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HIGH NONADDITIVE GENE ACTION CONTROLS SYNCHRONOUS MATURITY IN MUNG BEAN

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SUMMARY

In mung bean, synchronous maturity is one of the breeding objectives for harvest efficiency and revealing its potential as a catch crop between major cropping seasons. The genetic control of synchronous maturity can be estimated by using a line × tester mating design that provides information on gene action, combining ability, and generating segregated populations. The objectives of this study were to a) assess the combining ability of mung bean genotypes, b) estimate the nature and magnitude of genetic components and gene action through the line × tester method, and c) select F_1s for synchronous maturity in mung bean. This research was performed at IPB University Experimental Station, Bogor, Indonesia, from October 2018 to January 2019. The genetic material consisted of 10 lines, three testers, and 30 F_1s. The experiment was arranged in a randomized complete block design with three replications. Data were collected on days to flowering, days to the first harvest, days to 90% harvest, harvest period, degree of the indetermination of generative phase, and degree of the indetermination of harvest period. Data analysis was performed to estimate general combining ability (GCA), specific combining ability (SCA), additive variance, dominance variance, and heritability. Combining abilities (GCA and SCA) for synchronous maturity traits were selected on the basis of negative and significant values. Lom2, VR10, VR480B, VR422H, Kawur, and Vima 1 were the best combiners for synchronous maturity traits. The expression of all studied traits indicated the low control of additive genes. Delaying selection to later segregating generations is suggested, and the reliable selection of transgressive recombinants is possible. The hybrids that were selected as a source to exploit transgressive segregation for synchronous maturity traits were VR10 × Vima 1, Lom2 × Vima 1, VR480B × Vima 1, VR60 × No.129, Lom 1 × Vima 2, and VR82 × Vima 2. This step can thereafter be followed by bulk or single seed descent method.

Keywords: Indetermination degree, F_1, heritability, line × tester, overdominance

Key findings: Typical mung bean cultivars have a considerably long harvest period due to asynchronous pod maturity. Mung bean cultivars with a short harvest period will allow intercropping for sustainability in local cultivation. Cultivar development requires information on combining ability and gene action that can be provided by the line × tester

mating design to allow the exploitation of transgressive segregants in further segregating generations. These transgressive segregants can be selected further for developing improved mung bean cultivars with synchronous maturity.

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INTRODUCTION

Mung bean originated from Asia (India), then became widely cultivated in Africa, America, and Australia (Waniale *et al*., 2014; Pataczek *et al*., 2018). It has a protein content of up to 28% and is more digestible than some other protein-source legumes, such as chickpea (*Cicer arietinum*), pigeon pea (*Cajanus cajan*), and lentils (*Lens culinaris*) (Pataczek *et al*., 2018; Kakde *et al*., 2019). Recently, mung bean has also been targeted as a functional food to improve human nutritional quality, especially in countries where malnutrition and stunting are prevalent. However, low productivity is a problem for mung bean producers in Asian countries, namely China, India, Pakistan, Thailand, and Indonesia (Xin *et al*., 2003; Rahayu and Srimayanti, 2017; Schreinemachers *et al*., 2019). Low yield and asynchronous pod maturity are major problems in mung bean cultivation (Mondal *et al*., 2011). The average global grain yields of mung bean are low at 0.73 ton ha^{-1} (AVRDC, 2020).

According to Xin *et al*. (2003), the strategy for increasing mung bean productivity involves integrating mung bean into local cultivation systems. Mung bean is widely planted together with other crops, such as maize, sorghum, peanuts, and sugar cane, either by intercropping (Onuh *et al*., 2011; Shaker-Koohi and Nasrollahzadeh, 2014; Pataczek *et al*., 2018; Kakde *et al*., 2019) or catch cropping between wheat and rice seasons (Rani *et al*., 2018; Rehman *et al*., 2019). These cultivation systems require high-yielding mung bean cultivars with synchronous pod maturity or short harvest periods. Synchronous maturity in mung bean is characterized as a harvest period of approximately 20 days (Shanmugasundaram, 2011), an indetermination degree of harvest period of less than 20%, or an indetermination degree of plant height of less than 38.5% (Ullah *et al*., 2012).

Breeding for short harvest periods or synchronous maturity in mung bean through hybridization begins with parental selection. The parents should have a short harvest period, good agronomic traits, and good adaptability to generate high genetic variability in their recombinants. Therefore, a diverse collection of genetic materials with good combining ability is needed for developing new cultivars. This basic information can be obtained through the study of inheritance. Gene action and heritability determine the method for effective selection, trait selection, and genetic advancement in each generation. One of the mating designs suitable for inheritance studies is the line × tester design. This mating design allows the involvement of fewer genotypes than the other design while providing information on the combining ability of the parents for predicting superior hybrids (Yehia and El-Hashash, 2019).

Inheritance studies on several mung bean traits have been reported. Khattak *et al*. (2001) mentioned that additive genes control the days to flowering in mung bean, whereas nonadditive genes affect days to the first harvest, days to 90% maturity, and the indetermination degree of the generative phase. Iqbal *et al*. (2015) also reported that nonadditive genes control the indetermination degree of the harvest period and generative phase in mung bean. Rehman *et al*. (2013) also reported the involvement of nonadditive genes with dominant gene action for the degree of

indetermination plant height in mung bean.

The control of synchronous maturity in mung bean by nonadditive genes suggests that the delayed selection of advanced generations is better than that of other breeding strategies (Khattak *et al*., 2004; Rehman *et al*., 2013). A bulk method is one of the recommended selection methods for synchronous maturity traits in mung bean (Iqbal *et al*., 2015). The bulk method effectively handles traits with low to moderate heritability (Chahal and Gosal, 2003).

The development of mung bean cultivars with synchronous maturity and the availability of information on genetic control for this trait are limited in Indonesia. Since 1945, Indonesia has released 22 mung bean cultivars, among 16 cultivars, including No.129, Vima 1, and Vima 2 (Suhartina, 2005; Trustinah, 2014; ILETRI, 2016), have synchronous maturity. However, not all cultivars with synchronous maturity are harvested at once, and some are harvested 2–3 times (Sundari 2014). Compared with Indonesia, India has completed and published more and earlier reports on mung bean breeding for synchronous maturity and has released synchronous maturity cultivars (Chadda 2010; Nair *et al*. 2012, ICAR 2021). Therefore, the number of high-yielding mung bean cultivars with synchronous maturity should be increased. Indonesia has many local cultivars that can be developed further through hybridization and selection. During selection, inheritance studies can also be conducted for understanding the genetic control of the synchronous maturity trait in the population.

This study evaluated several mung bean germplasm accessions as lines, national cultivars as testers, and their recombinants (F_1) by using a line × tester mating design with a focused interest on synchronous maturity. This research aimed to assess combining ability, estimate genetic components and gene action, and select the best-performing F_1 for synchronous maturity in mung bean. The results of this study may provide some information on the genetic control of synchronous maturity or harvest periods in mung bean.

MATERIALS AND METHODS

The evaluated genetic materials consisted of 10 lines, three testers, and 30 F_1 genotypes. Table 1 describes the mung bean genotypes that were used as lines and testers in this research. According to the descriptions of mung bean cultivars from ILETRI (2016), Vima 1 and Vima 2 have synchronous maturity and No.129 has medium synchronous maturity. Ten genotypes from IPB and ICABIOGRAD have not been categorized (Safuan, 2018). This experiment was conducted from October 2018 to January 2019 at IPB University Experimental Station (106°43'32."E; 6°33'48.4"S), Bogor, Indonesia, at 234 m above sea level. The soil type of the experimental land was latosol with pH 6. The agro-meteorological variables during the study were as follows: temperatures of 22.99 °C–30.77 °C (T_{mean} = 25.83 °C), mean annual rainfall of 267.75 mm month^{-1}, and humidity of 83.30%. Genetic materials were evaluated by using a randomized complete block design with three replications. Each genotype was planted in one row with a length of 2.4 m length with a spacing of 40 cm between rows and 15 cm within a row. The ripening pods were harvested from individual plants every week beginning from the first to the eighth week. Mung bean cultivation was done in reference to the field technical guidelines provided by AVRDC (2014) and ILETRI (2015).

Data were collected for days to flowering (D1); days to the first harvest (D2); days to 90% harvest (D3); and synchronous maturity traits, namely, harvest period, degree of indetermination of the generative phase (DDd1), and degree of indetermination of the harvest periods (DDd2). The harvest period is the difference between days to 90% harvest

and days to the first harvest (D3-D2). DDd1 was formulated as:

$$DDd1 = \frac{D3 - D1}{D3} x100\%$$

and DDd2 as:

$$DDd2 = \frac{D3 - D2}{D3} x100\%$$

Both degrees of indetermination followed the formulations by Khattak *et al*. (2001), Khattak *et al*. (2004), and Tah (2009).

Observations were recorded from 10 plants for each experimental unit. The data analysis was performed by using analysis of variance (ANOVA) with lines and testers as random effects. Further tests through the Least Significance Difference (LSD) test at α = 5% were conducted if a significant difference was observed. The general combining ability (GCA), specific combining specific (SCA), and proportional contributions of the parents (lines, testers, and hybrids or F_1), additive variance, dominance variance, and heritability were estimated in accordance with Singh and Chaudhary (1985). Additive and dominance variances were calculated by taking the inbreeding coefficient (F) equal to one ($F = 1$) because both lines and testers were self-pollinated crops. The data were analyzed through the ANOVA of the line × tester. Significant effects were tested further by using the Least Significant Difference (LSD) test at α = 5%. The t-test was conducted to test combining ability under the null hypothesis that the estimate was equal to zero. Microsoft Excel and SAS version 9.0 software were used for statistical analyses.

Table 1. General descriptions of the mung bean genotypes as lines and testers in this research.

Geno-types	Sources	Origin	DTF50 (days)	DM50 (days)	HPT (days)	PHE (cm)
Lom2	IPB university	Local from Lombok, West Nusa Tenggara, Indonesia	44	65	22	70.4
Kawur	IPB university	Local from Bengkulu, Sumatera, Indonesia	53	65	25	88.7
KEFA	IPB university	Local from Kefamenanu, East Nusa Tenggara, Indonesia	48	61	29	76.2
Lom1	IPB university	Local from Lombok, West Nusa Tenggara, Indonesia	42	61	26	59.4
VR10	ICABIOGRAD	Introduction from India	42	64	26	66.4
VR60	ICABIOGRAD	Local from Malang, East Java, Indonesia	43	62	28	67.3
VR480B	ICABIOGRAD	Introduction from Taiwan	39	56	34	62.6
VR422H	ICABIOGRAD	Introduction from Taiwan	37	59	31	59.0
VR416	ICABIOGRAD	Introduction from Taiwan	42	62	28	69.2
VR82	ICABIOGRAD	Local from East Java, Indonesia	40	56	34	66.9
Vima 1	ILETRI	Indonesia national cultivar	33	57[1]	-	53.0[1]
Vima 2	ILETRI	Indonesia national cultivar	33	56[1]	-	64.3[1]
No.129	ILETRI	Indonesia national cultivar	32	58[1]	-	45.0[1]

Sources: Safuan (2018) and [1] ILETRI (2016).
DTF50 = days to 50% flowering based on population; DM50 = days to 50% maturity based on population, HPT = harvest period, PHE = plant height, IPB = IPB University (Division of Plant Genetics and Breeding, Department of Agronomy and Horticulture), ICABIOGRAD = Indonesian Center for Agricultural Biotechnology and Genetic Resources Research and Development, ILETRI = Indonesian Legumes and Tuber Crops Research Institute.

Table 2. Mean squares of days to flowering, days to harvest, and synchronous maturity in mung bean.

Source of variation	d.f.	DTF	DM1	DM90	HPT	DDd1	DDd2
Replication	2	8.63*	16.78**	8.69	25.79**	19.95*	25.34**
Genotype	42	33.95**	28.97**	54.09**	97.08**	51.79**	98.83**
Parent	12	88.21**	28.06**	52.49**	42.40**	95.73**	75.56**
F_1	29	11.62**	30.26**	37.56**	90.89**	21.47**	95.43**
Parent vs. F_1	1	30.49**	2.75	552.71**	312.70**	404.09**	476.89**
Line (L)	9	24.10**	44.37**	58.37**	116.95**	26.81**	119.85**
Tester (T)	2	3.40	43.56**	23.88*	129.75**	19.81*	147.72**
L×T	18	6.28**	21.72**	28.67**	73.56**	18.97**	77.40**
Error	84	2.36	2.37	5.41	4.22	4.22	3.92

*= significant at 5% probability level, ** = significant at 1% probability level, d.f = degrees of freedom, DTF = days to flowering, DM1 = days to the first harvest, DM90 = days to 90% harvest, HPT = harvest period, DDd1 = degree of indetermination of the generative phase, DDd2 = degree of indetermination of the harvest period.

RESULTS AND DISCUSSION

Variability and performance of the parents and F_1

The analysis of variance results for six mung bean traits is presented in Table 2. The genotype showed a highly significant effect ($P < 0.01$) for days to flowering, days to the first harvest, days to 90% harvest, harvest period, DDd1, and DDd2. The significant effect of the genotype indicated the variability of the genetic materials for the six traits studied. Further analysis could be performed by partitioning the genotype effect into the parent, F_1, and parent vs. F_1. These three components had a highly significant effect ($P < 0.01$) for all traits, except the parent vs. F_1 had contrasting days to the first harvest (Table 1). Cross-combinations between the parents will allow the formation of potential recombinants. Surashe *et al*. (2017) and Kakde *et al*. (2019) stated that crosses among genetically distant parents could produce F_1s that are better than the parents.

The highly significant effect ($P < 0.01$) of the F_1s for all six traits indicated the presence of genetic diversity among F_1 genotypes. Hence, the selection of F_1 genotypes possessing the targeted trait, namely, synchronous maturity, was possible. The F_1 effect could be further partitioned into the line GCA, tester GCA, and line × tester SCA effects (Fellahi *et al*., 2013; Kose, 2017). The line and tester main effects were significant ($P < 0.01$ and $P < 0.05$) for all traits, except for the tester effect of days to flowering (Table 2). The line × tester interaction effect was highly significant ($P < 0.01$) for all traits. These results indicated that variability existed for the GCA effects of the lines and testers and SCA effects. The variability among the F_1 genotypes suggested the potential of developing improved cultivars with shortened days to flowering and days to harvest, as well as synchronous maturity from selected populations.

Previous studies have also reported the significance of F_1s derived from line × tester in terms of several traits in mung bean, i.e., days to flowering and days to harvest (Surashe *et al*., 2017; Kakde *et al*., 2019), total pod number (Khattak *et al*., 2001), and plant height (Narasimhulu *et al*., 2014). Similar effects were also identified for other pulses, such as *Vigna mungo* for plant height (Chakraborty *et al*., 2010), and *Vigna umbellata* for days to flowering and days to harvest (Gill and Kumar, 2017). Other earlier studies revealed that if the line and tester effects are not significant, the F_1 effect may not be significant as was previously identified for yield in mung bean (Chakraborty *et al*., 2010) and *V. umbellata* (Gill and Kumar, 2017).

The parent vs. F_1 contrast was highly significant ($P < 0.01$) for days to flowering, days to 90% harvest, and synchronous maturity (Table 2), indicating the presence of heterosis (hybrid vigor) effect either in the positive or negative direction (Chakraborty *et al*., 2010; Katiyar and Kumar, 2015; Widyastuti *et al*., 2017). A similar phenomenon in the other line × tester populations of mung bean for days to flowering, days to 90% harvest (Narasimhulu *et al*., 2014), plant height, and yield components (Katiyar and Kumar, 2015), as well as in a mung bean's close relative, *V. mungo*, for days to flowering (Chakraborty *et al*., 2010), has been reported.

The genotype means for days to flowering, days to harvest, and synchronous maturity of parents are presented in Table 3. The lines showed earlier maturity, shorter harvest periods, and lower degrees of indetermination than the tester. Days to flowering did not differ among testers with a narrow range of 39.71–41.48 days after sowing (das). Genotypes VR422H, VR480B, and VR82 were early-flowering and early-first harvest genotypes.

Mung bean genotypes with pod harvest days < 60 das were categorized as early maturing, and those with harvest days > 60 das were categorized as late maturing (Xin *et al*., 2003; Hakim and Suyamto, 2012; Nair *et al*., 2012). All lines and testers, except for Lom2, No.129, Kefa, and Kawur, were classified as early maturing. Early-maturing mung bean cultivars may be suitable for intercropping (GRDC, 2017) and may be able to avoid exposure to drought and pest stresses (Hapsari *et al*., 2015). Early-maturing cultivars enable plants to escape from the onslaught of insects and hence minimize yield losses (Chahal and Gosal, 2003).

Parents were significantly different for synchronous maturity traits (Table 3). Mung bean cultivars with harvest periods < 15 days were classified as having synchronous maturity, those with harvest periods of 15–20 days were classified as having as partial synchronous maturity, and those with harvest periods > 20 days were classified as having as asynchronous maturity (Mondal *et al*., 2011). Lines VR10 and Lom2 had short harvest periods (17.16–17.32 days) and were not different from Kawur (19.35 days) but were different from VR422H (28.24 days). Vima 1 was one of the tester genotypes with a short harvest period of less than 20 days (19.87 days). Cultivars with a DDd2 of <20% are categorized as a synchronous maturity (Tah, 2009). Genotypes Lom2, Kawur, and VR10 were lines with a significantly lower DDd2 than other genotypes that nonetheless exceeded 20% and ranged from 21.79% to 22.12%. No one tester genotypes were classified as having synchronous maturity on the basis of DDd2 criteria (25.29 to 31.15%).

The performance of the F_1 genotypes for all observed traits is presented in Table 3. VR480B × Vima 2 was the earliest flowering F_1 genotype. VR480B, as a female parent, was the earliest flowering line (Table 3). Genotypes with early-flowering may be preferred in selection. All F_1 genotypes that had the latest flowering time were derived from Kawur: namely Kawur × Vima 2, Kawur × No.129, and Kawur × Vima 1. Cross-combination among VR60 or Lom1 as the female parent and Vima 1 as the male parent generated the earliest maturing F_1 but was not significantly different from VR60 × Vima 2, VR416 × Vima 2, and VR82 × No.129.

The VR10 × Vima 1 and Lom 2 × Vima 1 F_1 genotypes had short days to last harvest, a relatively short harvest period, and a low DDd1 (<50%) and harvest period (<20%). Therefore, they could be classified as synchronous maturity genotypes. Mung bean genotypes having synchronous maturity are favorable for growing as a catch crop between two seasons of major crops (Tah and Saxena, 2009; Rani *et al*., 2018; Rehman *et al*., 2019). By contrast, Kefa × Vima 2 had the longest harvest period and a high DDd2, whereas VR60 × Vima 1 had the highest DDd1.

Table 3. Average days to flowering, days to harvest, and synchronous maturity of mung bean parents (line and tester) and hybrids.

	Genotypes	DTF (das)	DM1 (das)	DM90 (das)	HPT (days)	DDd1 (%)	DDd2 (%)
Line	Lom2	44.58 bc	61.48 bc	78.64 d	17.16 d	43.27 f	21.79 e
	Kawur	58.00 a	68.00 a	87.35 a	19.35 cd	33.57 g	22.12 de
	VR10	43.08 c	60.72 cd	78.05 d	17.32 d	44.73 ef	22.12 de
	VR60	44.21 bc	60.90 cd	85.05 abc	24.14 ab	47.97 cde	28.34 bc
	KEFA	46.16 b	63.26 b	85.95 ab	22.69 cb	46.26 def	26.37 cd
	VR480B	38.93 d	57.51 e	81.89 cd	24.37 ab	52.43 abc	29.72 abc
	VR422H	38.69 d	57.03 e	85.27 abc	28.24 a	54.57 a	33.06 a
	VR416	42.30 c	58.88 de	84.52 abc	25.64 ab	49.90 bcd	30.29 abc
	VR82	39.18 d	58.48 de	82.65 bc	24.17 ab	52.55 ab	29.23 abc
	Lom1	42.25 c	57.82 e	83.96 abc	26.15 ab	49.69 bcd	31.14 ab
	Mean	43.74	60.41	83.33	22.92	47.49	27.42
	CV (%)	3.34	2.42	2.74	11.69	5.53	9.72
Tester	Vima 1	39.71	58.70 ab	78.58 b	19.87 c	49.49 b	25.29 c
	Vima 2	41.48	60.66 b	86.01 a	25.36 b	51.77 a	29.48 b
	No.129	40.24	62.26 a	90.44 a	28.18 a	55.49 a	31.15 a
	Mean	40.48	60.54	85.01	24.47	52.25	28.64
	CV (%)	3.79	3.35	2.02	8.39	3.14	7.80
	Parents mean	42.99	60.44	83.72	23.28	48.59	27.70
Hybrids	Lom2 × Vima 1	42.27 b–g	65.83 ab	82.03 i	16.20 j	48.50 kl	19.77 j
	Lom2 × Vima 2	40.27 e–k	59.33 f–h	88.73 b–e	29.43 c–f	54.63 a–e	33.17 c–f
	Lom2 × No.129	41.47 d–j	66.63 ab	84.33 g–i	17.73 ij	50.83 i–k	21.00 ij
	Kawur × Vima 1	44.67 ab	61.73 d–f	92.40 ab	30.70 b–d	51.60 e–k	33.13 c–f
	Kawur × Vima 2	46.47 a	62.47 c–e	90.43 bc	27.97 d–f	48.63 kl	30.97 e–g
	Kawur × No.129	46.07 a	64.23 b–d	87.77 c–g	23.53 h	47.50 lm	26.77 h
	VR10 × Vima 1	40.47 e–k	64.13 b–d	73.97 j	9.87 k	45.23 m	13.20 k
	VR10 × Vima 2	40.67 d–k	58.30 g–j	86.97 c–g	28.67 de	53.23 a–g	32.93 c–f
	VR10 × No.129	41.93 c–i	58.70 g–j	83.43 hi	24.73 gh	49.70 h–l	29.60 gh
	VR60 × Vima 1	39.03 i–k	56.43 j	89.27 b–d	32.83 ab	56.30 a	36.73 a
	VR60 × Vima 2	39.43 i–k	57.07 ij	86.80 c–h	29.73 c–f	54.60 a–e	34.23 a–d
	VR60 × No.129	44.10 a–c	60.30 e–g	86.90 c–h	26.57 f–h	49.23 i–l	30.60 fg
	Kefa × Vima 1	42.10 b–h	60.20 e–g	87.83 c–g	27.67 d–g	52.07 e–i	31.47 d–g
	Kefa × Vima 2	42.63 b–f	60.30 e–g	95.03 a	34.73 a	55.17 a–d	36.53 a
	Kefa × No.129	41.93 c–i	59.70 f–h	87.17 c–h	27.47 e–g	51.87 e–i	31.50 e–g
	VR480B × Vima 1	43.27 b–d	67.90a	84.47 f–i	16.57 j	48.77 j–l	19.63 j
	VR480B × Vima 2	38.80 k	57.57 h–j	85.63 d–h	28.07 d–f	54.67 a–e	32.73 c–f
	VR480B × No.129	40.60 e–k	58.17 g–j	86.73 c–h	28.57 d–f	53.20 a–g	32.93 c–f
	VR422H × Vima 1	39.90 f–k	58.63 g–j	85.90 d–h	27.27 e–g	53.53 a–g	31.73 c–g
	VR422H × Vima 2	42.07 be	59.20 g–i	86.23 d–h	27.03 e–g	51.23 f–k	31.37 e–g
	VR422H × No.129	39.60 h–k	64.70 bc	84.80 f–h	20.13 i	53.30 a–g	23.70 i
	VR416 × Vima 1	41.77 c–i	58.63 g–i	88.27 c–f	29.63 b–f	52.67 e–g	33.57 c–e
	VR416 × Vima 2	40.23 e–k	57.13 ij	84.73 i–h	27.67 d–g	52.57 e–g	32.50 c–g
	VR416 × No.129	42.73 b–e	59.53 g–j	87.57 c–g	28.07 e–f	51.13 f–k	32.00 c–g
	VR82 × Vima 1	40.93 d–k	58.80 g–j	86.47 e–g	27.67 d–g	52.63 c–f	32.00 c–g
	VR82 × Vima 2	40.03 f–k	57.87 g–j	85.13 e–h	27.27 e–g	52.97 b–g	32.00 c–g
	VR82 × No.129	39.33 i–k	57.07 ij	89.47 b–d	32.40 a–c	56.07 ab	36.23 ab
	Lom1 × Vima 1	39.63 h–k	56.63 j	88.80 b–d	32.23 a–c	55.40 a–c	36.27 ab
	Lom1 × Vima 2	40.77 d–k	57.67 i–h	87.33 c–g	29.67 c–f	53.27 a–g	33.97 a–d
	Lom1 × No.129	40.23 e–k	57.43 i–h	87.67 c–g	30.23 c–d	54.13 a–f	34.47 a–c
	Mean	41.45	60.08	86.74	26.68	52.15	30.56
	CV (%)	3.86	2.57	2.73	7.35	3.67	5.84

Means in the same column followed by the same letter are not significantly different based on LSD at the 5% probability level, DTF = days to flowering, DM1 = days to the first harvest, DM90 = days to 90% harvest, HPT = harvest period, DDd1 = degree of indetermination of the generative phase, DDd2 = degree of indetermination of the harvest period, CV = coefficient of variation.

Proportional contributions of lines, testers, and line × tester

The proportional contributions of the lines, the testers, and their interaction (F_1) to the total sum squares for each trait are shown in Table 4. For all six traits observed, the tester had a smaller contribution than the line and line × tester. The line had a higher contribution on days to flowering, days to the first harvest, and days to 90% harvest. The line and line × tester contributions were almost equal for days to the first harvest and days to 90% harvest. According to Fellahi *et al*. (2013), the large percentage of line, tester, or line × tester interaction indicates their major role in the expression, variability, and inheritance of a trait.

The line × tester interaction had the highest contribution (>50%) to the synchronous maturity traits, i.e., the harvest period, DDd1, and DDd2 (Table 4). The high contribution of the line × tester indicated a high SCA effect between the coupled parents, the major role of the nonadditive genes, and the opportunity to improve the synchronous maturity trait through effective selection. These results are supported by Widyastuti *et al*. (2017) and Makhdoom *et al*. (2017) for different crops. In self-pollinated crops with a considerably high percentage of cross-pollination, such as brassica (Afrose *et al*., 2019) and wheat (Din *et al*., 2020; Din *et al*., 2021), the high contribution of the line × tester interaction indicates the potential for hybrid development.

GCA of the lines and testers

Mungbean breeding focuses on early maturity improvement (Shanmugasundaram, 2011; Chauhan *et al*., 2011; Nair *et al*., 2012). Selection for days to flowering and synchronous maturity has a negative direction, i.e., favoring parents with low or negative GCA. The GCA of parents is shown in Table 5. VR82 and Lom1 were considered as potential combiners for early-flowering time and could be involved in hybridization. VR60, VR416, VR82, Lom1, and Vima 2 were the best combiners for early maturity based on days to the first harvest, whereas VR10 and Lom2 were the best combiners based on days to 90% harvest. In mung bean, early maturity supports achieving optimum yield (Hapsari *et al*., 2015). By contrast, the Kawur genotype showed a positive and significantly different GCA. Therefore, this genotype was the best combiner for late flowering and maturity.

Four of the lines and one tester were genotypes with significant and negative GCA (low GCA), including Lom2, VR10, VR480B, VR422H, and Vima 1 for harvest period and DDd2. VR10 and Kawur were significant and negative for DDd1. Their involvement in mung bean breeding programs will provide offspring with synchronous maturity. The selection of the parents with negative GCA (low GCA) and crossing partners to improve synchronous maturity in mung bean has been reported by Khattak *et al*. (2001) and the early maturity trait in mung bean has been reported by Khattak *et al*. (2001) and Kakde *et al*. (2019) and that in soybeans has been reported by Susanto (2018).

SCA of the lines and testers

The interaction effect of lines and testers might contribute to trait expression and measured by SCA values. Although the SCA effect does not directly contribute to the improvement of self-pollinated crops, a superior F_1 is expected to exploit transgressive segregants for further generating superior homozygous lines. The best F_1 for early flowering, early maturity, and synchronous maturity was selected on the basis of negative and significant SCA. Lom2 × Vima 1, VR10 × Vima 1, and VR82 × Vima 2 had a negative and significant SCA for days to 90% harvest (early maturity), harvest period, DDd1, and DDd2. VR60 × No.129, VR480B × Vima 1, and Lom 1 × Vima 2 were other candidate hybrids for the three synchronous maturity traits with late flowering and maturity (Table 6).

Table 4. Proportional contribution of lines, testers, and their interaction to genetic variances for six mung bean traits.

Traits	Contribution (%)			Genetic parameters							
	Line (L)	Tester (T)	L × T	Σ^2_{GCA}	Σ^2_{SCA}	$\Sigma^2_{GCA}/\sigma^2_{SCA}$	Σ^2_A	Σ^2_D	$(\sigma^2_D/\sigma^2_A)^{1/2}$	h^2_{bs}	h^2_{ns}
DTF	64.40	2.02	33.58	0.10	1.31	0.08	0.20	1.31	2.56	0.93	0.02
DM1	45.52	9.93	44.55	0.16	6.45	0.02	0.32	6.45	4.49	0.94	0.02
DM90	48.23	4.38	47.39	0.17	7.75	0.02	0.33	7.75	4.83	0.90	0.02
HPT	39.92	9.85	50.23	0.32	23.05	0.01	0.65	23.05	5.96	0.96	0.02
DDd1	38.78	6.37	54.86	0.05	4.92	0.01	0.09	4.92	7.26	0.92	0.01
DDd2	38.98	10.68	50.34	0.34	24.51	0.01	0.67	24.51	6.03	0.97	0.02

σ^2_{GCA} = general combining ability variance, σ^2_{SCA} = specific combining ability variance, σ^2_A = additive genetic variance, σ^2_D = dominance genetic variance, h^2_{bs} = broad-sense heritability, h^2_{ns} = narrow-sense heritability, DTF = days to flowering, DM1 = days to the first harvest, DM90 = days to 90% harvest, HPT = harvest period, DDd1 = degree of indetermination of the generative phase, DDd2 = degree of indetermination of the harvest period.

Table 5. General combining ability of mung bean parents for days to flowering, days to harvest, and synchronous maturity.

Genotypes	DTF (das)	DM1 (das)	DM90 (das)	HPT (days)	DDd1 (%)	DDd2 (%)
Lines						
Lom2	−0.11	3.86**	−1.71*	−5.57**	−0.85	−5.92**
Kawur	4.29**	2.73**	3.45**	0.72	−2.91**	−0.26
VR10	−0.42	0.31	−5.29*	−5.60**	−2.77**	−5.32**
VR60	−0.60	−2.14**	0.90	3.05**	1.22	3.32**
KEFA	0.77	−0.01	3.27**	3.28**	0.88	2.62**
VR480B	−0.56	1.14*	−1.14	−2.28**	0.07	−2.12**
VR422H	−0.92	0.77	−1.10	−1.87*	0.53	−1.62*
VR416	0.13	−1.65**	0.13	1.77*	−0.02	2.13**
VR82	−1.34*	−2.17**	0.29	2.46**	1.72*	2.84**
Lom1	−1.25*	−2.83**	1.20	4.03**	2.12**	4.34**
GCASE	0.49	0.49	0.74	0.66	0.65	0.63
Testers						
Vima 1	−0.04	0.82	−0.80	−1.62*	−0.49	−1.81*
Vima 2	−0.31	−1.38*	0.96	2.35*	0.94	2.48*
No.129	0.36	0.57	−0.16	−0.73	−0.45	−0.67
GCASE	0.23	0.23	0.35	0.31	0.31	0.29

*, **= significant at the 5% and 1% probability levels, respectively, based on t-test, DTF = days to flowering, DM1 = days to the first harvest, DM90 = days to 90% harvest, HPT = harvest period, DDd1 = degree of indetermination of the generative phase, DDd2 = degree of indetermination of the harvest period, GCASE = standard error of GCA.

Selected candidate hybrids were derived from low GCA × low GCA (Lom2 × Vima 1, VR10 × Vima 1, and VR480B × Vima 1), high GCA × low GCA (VR60 × No.129), and high GCA × high GCA (Lom 1 × Vima 2 and VR82 × Vima 2) for the three synchronous maturity traits. The cross-combination of low GCA × low GCA had a high chance of superior derived offspring for synchronous maturity. However, high × low and high × high cross patterns could provide a good chance as long as the direction of genes to express synchronous maturity traits is the same. Ghiday *et al.* (2016) and Ghiday and Tizzazu (2017) explained that superior hybrids from high GCA × low GCA can provide desirable transgressive segregants if the additive effects of one parent and the complementary epistasis effects act in the same direction and maximize performance under selection.

Table 6. Specific combining ability of crosses (F_1) for days to flowering, days to harvest, and synchronous maturity in mung bean.

Genotypes	DTF (das)	DM1 (das)	DM90 (das)	HPT (days)	DDd1 (%)	DDd2 (%)
Lom2 × Vima 1	0.94	1.09	−2.19*	−3.29**	−2.33*	−3.09**
Lom2 × Vima 2	−0.74	−3.21**	2.74*	5.96**	2.37*	6.03**
Lom2 × No.129	−0.21	2.12**	−0.55	−2.67**	−0.04	−2.94**
Kawur × Vima 1	−1.02	−1.89**	3.00**	4.89**	2.86**	4.66**
Kawur × Vima 2	1.05	1.03	−0.73	−1.76	−1.57	−1.83*
Kawur × No.129	−0.03	0.86	−2.27*	−3.13**	−1.29	−2.83**
VR10 × Vima 1	−0.52	2.92**	−6.69**	−9.61**	−3.68**	−10.23**
VR10 × Vima 2	−0.04	−0.69	4.55**	5.23**	2.90**	5.22**
VR10 × No.129	0.55	−2.23**	2.14*	4.37**	0.78	5.01**
VR60 × Vima 1	−1.78**	−2.30**	2.42*	4.72**	3.40**	4.69**
VR60 × Vima 2	−1.11	0.51	−1.82	−2.32*	0.28	−2.08*
VR60 × No.129	2.89**	1.79**	−0.60	−2.39*	−3.67**	−2.61**
Kefa × Vima 1	−0.07	−0.70	−1.38	−0.68	−0.50	0.10
Kefa × Vima 2	0.71	1.62*	4.06**	2.44*	1.20	0.91
Kefa × No.129	−0.64	−0.92	−2.68*	−1.76	−0.71	−1.01
VR480B × Vima 1	2.42**	5.86**	−0.35	−6.21**	−2.96**	−7.01**
VR480B × Vima 2	−1.77*	−2.24**	−0.93	1.31	1.53	1.82*
VR480B × No.129	−0.64	−3.62**	1.28	4.90**	1.44	5.18**
VR422H × Vima 1	−0.58	−3.02**	1.05	4.07**	1.34	4.60**
VR422H × Vima 2	1.84**	−0.24	−0.37	−0.13	−2.41*	−0.06
VR422H × No.129	−1.27	3.26**	−0.68	−3.94**	1.06	−4.54**
VR416 × Vima 1	0.25	−0.59	2.21*	2.79**	1.02	2.67**
VR416 × Vima 2	−1.05	0.07	−3.07**	−3.14**	−0.51	−2.67**
VR416 × No.129	0.80	0.51	0.86	0.35	−0.50	0.00
VR82 × Vima 1	0.90	0.07	0.26	0.19	−0.75	0.42
VR82 × Vima 2	0.23	1.34	−2.86**	−4.20**	−1.86*	−3.91**
VR82 × No.129	−1.12	−1.41*	2.60*	4.02**	2.61**	3.50**
Lom1 × Vima 1	−0.54	−1.45*	1.67	3.12**	1.61	3.18**
Lom1 × Vima 2	0.88	1.81**	−1.56	−3.37**	−1.93*	−3.42**
Lom1 × No.129	−0.34	−0.36	−0.11	0.25	0.32	0.24
SCASE	0.69	0.69	1.04	0.94	0.92	0.89

*, ** = significant at the 5% and 1% probability levels, respectively, based on t-test, DTF = days to flowering, DM1 = days to the first harvest, DM90 = days to 90% harvest, HPT = harvest period, DDd1 = degree of indetermination of the generative phase, DDd2 = degree of indetermination of the harvest period, SCASE = standard error of SCA.

The hybrid VR10 × Vima 1 showed the best performance or early maturity and synchronous maturity (Table 3). Vima 1, a local cultivar, is early and synchronous maturing, determinate, and high yielding (Trustinah, 2014). Introducing this hybrid into advanced breeding programs to develop lines with synchronous maturity will be a good decision. This present study proved that parents with low GCA × low GCA could provide superior hybrids. F_1 selection from combining low GCA × low GCA parents has been reported for mung bean (Narasimhulu *et al*., 2014) and soybean (Ghiday *et al.*, 2016; Ghiday and Tizzazu, 2017). Trait improvement from these cross-combinations can be expected after delaying the selection to further generations by exploiting desirable transgressive segregants, as suggested by Narasimhulu *et al*. (2014), Ghiday *et al.* (2016), and Ghiday and Tizzazu (2017).

Estimation of genetic components and gene action

GCA reflects the control of additive genes, whereas SCA is related to nonadditive genes. The SCA variance (σ^2_{SCA}) was greater than the GCA variance (σ^2_{GCA}) for all traits studied (Table 4). The $\sigma^2_{GCA}/\sigma^2_{SCA}$

ratio indicates the type of gene action controlling the trait. A ratio of<1 indicates an appreciable nonadditive gene effect, namely, dominant, over-dominance, and epistasis, and a ratio of >1 indicates a considerable additive gene effect (Nath *et al*., 2018). Days to flowering, days to the first harvest, days to 90% harvest, harvest period, DDd1, and DDd2 had $\sigma^2_{GCA}/\sigma^2_{SCA}$ ratios ranging from 0.01 to 0.08 (<1). These results suggested the preponderance of nonadditive gene effects.

The line × tester mating design allows the estimation of total genetic variance, as well as additive and dominant variances. The magnitude of genetic parameters in Table 4 shows that the dominant variance (σ^2_D) was always higher than the additive variance (σ^2_A) for the six traits studied. This result supported the ratio of GCA variance to SCA variance, i.e., ($\sigma^2_{GCA}/\sigma^2_{SCA}$) < 1 (0.01–0.08), indicating that the nonadditive genes played a major role and confirming that dominant genes controlled the expression of days to flowering, days to harvest, and synchronous maturity.

The gene action that controls a trait can also be determined on the basis of the degree of dominance $(\sigma^2_D/\sigma^2_A)^{1/2}$. Petr and Frey (1966) distinguished the degree of dominance as incomplete–positive dominance (0–1), incomplete–negative dominant gene with no perfect (–1 and 0), no dominance (= 0), complete dominance (= 1 or = –1), and over-dominance (<-1 or >1). Table 4 shows that the degree of dominance ranged from 2.56 and 7.26 among all traits, indicating that over-dominance gene action controlled days to flowering, days to the first harvest, days to 90% harvest, harvest period, DDd1, and DDd2. Over-dominance gene action has been reported to control yield-contributing traits in mung bean (Khattak *et al*. 2002; Katiyar and Kumar, 2015), as well as the flowering and harvesting days in *V. mungo* (Chakraborty *et al*., 2010), and panicle weight in rice (Widyastuti *et al*., 2017).

Over-dominance gene action indicates that heterozygous superiority can serve in the development of hybrid cultivars (Chahal and Gosal 2003; Xin *et al*., 2003; Surashe *et al*., 2017; Kakde *et al*., 2019) or as a basis for exploiting transgressive segregants (Fellahi *et al*., 2013). Superior F_1 are selected in several self-pollinated crops, such as sorghum (Mohammed, 2009; Ingle *et al*., 2018) and tomatoes (Shankar *et al*., 2013) to develop hybrid cultivars. However, the development of hybrid mung bean cultivars is not economically beneficial at the moment because performing the manual emasculation of the female parent is challenging. The cleistogamous mechanism is a natural limit encountered in developing mung bean hybrids (Nair *et al*., 2012). The hybrid cultivars of *V. mungo* are made possible through genetic modification from cleistogamous to chasmogamous via mutation followed by inducing male sterility (Chakraborty *et al*., 2010). The pure line cultivar is the most common type for mung bean (Xin *et al*., 2003).

Broad-sense heritability (h^2_{bs}) is the proportion of genetic variance to total phenotypic variance, whereas narrow-sense heritability (h^2_{ns}) is additive-genetic to total phenotypic variance. The ratio of additive-genetic to phenotype reflects the fixable component of variance through selection to improve a target quantitative trait. The estimation of heritability for the six traits studied in mung bean is presented in Table 4. The low estimates of h^2_{ns} for all traits ranged from 0.01 to 0.02, indicating the low control of additive genes for trait expression. The estimation of h^2_{ns} affirms the discussion of genetic parameters that previously showed nonadditive gene control. The breeding strategy for low narrow-sense heritability is to delay selection to later segregating generations. The reliable selection of transgressive recombinants is possible. Inbreeding for several generations will lead to the accumulation of additive genes until sufficient homozygosity is observed in a higher proportion.

The best F_1s are selected on their basis of their performance. F_1 selection followed by selection in further

generations is commonly practiced in the breeding of self-pollinated crops. Previous studies reported a similar approach for mung bean (Tantasawat *et al*., 2015; Surashe *et al*., 2017; Kakde *et al*., 2019), soybean (Ghiday *et al*., 2016; Ghiday and Tizzazu, 2017), and wheat (Hama-Amin and Towfiq, 2019). When additive genes have low contributions, selection should be delayed and an appropriate breeding method should be applied. The recurrent selection method (Khattak *et al*. 2001; Ghiday and Tizzazu, 2017) or diallel selective mating (Narasimhulu *et al*., 2014) has been reported for mung bean and soybean. Nonadditive genes may not be directly beneficial for breeding self-pollinated crops with autogamy and cleistogamous mechanisms, such as mung bean. Chahal and Gosal (2003) described the bulk and single seed descent methods for breeding short annual crops, such as legumes, with low narrow-sense heritability and limited resources.

CONCLUSIONS

The significance of the line, tester, and F_1 effects indicated the presence of genetic variability among genotypes. Therefore, the GCA and SCA effects could be estimated. The best combiners and superior hybrids for synchronous maturity traits were selected on the basis of negative and significant values, respectively. Lom2, VR10, VR480B, VR422H, and Vima 1 were the best combiners for harvest period and DDd2, whereas VR10 and Kawur were the best combiners for DDd1. The expression of all traits studied indicated the low control of additive genes. Thus, delaying selection to later segregating generations is suggested. The reliable selection of transgressive recombinants is possible. The hybrids selected as a source to exploit transgressive segregants for synchronous maturity traits were VR10 × Vima 1, Lom2 × Vima 1, VR10 × Vima 1, VR480B × Vima 1, VR60 × No.129, Lom 1 × Vima 2, and VR82 × Vima 2. This approach should be followed by bulk or single seed descent.

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