (2020). Bioguma 1 Agritan × Pulut 3 is the progeny with the lowest MPH and BPH values (Figure 1). The MPH and BPH values for panicle diameter ranged from -12.75% to 3.10% and -17.14% to 2.69%, respectively. Kawali × Pulut 3 was the hybrid with the highest MPH and BPH values. Wirnas et al. (2021) stated that panicle diameter was one of the important morphological ideotypes related to high grain yielding. At the same time, PI-150-20A × Pulut 3 was the progeny with the lowest MPH and BPH values.

The MPH and BPH values for dry panicle weight ranged from -0.84% to 72.60% and -19.23% to 51.54%, respectively. All hybrids had positive MPH values except for Bioguma 1 Agritan × Pulut 3. While hybrids of Bioguma 1 Agritan × Pulut 3 and Kawali × Pulut 5 had negative BPH values. The best heterosis for dry panicle weight was found in the Soraya 3 IPB × Pulut 5 hybrid (Figure 1), so this combination would potentially produce sorghum hybrids with high yield. In the present study, positive heterosis for panicle weight might improve the traits of sorghum for high grain yielding. It is in agreement with Khadi et al. (2018) and Mengistu et al. (2020).

The MPH and BPH values of grain yield per panicle ranged from -6.38% to 64.12% and -20.86% to 46.98%, respectively. Similar results were also reported by Jaikishan et al. (2018) and Schaffasz et al. (2019). The hybrid with the highest heterosis for grain yield per panicle is Soraya 3 IPB × Pulut 5, which also had the highest heterosis for dry panicle weight. According to Enyew et al. (2021), grain yield per panicle had a highly significant positive correlation with panicle weight.

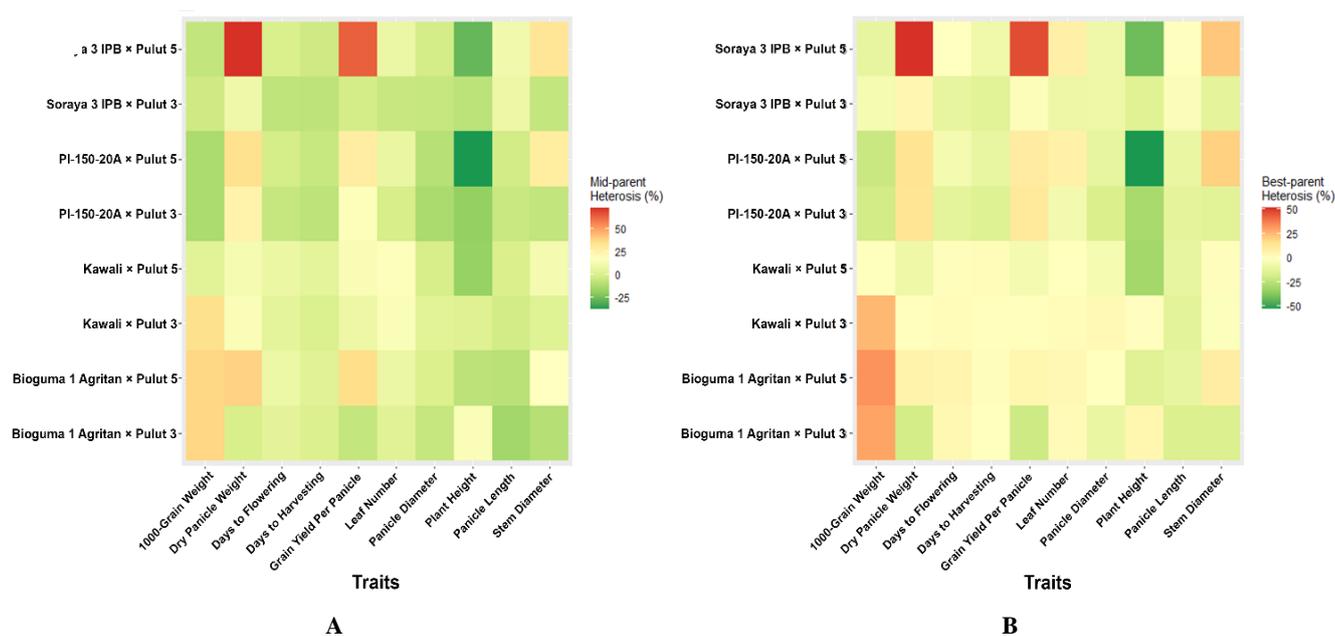


Figure 1. Heterosis heatmap from each cross combination for various agronomic traits in sorghum. A. Mid-parent heterosis, B. Best-parent heterosis

The MPH values range from -12.69% to 37.92% for 1000-grain weight. Four out of eight hybrids were found to have positive MPH values, namely Kawali × Pulut 3, Kawali × Pulut 5, Bioguma 1 Agritan × Pulut 3, and Bioguma 1 Agritan × Pulut 5. The BPH values ranged from -21.62% to 33.01%. Three hybrids were found to have positive BPH, namely Kawali × Pulut 3, Bioguma 1 Agritan × Pulut 3, and Bioguma 1 Agritan × Pulut 5. Sorghum yield is influenced by several traits such as the number of plants in an area, the number of seeds per plant, grain yield per panicle, and the weight of 1000 grains as stated by Wang et al. (2019). Also, 1000-grain weight is highly correlated to yield (Mofokeng et al. 2019), and it is caused by the efficiency of photosynthetic accumulation in the seed endosperm (Putri et al. 2013). Overall, the present study revealed that hybrid development from local Indonesian sorghum cultivars and national varieties could improve sorghum grain productivity.

Based on heterosis Pearson's correlation analysis (Table 6), grain yield per panicle had a significant and positive correlation with stem diameter ($r = 0.87$ for MPH) and dry panicle weight ($r = 0.98$ for MPH and $r = 0.99$ for BPH). This result indicated that hybrids developed for high grain yield heterosis could improve other desirable traits, such as large stem diameter and high panicle weight. Heterosis of 1000-grain weight showed a significant and positive correlation with undesirable traits for grain yielding sorghum, such as plant height ($r = 0.82$ for MPH and $r = 0.84$ for BPH), days to flowering ($r = 0.71$ for MPH and $r = 0.77$ for BPH), and days to harvesting ($r = 0.79$ for BPH). Similarly, heterosis of panicle diameter was also correlated with days to harvesting ($r = 0.74$ for BPH). Hybrid development for high 1000-grain weight should be taken into consideration because it will have undesirable traits, such as tall plant height and late maturity. Wirnas et al. (2021) explained that the ideotype for selecting high-yielding sorghum was indicated by medium plant height (150-235 cm). Meanwhile, dual-purpose sorghum for grain and biomass yielding hybrids might be potentially developed due to this study revealed that an increase in

vegetative (plant height, stem diameter, leaf number) and maturity traits value has provided an increase in grain yield-related traits. This study is in agreement with the findings of Burks et al. (2013) which stated that late-maturing sorghum hybrids would produce higher biomass. Dual-purpose sorghum can be used as food from grain yield, feed and biofuel from biomass yield as reported by Chikuta et al. (2017) and He et al. (2020).

In conclusion, plant height, leaf number, days to flowering, days to harvesting, panicle length, panicle diameter, and 1000-grain weight in sorghum were significantly affected by additive gene action than non-additive gene action. Meanwhile, non-additive gene action had a significant effect on stem diameter, panicle dry weight, and grain yield per panicle. The broad-sense heritability for the traits ranged from 63-98%, and the narrow-sense heritability ranged from 0-98%. Based on field observation, three out of six parental lines showed the best performance of grain yields related traits. Of these, Soraya 3 IPB × Pulut 5 and Bioguma 1 Agritan × Pulut 5 crosses were the best cross combination showing high values for both combining ability and heterosis parameters. These findings would help breeders to determine the selection methods for desirable traits and cross combinations to develop a new variety with high yield performance.

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Table 6. Pearson's correlation of mid-parent heterosis (*below the diagonal*) and best-parent heterosis (*above the diagonal*) between various agronomic traits in sorghum

Traits	Correlation coefficient (r)									
	PH	LN	SD	DTF	DTH	PL	PD	DPW	GYP	1000-GW
PH		-0.31 ^{ns}	-0.69 ^{ns}	0.37 ^{ns}	0.46 ^{ns}	-0.47 ^{ns}	0.45 ^{ns}	-0.64 ^{ns}	-0.65 ^{ns}	0.84 ^{**}
LN	-0.09 ^{ns}		0.79 [*]	0.64 ^{ns}	0.42 ^{ns}	-0.04 ^{ns}	0.27 ^{ns}	0.35 ^{ns}	0.40 ^{ns}	0.13 ^{ns}
SD	-0.74 [*]	0.49 ^{ns}		0.29 ^{ns}	0.08 ^{ns}	0.43 ^{ns}	0.22 ^{ns}	0.67 ^{ns}	0.70 ^{ns}	-0.25 ^{ns}
DTF	0.32 ^{ns}	0.78 [*]	0.23 ^{ns}		0.93 ^{**}	-0.33 ^{ns}	0.68 ^{ns}	-0.22 ^{ns}	-0.15 ^{ns}	0.77 [*]
DTH	0.38 ^{ns}	0.75 [*]	0.13 ^{ns}	0.98 ^{**}		-0.47 ^{ns}	0.74 [*]	-0.46 ^{ns}	-0.37 ^{ns}	0.79 [*]
PL	-0.52 ^{ns}	-0.06 ^{ns}	0.37 ^{ns}	-0.47 ^{ns}	-0.41 ^{ns}		-0.06 ^{ns}	0.74 [*]	0.70 ^{ns}	-0.49 ^{ns}
PD	0.35 ^{ns}	0.68 ^{ns}	0.21 ^{ns}	0.71 [*]	0.72 [*]	0.08 ^{ns}		-0.18 ^{ns}	-0.12 ^{ns}	0.71 ^{ns}
DPW	-0.65 ^{ns}	0.16 ^{ns}	0.82 [*]	-0.05 ^{ns}	-0.17 ^{ns}	0.48 ^{ns}	0.08 ^{ns}		0.99 ^{**}	-0.54 ^{ns}
GYP	-0.65 ^{ns}	0.29 ^{ns}	0.87 ^{**}	0.10 ^{ns}	-0.01 ^{ns}	0.41 ^{ns}	0.16 ^{ns}	0.98 ^{**}		-0.51 ^{ns}
1000-GW	0.82 [*]	0.30 ^{ns}	-0.28 ^{ns}	0.71 [*]	0.69 ^{ns}	-0.63 ^{ns}	0.65 ^{ns}	-0.35 ^{ns}	-0.29 ^{ns}	

Notes: **significant at level 1%, *significant at level 5%, ^{ns}: not significant at level 5%, PH: plant height, LN: leaf number, SD: stem diameter, DTF: days to flowering, DTH: days to harvesting, PL: panicle length, PD: panicle diameter, DPW: dry panicle weight, 1000-GW: 1000-grain weight, GYP: grain yield per panicle

REFERENCES

- Abebe A, Wolde L, Gebreselassie W. 2020. Standard heterosis and trait association of maize inbred lines using line x tester mating design in Ethiopia. *Afr J Plant Sci* 14 (4): 192-204. DOI: 10.5897/AJPS2019.1839.
- Abubakar L, Bubuche TS. 2013. Correlation analysis of some agronomic traits for biomass improvement in sorghum (*Sorghum bicolor* L. Moench) genotypes in north-western Nigeria. *Afr J Agric Res* 8 (28): 3750-3756. DOI: 10.5897/AJAR2013.6858.
- Acquaah G. 2007. Principles of Plant Genetics and Breeding. Blackwell Publishing, Oxford.
- Agung IGAMS, Sardiana IK, Diara IW, Nurjaya IGMO. 2014. Residual effect of compost on ethanol production of sweet sorghum [*Sorghum bicolor* (L.) Moench] varieties and soil organic carbon at dryland farming area in Bali, Indonesia. *J Biol Agric Health* 4 (13): 96-102.
- Amelework B, Shimelis H, Laing M. 2017. Genetic variation in sorghum as revealed by phenotypic and SSR markers: Implications for combining ability and heterosis for grain yield. *Plant Genet Res* 15 (4): 335-347. DOI: 10.1017/S1479262115000696.
- Andriani A, Isnaini M. 2013. Morphology and growth phase of sorghum. In: Sumarno, Damardjati DS, Syam M, Hermano (Eds.). Sorghum: Innovation Technology and Development. IAARD Press, Jakarta. [Indonesian]
- Ardiyanti SE, Sopandie D, Wirnas D, Trikoesoemaningtyas. 2019. Ratoon productivity of sorghum breeding lines (*Sorghum bicolor* (L.) Moench). *IOP Conf Ser: Earth Environ Sci* 399: 012030. DOI: 10.1088/1755-1315/399/1/012030.
- Boeven PHG, Zhao Y, Thorwarth P, Liu F, Maurer HP, Gils M, Schachschneider R, Schacht J, Ebmeyer E, Kazman E, Mirdita V, Dörnte J, Kontowski S, Horbach R, Cöster H, Holzapfel J, Jacobi A, Ramgraber L, Reinbrecht C, Starck N, Varenne P, Starke A, Schürmann F, Ganal M, Polley A, Hartung J, Beier S, Scholz U, Longin CFH, Reif JC, Jiang Y, Würschum T. 2020. Negative dominance and dominance-by-dominance epistatic effects reduce grain-yield heterosis in wide crosses in wheat. *Sci Adv* 6: eaay4897. DOI: 10.1126/sciadv.aay4897.
- Benggu YI, Nguru ESO. 2018. Short communication: The tolerance level of local sorghum genotypes from Sabu-Raijua and Belu Districts, Indonesia to saline soil. *Trop Drylands* 2 (1): 1-4. DOI: 10.13057/tropdrylands/t020101.
- BMKG [Meteorology, Climatology, and Geophysical Agency of Indonesia]. 2021. Bogor Climatology Station Climatic Data. <http://dataonline.bmkg.go.id>.
- Burks PS, Felderhoff TJ, Viator HP, Rooney WL. 2013. The influence of hybrid maturity and planting date on sweet sorghum productivity during a harvest season. *Agron J* 105 (1): 263-267. DOI: 10.2134/agronj2012.0317.
- Crozier D, Hoggmann Jr L, Klein PE, Klein RR, Rooney WL. 2020. Predicting heterosis in grain sorghum hybrids using sequence-based genetic similarity estimates. *J Crop Improv* 34 (5): 600-617. DOI: 10.1080/15427528.2020.1748152.
- Chikuta S, Odong T, Kabi F, Rubaihayo P. 2017. Combining ability and heterosis of selected grain and forage dual purpose sorghum genotypes. *J Agric Sci* 9 (2): 122-130. DOI: 10.5539/jas.v9n2p122.
- de Mendiburu F, Simon R. 2015. *Agricolae*-Ten years of an open source statistical tool for experiments in breeding, agriculture and biology. *PeerJ* 3: e1404v1. DOI: 10.7287/peerj.preprints.1404v1.
- de Mendiburu F. 2021. *Agricolae*: Statistical Procedures For Agricultural Research. <https://cran.r-project.org/web/packages/agricolae/index.html>.
- Devesh P, Moitra PK, Shukla RS, Shukla SS, Pandey S, Arya G. 2018. Analysis of variability, heritability and genetic advance of yield, its components and quality traits in wheat. *Intl J Agric Environ Biotechnol* 754: 855-859.
- Derese SA, Shimelis H, Mwadzingeni L, Laing M. 2018. Agromorphological characterisation and selection of sorghum landraces. *Acta Agric Scand* 68 (7): 585-595. DOI: 10.1080/09064710.2018.1448884.
- Dubey S, Rangaiah S. 2019. Broad sense and narrow sense heritability in F4 and F5 generations of finger millet, *Eleusine coracana* (L.) Gaertn. *Electron J Plant Breed* 10 (1): 66-75. DOI: 10.5958/0975-928X.2019.00008.5.
- Enyew M, Feyissa T, Geleta M, Tesfaye K, Hammenhag C, Carlsson AS. 2021. Genotype by environment interaction, correlation, AMMI, GGE biplot and cluster analysis for grain yield and other agronomic traits in sorghum (*Sorghum bicolor* L. Moench). *PLoS One* 16 (10): e0258211. DOI: 10.1371/journal.pone.0258211.
- Etuk E, Ifeduba AV, Okata UE, Chiaka I, Charles OI, Okeudo NJ, Esonu BO, Udedibie ABI, Moreki J. 2012. Nutrient composition and feeding value of sorghum for livestock and poultry: A review. *J Anim Sci Adv* 2: 510-524.
- Fang X, Li Y, Nie J, Wang C, Huang K, Zhang Y, Zhang Y, She H, Liu X, Ruan R, Yuan R, Yi Z. 2018. Effects of nitrogen fertilizer and planting density on the leaf photosynthetic characteristics, agronomic traits and grain yield in common buckwheat (*Fagopyrum esculentum* M.). *Field Crop Res* 219: 160-168. DOI: 10.1016/j.fcr.2018.02.001.
- FAO [Food and Agriculture Organization of The United Nations]. 1995. Sorghum and Millets in Human Nutrition. Food and Agriculture Organization of The United Nations, Rome.
- Fitrahtunnisa, Mardian I, Rahmatullaila. 2020. Performance and utilization of local sorghum (*Sorghum bicolor* L.) in West Nusa Tenggara. *IOP Conf Ser: Earth Environ Sci* 484: 012092. DOI: 10.1088/1755-1315/484/1/012092
- Gaddameedi A, Phuke RM, Polavarapu KKB, Gorthy S, Subhasini V, Jagannathan J, Are AK. 2020. Heterosis and combining ability for grain Fe and Zn concentration and agronomic traits in sorghum [*Sorghum bicolor* (L.) Moench]. *J King Saud Univ* 32 (7): 2989-2994. DOI: 10.1016/j.jksus.2020.08.003.
- Hashimoto S, Wake T, Nakamura H, Minamiyama M, Araki-Nakamura S, Ohmae-Shinohara K, Koketsu E, Okamura S, Miura K, Kawaguchi H, Kasuga S, Sazuka T. 2021. The dominance model for heterosis explains culm length genetics in a hybrid sorghum variety. *Sci Rep* 11 (1): 4532. DOI: 10.1038/s41598-021-84020-3.
- He S, Tang C, Wang ML, Li S, Diallo B, Xu Y, Zhou F, Sun L, Shi W, Xie GH. 2020. Combining ability of cytoplasmic male sterility on yield and agronomic traits of sorghum for grain and biomass dual-purpose use. *Ind Crop Prod* 157: 112894. DOI: 10.1016/j.indcrop.2020.112894.
- Hidayanti N. 2020. Characterization of local varieties, national varieties and breeding lines of sorghum. [Thesis]. IPB University, Bogor. [Indonesian]
- Huang M, Chen L, Chen Z. 2015. Diallel analysis of combining ability and heterosis for yield and yield components in rice by using positive loci. *Euphytica* 205: 37-50. DOI: 10.1007/s10681-015-1381-8.
- Ingle KP, Gahukar SJ, Khelurkar VC, Ghorade RB, Kalpande VV, Jadhav PV, Moharil MP. 2018. Heterosis and combining ability for grain yield trait in Rabi sorghum [*Sorghum bicolor* (L.) Moench] using line x tester mating design. *Int J Curr Microbiol App Sci* 6: 1925-1934.
- Jaikishan I, Rajendrakumar P, Hariprasanna K, Bhat BV. 2018. Gene expression analysis in sorghum hybrids and their parental lines at critical developmental stages in relation to grain yield heterosis by exploiting heterosis-related genes from major cereals. *Plant Mol Biol Report* 36: 418-428. DOI: 10.1007/s11105-018-1079-x.
- Jarwar AH, Wang X, Wang L, Ma Q, Fan S. 2017. Line x tester analysis of estimating heterosis and combining ability in F₁ generation of sunflower. *Asian Agric Res* 9 (8): 70-74. DOI: 10.19601/j.cnki.issn1943-9903.2017.08.017.
- Kamara MM, Ghazy NA, Mansour E, Elsharkawy MM, Kheir AMS, Ibrahim KM. 2021. Molecular genetic diversity and line × tester analysis for resistance to late wilt disease and grain yield in maize. *Agron* 11: 898. DOI: 10.3390/agronomy11050898.
- Kempthorne O. 1957. An Introduction to Genetic Statistics. John Wiley and Sons, New York.
- Kenga R, Alibi SO, Gupta SC. 2004. Combining ability studies in tropical sorghum (*Sorghum bicolor* (L.) Moench). *Field Crop Res* 88: 251-260. DOI: 10.1016/j.fcr.2004.01.002.
- Khadi PS, Biradar BD, Pattanashetti SK. 2018. Heterosis studies for yield and yield components in rabi sorghum [*Sorghum bicolor* (L.) Moench]. *J Farm Sci* 31 (3): 342-343.
- Kose A. 2017. Gene action and combining ability in line x tester population of safflower (*Carthamus tinctorius* L.). *Turkish J Field Crop* 22 (2): 197-203. DOI: 10.17557/tjfc.356216.
- Krystkowiak K, Adamski T, Surma M, Kaczmarek Z. 2009. Relationship between phenotypic and genetic diversity of parental genotypes and the specific combining ability and heterosis effects in wheat (*Triticum aestivum* L.). *Euphytica* 165: 419-434. DOI: 10.1007/s10681-008-9761-y.
- Kumar A, Mishra VK, Vyas RP, Singh V. 2011. Heterosis and combining ability analysis in bread wheat (*Triticum aestivum* L.). *J Plant Breed Crop Sci* 3 (10): 209-217. DOI: 10.5897/JPBCS.9000075.

- Lestari T, Sopandie D, Trikoesoemaningtyas, Ardie SW. 2014. Screening of several sorghum genotypes on acid soil tolerance. *Intl J Agron Agric Res* 5 (5): 170-176.
- Maftuchah, Febriana L, Sulistyawati, Reswari HA, Septia ED. 2021. Morphological diversity and heritability of nine local sorghum (*Sorghum bicolor*) genotypes in East Java, Indonesia. *Biodiversitas* 22 (3): 1310-1316. DOI: 10.13057/biodiv/d220330.
- Makanda I, Tongoona P, Derera J. 2009. Combining ability and heterosis of sorghum germplasm for stem sugar traits under off-season conditions in tropical lowland environments. *Field Crop Res* 114: 272-279. DOI: 10.1016/j.fcr.2009.08.009.
- Makanda I. 2017. Development of dual purpose sorghum: Correlation and path-coefficient analysis of grain yield and stem sugar traits. *Afr Crop Sci J* 25 (3): 263-275. DOI: 10.4314/acsj.v25i3.1.
- Martwi INA, Nugroho LH, Daryono BS, Susandarini R. 2020. Morphological variability and taxonomic relationship of *Sorghum bicolor* (L.) Moench accessions based on qualitative characters. *Annu Res Rev Biol* 35 (6): 40-52. DOI: 10.9734/arrb/2020/v35i630234.
- Melati M, Ari ANHG, Aziz SA. 2021. Plant growth and morphological characters of *Sonchus arvensis* L. from different chicken manure rates and harvest intervals with ratooning practices. *J Trop Crop Sci* 8 (2): 60-70. DOI: 10.29244/jtcs.8.02.60-70.
- Mengistu G, Shimelis H, Laing M, Lule D, Mashilo J. 2020. Combining ability and heterosis among sorghum (*Sorghum bicolor* [L.] Moench) lines for yield, yield-related traits, and anthracnose resistance in western Ethiopia. *Euphytica* 216: 33. DOI: 10.1007/s10681-020-2563-6.
- Mofokeng AM, Shimelis H, Laing M, Shargie N. 2019. Genetic variability, heritability and genetic gain for quantitative traits in South African sorghum genotypes. *Aust J Crop Sci* 13 (1): 1-10. DOI: 10.21475/ajcs.19.13.01.p718.
- Mohammed MI. 2009. Line x tester analysis across locations and years in Sudanese x exotic lines of forage sorghum. *J Plant Breed Crop Sci* 1 (9): 311-319. DOI: 10.5897/JPCS.9000089.
- Mohammed R, Are AK, Bhavanasi R, Munghate RS, Kavi Kishor PB, Sharma HC. 2015. Quantitative genetic analysis of agronomic and morphological traits in sorghum, *Sorghum bicolor*. *Front Plant Sci* 6: 945. DOI: 10.3389/fpls.2015.00945.
- Mondal C, Sarkar S, Hazra P. 2009. Line x tester analysis of combining ability in tomato (*Lycopersicon esculentum* Mill.). *J Crop Weed* 5 (1): 53-57.
- Mukkun L, Lalel HJD, Kleden YL. 2021. The physical and chemical characteristics of several accessions of sorghum cultivated on drylands in East Nusa Tenggara, Indonesia. *Biodiversitas* 22 (5): 2520-2531. DOI: 10.13057/biodiv/d220509.
- Mukkun L, Lalel HJD, Richana N, Pabendon MB, Kleden SR. 2018. The diversity of local sorghum (*Sorghum bicolor* L. Moench) in Nusa Tenggara Timur province. *IOP Conf Ser: Earth Environ Sci* 144: 012065. DOI: 10.1088/1755-1315/144/1/012065.
- Muturi PW, Mgonja M, Rubaihayo P. 2019. Gene action conditioning resistance traits to spotted stem borer, *Chilo partellus*, in grain sorghum. *Intl J Trop Insect Sci* 39: 147-155. DOI: 10.1007/s42690-019-00020-x.
- Narasimhamurthy YK, Gowda PHR. 2013. Line x tester analysis in tomato (*Solanum lycopersicum* L.): Identification of superior parents for fruit quality and yield-attributing traits. *Intl J Plant Breed* 7 (1): 50-54.
- Nduwumuremyi A, Tongoona P, Habimana S, Husbandry A. 2013. Mating designs: Helpful tool for quantitative plant breeding analysis. *J Plant Breed Genet* 1 (3): 117-129.
- Ni X, Zhao G, Liu T, Hu J, Chen G, Ding G. 2012. Analysis on the combining ability and heritability of main agronomic traits of hybrid glutinous sorghum. *J Agric Sci Technol* 13 (10): 2104-2109.
- Paliwal A, Shrotria PK, Verma JS. 2016. Estimation of heterosis in milo and non-milo based forage sorghum hybrids [*Sorghum bicolor* (L.) Moench]. *Adv Life Sci* 5(21): 9792-9798.
- Panwar LL. 2005. Line x tester analysis of combining ability in rice (*Oryza sativa* L.). *Indian J Genet* 65 (1): 51-52.
- Prabhakar, Elangovan M, Bahadure DM. 2013. Combining ability of new parental lines for flowering, maturity and grain yield in *Rabi* sorghum. *Electron J Plant Breed* 4 (3): 1214-1218.
- Prakash R, Ganesamurthy K, Nirmalakumari A, Nagarajan P. 2010. Heterosis for fodder yield in sorghum (*Sorghum bicolor* L. Moench). *Electron J Plant Breed* 1 (3): 319-327.
- Putri NE, Chaniago I, Suliansyah I. 2013. Selection to several wheat genotypes based on yield component in a high rainfall area. *J Agroteknologi* 4 (1): 1-6. DOI: 10.24014/ja.v4i1.56. [Indonesian]
- Rehana S, Ullah MZ, Zeba N, Narzis, Husna A, Siddique AB. 2019. Estimation of heterosis for yield and yield attributing traits in tomato crossed with line and tester method. *Progress Agric* 30 (2): 179-185.
- Rini EP, Wirnas D, Trikoesoemaningtyas, Sopandie D. 2017. Genetic analysis on agronomic and quality traits of sorghum hybrids in Indonesia. *SABRAO J Breed Genet* 49 (2): 192-200.
- Rivera-Burgos LA, Volenec JJ, Ejeta G. 2019. Biomass and bioenergy potential of brown midrib sweet sorghum germplasm. *Front Plant Sci* 10: 1142. DOI: 10.3389/fpls.2019.01142.
- Rodríguez F, Alvarado G, Pacheco Á, Crossa J, Burgueño J. 2015. AGD-R (Analysis of Genetic Designs with R for Windows) Version 4.0. <https://data.cimmyt.org/dataset.xhtml?persistentId=hdl:11529/10202>.
- SaadAbdel-Aty M, Yousef SA, Ghazy MM, Hatab SH. 2018. Combining ability of forage yield for sorghum-sudangrass hybrids under water stress using line x tester. *Fresenius Environ Bull* 27 (12): 8367-8379.
- Sanghera GS, Hussain W. 2012. Heterosis and combining ability estimates using line x tester analysis to develop rice hybrids for temperate conditions. *Not Sci Biol* 4 (3): 131-142. DOI: 10.15835/nsb437873.
- Schaffasz A, Windpassinger S, Snowdon R, Wittkop B. 2019. Reproductive cold stress tolerance in sorghum F1 hybrids is a heterotic trait. *Agron* 9: 508. DOI: 10.3390/agronomy9090508.
- Sen R, Saini RK, Singh SK, Kumar A. 2019. Study of genetic variability of fodder yield and it's components in forage sorghum [*Sorghum bicolor* (L.) Moench]. *Forage Res* 45 (2): 156-158.
- Shah AN, Tanveer M, ur Rehman A, Anjum SA, Iqbal J, Ahmad R. 2016. Lodging stress in cereal—effects and management: An overview. *Environ Sci Pollut Res* 24: 5222-5237. DOI: 10.1007/s11356-016-8237-1.
- Sheunda P, Nzuve FM, Manyasa EO, Chemining'wa GN. 2019. Heterosis and combining ability for grain and biomass yield in sorghum hybrids for the semi-arid lowlands of Eastern Kenya. *Acad Res J Agric Sci Res* 7 (4): 176-189. DOI: 10.14662/ARJASR2019.035.
- Singh RK, Chaudary BD. 1979. *Biometrical Methods in Quantitative Genetic Analysis*. Kalyani Publishers, Ludhiana.
- Sitanggang PA. 2013. The performance of sorghum (*Sorghum bicolor* (L.) Moench) under acid soil stress conditions in South Lampung. [Thesis]. IPB University, Bogor. [Indonesian]
- Sofiah II. 2021. Performance of characters from local varieties, national varieties, and breeding lines of sorghum. [Thesis]. IPB University, Bogor. [Indonesian]
- Su J, Zhang F, Yang X, Feng Y, Yang X, Wu Y, Guan Z, Fang W, Chen F. 2017. Combining ability, heterosis, genetic distance and their intercorrelations for waterlogging tolerance traits in chrysanthemum. *Euphytica* 213: 42. DOI: 10.1007/s10681-017-1837-0.
- Subagio H, Aqil M. 2013. Development of sorghum production in Indonesia. In: Yasin M, Noor A, Suryana, Hasbianto A, Amali N, Pribadi Y (Eds.). *Proceeding of National Seminar on Agriculture Innovation*. Assessment Institutes for Agricultural Technology of South Kalimantan, Banjarbaru, 26-27 March 2013.
- Suguna M, Aruna C, Deepika C, Ratnavathi CV, Tonapi VA. 2021. Genetic analysis of semolina recovery and associated traits- a step towards breeding for specific end uses in sorghum (*Sorghum bicolor* (L.) Moench). *J Cereal Sci* 100: 103226. DOI: 10.1016/j.jcs.2021.103226.
- Sulistyawati, Roeswitawati D, Ibrahim JT, Maftuchah. 2019. Genetic diversity of local sorghum (*Sorghum bicolor*) genotypes of East Java, Indonesia for agro-morphological and physiological traits. *Biodiversitas* 20 (9): 2503-2510. DOI: 10.13057/biodiv/d200910.
- Syukur M, Sujiprihati S, Yunianti R. 2012. *Plant Breeding Technique*. Penebar Swadaya, Jakarta. [Indonesian]
- Tabri F, Zubachtirodin. 2013. Sorghum cultivation. In: Sumarno, Damardjati DS, Syam M, Hermano (Eds.). *Sorghum: Innovation Technology and Development*. IAARD Press, Jakarta. [Indonesian]
- Talanca AH, Andayani NN. 2013. Development of sorghum variety in Indonesia. In: Sumarno, Damardjati DS, Syam M, Hermanto (Eds.). *Sorghum: Innovation Technology and Development*. IAARD Press, Jakarta. [Indonesian]
- Tnunay IMY, Chikmawati T, Miftahudin. 2019. Morphological diversity of local sorghum cultivar (*Sorghum bicolor*) of East Nusa Tenggara, Indonesia. *Biosaintifika* 11 (1): 47-54. DOI: 10.15294/biosaintifika.v11i1.15199.

- Trikoesoemaningtyas, Wirnas D, Saragih EL, Rini EP, Sari M, Marwiyah S, Sopandie D. 2017. Genetic control of morphology and agronomic characters in three sorghum (*Sorghum bicolor* (L.) Moench) populations. *J Agron Indones* 45 (3): 285-291. DOI: 10.24831/jaiv45i3.18387. [Indonesian]
- UPOV [International Union for the Protection of New Varieties of Plants]. 2014. Sorghum Guidelines for the Conduct of Tests for Distinctness, Uniformity and Stability. https://www.upov.int/meetings/en/doc_details.jsp?meeting_id=35045&doc_id=295796
- Usman MG, Rafii MY, Martini MY, Oladosu Y, Pedram K. 2017. Genotypic character relationship and phenotypic path coefficient analysis in chili pepper genotypes grown under tropical condition. *J Sci Food Agric* 97 (4): 1164-1171. DOI: 10.1002/jsfa.7843.
- Veldandi S, Shivani D, Maheswaramma S, Sujatha K, Sravanthi K, Ramesh S, Yamini KN, Kumar CVS. 2021. Combining ability and heterosis studies in different crop sites for yield and yield contributing traits in sorghum (*Sorghum bicolor* (L.) Moench). *Electron J Plant Breed* 12 (4): 1351-1358. DOI: 10.37992/2021.1204.185.
- Wang C, Zhou L, Zhang G, Xu Y, Gao X, Jiang N, Zhang L, Shao M. 2019. Effects of sowing time and growing density on agronomic traits, grain yield, and grain quality of waxy sorghum cultivar Hongliangfeng 1. *J Agric Sci* 11 (6): 12-21. DOI: 10.5539/jas.v11n6p12.
- Wickham H. 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.
- Widowati S. 2010. Characteristics of nutritional quality and diversification of sorghum-based food (*Sorghum vulgare*). *Jurnal Pangan* 19 (4): 373-382. DOI: 10.33964/jp.v19i4.170. [Indonesian]
- Wirnas D, Oktanti N, Rahmi HN, Andriani D, Faturrahman, Rini EP, Marwiyah S, Trikoesoemaningtyas, Sopandie D. 2021. Genetic analysis for designing an ideotype of high-yielding sorghum based on existing lines performance. *Biodiversitas* 22 (12): 5286-5292. DOI: 10.13057/biodiv/d221208.
- Yehia H, El-Hashash EF. 2019. Combining ability effects and heterosis estimates through line x tester analysis for yield, yield components and fiber traits in Egyptian cotton. *Elixir Agric* 131: 53238-53246.