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Inheritance and combining ability of cowpea resistance to bruchid (*Callosobruchus maculatus* F.)

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The bruchid, *Callosobruchus maculatus* (F.) is one of the most destructive pests and causes substantial losses to cowpea during storage in tropical and subtropical regions. The development of successful breeding strategy requires knowledge on gene action and trait inheritance in local and improved sources. In this study, the mode of inheritance, the types of gene action and maternal effects of cowpea resistance to bruchid was investigated. Nine parental lines and their 72 F₂ segregating populations, created in a full diallel Griffing's method 1 approach, were evaluated for resistance to bruchid attack in a randomized complete block design (RCBD) with three replications. Data were recorded on number of eggs laid by the bruchid (NE), adult bruchid emergence (NEI), median development period (MDP) and Dobie Susceptibility index (DSI) was computed. Genotype had highly significant effects on NE, NEI and MDP and DSI. General combining ability (GCA) effects of parents, specific combining ability (SCA) effects of crosses, and maternal and reciprocal effects were highly significant for all the traits. The ratios of GCA to SCA for all the traits were greater than 50% suggesting the preponderance of additive over non-additive gene action in the expression of the traits. Narrow sense heritability estimates were 64.12, 77.69 and 80.99% for NE, NEI and MDP, respectively. Parents 2419, TVu-2027 and IT84s-2246 were identified as promising general combiners for resistance to bruchid and the seven best selected crosses based on their SCA and DSI values were, IT84s-2246 × 2419, 2419 × MU9, TVu-2027 × SECOW2W and 2419 × IT90K-76, 2419 × WC69, 2419 × SECOW5T and 2419 × SECOW2W. The selected parents and/or crosses could be valuable genetic materials for breeding cowpea resistance to bruchid in Uganda or similar environments.

Key words: Additive gene action, heritability, median development period, reciprocal effects.

INTRODUCTION

Cowpea, *Vigna unguiculata* (L. Walp.) (Fabaceae) is one of the most important legume crops in arid and semiarid

regions of Africa (NRC, 2006). It is a warm-weather crop, drought tolerant and well- adapted to the drier regions

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of the tropics (Aliyu and Wachap, 2014). The crop represents one of the main sources of protein in human diet (Lima et al., 2014). Despite its relevance to agriculture in the developing world and its stress resilience, actual yields of cowpea are much lower than the known yield potential (Amatriaín et al., 2016). Production of this important crop has been constrained by insect pests among other factors (Boukar et al., 2012) and devastating effects in storage due to bruchid (Adebayo and Anjorin, 2018).

The cowpea bruchid, *Callosobruchus maculatus* F. (Coleoptera: Bruchidae), widely distributed in the tropical and subtropical regions (Adebayo and Anjorin, 2018), is the most destructive pest of cowpea during storage (Deshpande et al., 2011). *C. maculatus* attack cowpea in the field and continues after harvest, and if left unattended, cause up to 44.7% loss in weight, reduction in the germination ability, and the market and nutritional values of cowpea seeds (Oluwafemi, 2012; NARO, 2012; Adekunle and Ayodele, 2014; Miesho et al., 2018). Although several control measures for bruchids are available, such as, synthetic insecticides, plant extracts and other traditional methods such as mixing the cowpea seeds with ash (MBAZARDI, 2014), the use of host-plant resistant cultivar is currently viewed as the most economical and eco-friendly option (Orawu et al., 2013; Adebayo et al., 2016). To develop an appropriate breeding strategy, the search for sources of resistance to bruchids in cowpea must be followed with the study of the inheritance of resistant genes.

In an earlier study (Miesho et al., 2018), 18 bruchid resistant genotypes were identified from local and introduced cowpea genotypes; for example, 2419, IT84s-2046 and TVu-2027. However, knowledge regarding the genetic control and heritability of the resistance to *C. maculatus* was not studied and yet it is needed to optimize breeding pipeline for bruchid resistance (Barelli et al., 1999; Viana et al., 1999). Previous genetic studies using TVu-2027 as donor suggested that maternal genes are involved in the inheritance of resistance to bruchid (Dobie, 1981). The same study highlighted involvement of a major recessive gene and modifiers, and also noted that either dominant or interactive effects were more important than additive types of gene effects (Dobie, 1981). Redden (1983) reported paternal and embryonic genotypic effect in certain backcross combinations of F₃ generation and digenic control of resistance in one of their cross and monogenic control in another cross, in conjunction with one or more modifier or minor gene loci. In contrast, Kitch (1987) and Adjadi et al. (1985) reported that resistance to bruchid resulted from two recessive genes. In Uganda, studies on inheritance of resistance to bruchid are scarce. It is important to understand the heritability of resistance to bruchid character and the gene action controlling it to help breeders select suitable parents for the breeding program. Therefore, the aims of the present study were to identify the mode of

inheritance, estimate the gene effects as well as identify parents and crosses with good combining abilities for cowpea resistance to bruchid under the Uganda growing condition.

MATERIALS AND METHODS

Experimental procedures and diallel mating scheme

Nine cowpea genotypes comprising of five bruchid resistant (IT90K-76, IT97K-499-35, TVU-2027, 2419 and IT84s-2246) and four susceptible (SECOW2W, WC69, MU9 and SECOW5T) lines used as parents were selected from out of 145 cowpea genotypes by a no-choice laboratory bruchid damage bioassay (Miesho et al., 2018). These genotypes were selected based on their adaptation to wider agro-ecology, preference by farmers and resistance to other biotic and abiotic stresses.

The nine cowpea parental lines were each planted separately in a five-litter bucket (two seeds per bucket) in September 2015 in a screen house at Makerere University Agricultural Research Institute Kabanyolo (MUARIK), Uganda, located at 0°28'N and 32°37'E, at approximately 1200 m a. s. l. Each line was hand emasculated before pollen shading and crossed at flowering in all possible combinations following Griffing's (1956) method 1 approach to produce 36 F₁ plants and 36 reciprocal crosses. The F₁ seeds and the reciprocal crosses were selfed to produce F₂ generation in a screen house. The F₁ seeds were planted along with their parents to identify true crosses. The F₂ seeds were harvested and bulked for each of the 36 crosses and 36 reciprocal crosses.

Bruchid laboratory culture

Adults of *C. maculatus* (F.) were obtained from the National Agricultural Research Laboratory, Kawanda. A permanent laboratory culture of the insect was established at MUARIK by allowing the insects to lay eggs on a susceptible inbred line IT71. Insects were reared on 12 kg seeds kept in four transparent plastic buckets of 5 L capacity whose tops were covered with muslin cloth to provide aeration and prevent the insects from escaping. The insects were allowed to oviposit, and their progeny maintained by regularly replacing the infested seeds with fresh seeds.

Screening of cowpea seeds for resistance to *C. maculatus*

To evaluate for resistance to bruchids, 10 F₂ generation seeds of each of the 36 F₁ and 36 reciprocal crosses and the nine parents were weighed and separately put in a Petri-dish of 90 × 15 mm. Thirty seeds were randomly selected from each of the bulked F₂s and parental seeds and oven dried at 40°C for 24 h to destroy any insects or eggs that could have been present and to standardize moisture levels of the seeds (Amusa et al., 2014). The experiment was laid in randomized complete block design with three replications. Time was used as blocking factor and infestation was done at an interval of eight days in order to ease data collection. To each Petri dish containing the ten seeds, two pairs of three-day old male and female adult bruchids from laboratory culture were introduced and the top covered to prevent the insects from escaping. The insects were left undisturbed in the Petri-dishes for three days to allow for mating and oviposition and then removed (Amusa et al., 2013). Data on number of eggs, daily insect emergence, number of exit holes, number of damaged and undamaged seeds, initial seed weight (g) and residual seed weight (g) were recorded for 44 days after insect introduction, and percentage weight loss and percentage pest tolerance computed.

Table 1. Analysis of variance for resistance of cowpea genotypes to *C. maculatus* infestation.

Source of variation	df	NE	NEI	ANH	MDP	PWL	PPT	DSI
Genotype	80	1831.45***	888.50**	9.14***	155.00***	543.23**	2766.76**	16.45**
Replication	2	16.807ns	5.94ns	0.75*	4.49*	0.45ns	153.10ns	0.95***
Residual	160	7.32	3.55	0.64	1.45	1.96	61.42	0.11

NE= Number of eggs; NEI= Number of emerged insects; ANH= Average number of holes; MDP= Median development period; PWL= percentage weight loss; PPT= percentage pest tolerance; DSI= Dobie susceptibility index. ***, **, * and ns; significant at $P \leq 0.001$, $P \leq 0.01$, $P \leq 0.05$ and non-significant, respectively.

The number of emerged adult bruchids was recorded daily until no more adults emerged for five days. At the end of the experiment, Dobie Susceptibility Index (DSI) was calculated for each genotype using the data on total number of adult bruchid that emerged on each genotype and their median development period (that is the time from the middle of oviposition to the emergence of 50% of adult bruchids) using the formula of Dobie (1974):

$$DSI = \frac{\text{Loge F1} \times 100}{MDP}$$

Where, F1 is the total number of emerging adults and MDP is the median developmental period (days).

The susceptibility index ranging from 0 to 11 was used to categorize the cowpea genotypes; where; 0-3 = resistant, 4-7 = moderately resistant, 8-10 = susceptible and ≥ 10 = highly susceptible (Dobie, 1974).

Data analysis

General analysis of variance, using GenStat discovery 16.1th Edition statistical package, was performed for all quantitative data.

Diallel analysis was performed for all quantitative data of the populations developed by Griffing's (1956) Method 1 using Genetic Designs in R (AGD-R) Version 3.0 (Rodríguez et al., 2015). In this model, genotypes were considered as a fixed effect whereas replication effects were regarded as random.

Estimation of heritability, general and specific combining ability, reciprocal and maternal effects, and Bakers ratio

The general combining ability (GCA) effects were analyzed for each parent. Specific combining ability (SCA) and reciprocal effects were analyzed for the F₂ crosses and their reciprocals, respectively. Similarly, maternal effects were analyzed for each parent. Confirmation of the adequacy of the additive and non-additive variances was estimated. Coefficient of genetic determination in the narrow (CGD-NS) and broad sense (CGD-BS), analogues of the narrow sense (h²) and broad sense heritability (H²), respectively were estimated. All the analysis was done using Genetic Designs in R (AGD-R) Version 3.0 (Rodríguez et al., 2015).

Phenotypic correlation analysis was used to investigate the relationship among number of eggs, adult bruchid emergence, median development period, percentage pest tolerance and Dobie susceptibility index. The analysis was done with GenStat Discovery, 16th Edition statistical package using data from the reciprocals, crosses and the nine parents.

RESULTS

There were significant differences in the responses of the

parents and the F₂ segregating populations to bruchid infestation for all the traits measured (Table 1).

The observed significant differences among progenies were for number of eggs laid (NE), number of holes per seed (AHS), median development period (MDP), adult bruchid emergence (NEI), percentage seed weight loss (PWL), percentage pest tolerance (PPT) and Dobie susceptibility index (DSI) suggested the presence of genetic variability among the cowpea parental lines and the populations tested.

Total number of genotypes identified as susceptible, moderately resistant and resistant based on the DSI value were 15, 38 and 28, respectively (Table 5), indicating their continuous distribution to the different resistance classes (Table 2).

The Highest Dobie susceptibility index and adult emergence was recorded from the parental genotypes WC69, MU9, SECOW2W and SECOW5T than their crosses and reciprocals. The Dobie susceptibility ranged from zero for the resistant (TVu-2027 × IT97K-499-35) to 8.46 for the susceptible genotype (WC69). The number of emerged insects ranged from zero (2419 × IT84s-2246, IT84S-2246, IT84S-2246 × 2419, TVu-2027, TVu-2027 × 2419 and TVu-2027 × IT97K-499-35) to 69 (SECOW2W). Similarly, number of holes per seed was low for the resistant and high for the susceptible suggesting resistance. The correlation coefficients (r) of cowpea bruchid resistance parameters are presented in Table 3.

Percentage grain weight loss was significant ($P < 0.001$) and positively correlated with the number of eggs ($r = 0.70$) and number of holes (0.80). Number of emerged insects showed significant ($P < 0.001$) but negative correlations with MDP (-0.53) and PPT (-0.78). Dobie Susceptibility index showed significant ($P < 0.001$) but negative correlations with insect development period (-0.81) and pest tolerance (-0.86); and positively correlated with number of eggs (0.80), growth index (0.7), number of emerged insects (0.88), number of holes (0.88), and weight loss (0.57). These results imply that number of emerged insects and insect development period could be used as good indicators of cowpea resistance to bruchid.

Combining ability and maternal effects

The results of diallel analysis for the parents and F₂

Table 2. Evaluation of F₂ generation and parental seeds for bruchid resistance (some representative parental and F₂ populations).

Genotypes	Type of cross	NE	NEI	AHS	MDP	PWL	PPT	DSI
WC69	Parent	130	61.33	6.2	21.17	35	0	8.46
MU9	Parent	70	65	6.5	22	19	10	8.24
SECOW2W	Parent	95	69	6.9	23	30	3.33	7.99
SECOW5T	Parent	61	55	5.2	22	26	6.67	7.91
MU9 × SECOW5T	S×S	57	55	5.4	24	22	3.33	7.25
SECOW5T × WC69	S×S	45	36	3.5	22	38	3.33	7.07
MU9 × 2419	S×R	74	39	3.9	23	12	20	6.92
MU9 × SECOW2W	S×S	63	49	5	25.5	50	3.33	6.63
SECOW2W × 2419	S×R	40	27	2.9	24.5	15.63	30	5.84
SECOW2W × TVu-2027	S×R	32	15	1.6	23	5.42	43.33	5.11
SECOW5T × 2419	S×R	28	14	1.4	25	14.18	50	4.58
2419 × WC69	R×S	25	10.67	1.07	37.67	6.36	43.33	2.72
2419 × SECOW5T	R×S	12	9	0.8	38	2.37	56.67	2.63
2419 × SECOW2W	R×S	12	8	0.8	34.67	3.94	50	2.6
TVu-2027 × IT90K-76	R×R	12	5	0.5	28	1	76.67	2.5
TVu-2027 × SECOW2W	R×S	16	5	0.5	34	5	60	2.06
2419 × MU9	R×S	13	4	0.4	37	3.47	73.33	1.63
WC69 × 2419	S×R	5	2	0.2	21	5	70	1.43
2419	Parent	43.33	0.67	0.07	40.67	0.09	96.67	0.24
IT84S-2246	Parent	0	0	0	44	0	100	0
IT84S-2246 × 2419	R×R	0	0	0	44	0	100	0
TVu-2027	Parent	4	0	0	44	0	96.67	0
TVu-2027 × 2419	R×R	14	0	0	44	0	100	0
LSD		4.36	3.04	1.29	1.94	2.26	12.64	0.54

R= Resistance; S= susceptible.

Table 3. Correlation coefficients (r) for cowpea genotype bruchid resistance parameters under *C. maculatus* artificial infestation.

	NE	NEI	ANH	MDP	PWL	PPT	DSI
NE	1						
NEI	0.89***	1					
ANH	0.80***	0.90***	1				
MDP	-0.48***	-0.53***	-0.48***	1			
PWL	0.70***	0.78***	0.69***	-0.50***	1		
PPT	-0.71***	-0.78***	-0.71***	0.63***	-0.75***	1	
DSI	0.80***	0.88***	0.80***	-0.81***	0.76***	-0.86***	1

*** = significant at P ≤ 0.0001.

segregating populations and the different genetic variance components for number of eggs, adult emergence, and median development period are presented in Table 4.

The GCA and the SCA effects were both significant (P ≤ 0.001). Highly significant (P ≤ 0.001) difference was also observed among the reciprocal crosses for the traits measured, indicating significant diversity among the

genotypes. Additionally, maternal effect was significant (P ≤ 0.001) for NE, NEI and MDP. The number of eggs laid by the bruchid, adult bruchid emergence, and median development period accounted for 52.42, 64.34, 64.11 and 51.51% of the sum of squares for the parents and 29.15, 18.24 and 11.69% of the sum of squares for the crosses, respectively (Table 4). The result also provided evidence for the existence of wide variation among both

Table 4. Combined ANOVA for GCA and SCA, heritability and degree of dominance of F₂ population and parents' diallel analysis for number of eggs, *C. maculatus* emergence and median development period.

Source	DF	NE	NEI	MDP
GCA	8	10056.36***	6031.5***	917.94***
SCA	36	1242.39***	379.94***	46.29***
Reciprocal	36	592.76***	234.49***	94.37***
Maternal	8	867.85***	577.82***	231.05***
Residual	160	7.32	4.6	1.52
σ^2_{GCA}		186.09	111.61	16.97
σ^2_{SCA}		205.84	62.56	7.46
BR		0.64	0.78	0.82
CGDNS (%)		64.12	77.69	80.99
CGDBS (%)		99.74	99.92	98.53
Degree of dominance		1.05	0.75	0.66

*** Data significant at $P \leq 0.001$; GCA, the general combining ability; SCA, the specific combining ability; Reciprocal the reciprocal crosses; BR the Baker's ratio; σ^2_{GCA} = variance of general combining ability; σ^2_{SCA} = variance of specific combining ability of parents; CGDNS, the coefficient of genetic determination – narrow-sense heritability estimates; CGDBS, the coefficient of genetic determination – broad sense heritability estimates.

the parents and the resultant crosses, suggesting a high potential for selections for improvement in the resistance to bruchid. Values of Baker's ratio estimated for all the traits were greater than 50% suggesting the predominance of additive over non-additive gene action in the expression of these traits.

The observed high level of coefficient of genetic determination – broad sense (H^2) also corroborated the finding that both additive and non-additive gene effects conditioned the inheritance of bruchid resistance. The coefficient of genetic determination – narrow sense (h^2) estimates for number of eggs (64.12%), emerged insects (77.69%) and median development period (80.99%) were also high, supporting the Baker's ratio which revealed that additive gene effect was more important than non-additive gene effects for controlling the inheritance of the traits.

General combining ability (GCA) effects

Results of the general combining ability effects for the nine selected parents for bruchid resistance traits are shown in Table 5.

All the parents, except IT97k-499-35 for median development period, showed significant ($P \leq 0.001$) GCA effects for number of eggs laid by the bruchid, adult bruchid emergence and median development period suggesting a greater contribution of additive gene effects in determining resistance to *C. maculatus* among the studied genotypes. Lines 2419, TVu-2027 and IT84s-2246 contributed significant ($P < 0.001$) GCA effects of -10.55, -10.03 and -8.57 for number of emerged insects

and 6.19, 4.98 and 4.49 for median development period, respectively, suggesting that the genotype performed far better in the crosses for these specific traits. Conversely, genotypes SECOW2W, WC69, SECOW5T and MU9 contributed significant ($P \leq 0.001$) and positive GCA effects of 10.97, 11.58, 13.34 and 8.10 for number of emerged insects and -3.35, -3.68, -3.17 and -4.02 GCA effects for median development period, respectively indicating their negative contribution to resistance.

Specific combining ability (SCA) and maternal effects

The majority of the F₂ generation seeds showed significant ($P < 0.001$) SCA effects for median development period, adult bruchid emergence and number of eggs laid by the bruchid (Table 6).

Significant SCA effects for median development period (MDP) were observed in 25 crosses, indicating the presence of non-additive gene effects. The lowest SCA values for MDP were observed from crosses 2419 × TVu-2027 (-5.04), IT84s-2246 × SECOW5T (-4.49), IT84s-2246 × IT90K-76 (-3.73) and 2419 × SECOW2W (-2.79), and the highest were recorded from TVu-2027 × IT97K-499-35 (6.64). Likewise, significant SCA effects for number of emerged insects were observed in 29 crosses ranging from -14.93 (2419 × WC69) to 18.45 (SECOW2W). These results suggested that resistance of these genotypes was higher or lower than would be expected from the average resistance of their respective parents and therefore, these crosses could be selected for the improvement of resistance to bruchid.

All parents, except IT84s-2246, showed significant ($P \leq$

Table 5. Estimates of general combining ability effects for median development period, adult bruchid emergence and number of eggs laid by the bruchid in the F₂ population diallel analysis.

Parent	NE	NEI	MDP
SECOW2W	11.66***	10.97***	-3.35***
WC69	19.99***	11.58***	-3.68***
MU9	16.95***	13.34***	-3.17***
SECOW5T	5.47***	8.10***	-4.02***
IT90K-76	-7.80***	-7.64***	-1.29***
IT97k-499-35	-7.71***	-7.20***	-0.15ns
TVu-2027	-15.06***	-10.03***	4.98***
2419	-9.16***	-10.55***	6.19***
IT84s-2246	-14.34***	-8.57***	4.49***

***, **, * and ns; significant at $P \leq 0.001$, $P \leq 0.01$, $P \leq 0.05$ and non-significant, respectively.

Table 6. Estimates of specific combining ability effects for median development period, adult bruchid emergence and number of eggs laid by the bruchid in the F₂ population diallel analysis.

Female	Male	MDP	NEI	NE
SECOW2W	Secow2W	2.47*	18.45***	36.27***
WC69	Secow2W	0.42ns	5.55***	-4.07***
WC69	WC69	-0.01 ns	17.11***	52.27***
MU9	Secow2W	1.83***	-4.71***	-7.86***
MU9	WC69	-0.27 ns	-1.82*	25.97***
MU9	MU9	-0.19 ns	13.25***	-0.99ns
SECOW5T	Secow2W	1.81***	12.40***	11.62***
SECOW5T	WC69	-0.58***	-2.58***	-13.05***
SECOW5T	MU9	1.91***	2.16***	-4.68***
SECOW5T	SECOW5T	2.19***	15.39***	12.30***
IT90K-76	Secow2W	0.28***	-5.23***	-7.10***
IT90K-76	WC69	1.6***	-8.51***	-15.60***
IT90K-76	MU9	-0.41***	0.40***	-0.23ns
IT90K-76	SECOW5T	-0.80 ns	-12.53***	-5.58***
IT90K-76	IT90K-76	-0.95ns	0.22ns	-6.14***
IT97k-499-35	Secow2W	-0.86ns	-7.01***	-0.36ns
IT97k-499-35	WC69	1.21**	0.22ns	-2.53**
IT97k-499-35	MU9	-1.54***	-10.38***	-20.99***
IT97k-499-35	SECOW5T	-0.61ns	-10.47***	-13.01***
IT97k-499-35	IT90K-76	-1.76ns	11.77***	11.27***
Female	Male	MDP	NEI	NE
IT97k-499-35	IT97k-499-35	-1.56*	-4.34***	2.01ns
TVu-2027	Secow2W	-2.66***	-9.84***	-8.68***
TVu-2027	WC69	1.17***	1.38ns	-9.84***
TVu-2027	MU9	-2.34***	2.96***	5.36***
TVu-2027	SECOW5T	-0.15ns	0.36ns	7.84***
TVu-2027	IT90K-76	-0.72ns	4.27***	7.45***
TVu-2027	IT97k-499-35	6.64***	-1.34ns	-4.64***
TVu-2027	TVu-2027	5.51***	-0.67ns	0.05ns
2419	Secow2W	-2.79***	-2.99***	-14.08***
2419	WC69	-1.21*	-14.93***	-29.92***
2419	MU9	-0.72***	-3.52***	-0.71ns

Table 6. Contd.

2419	SECOW5T	0.72ns	-5.79***	-10.73***
2419	IT90K-76	6.48***	8.46***	17.38***
2419	IT97k-499-35	-1.99***	16.85***	22.12***
2419	TVu-2027	-5.04***	2.51***	0.30ns
2419	2419	-0.25ns	1.36ns	26.90***
IT84s-2246	Secow2W	-0.50ns	-6.64***	-5.73***
IT84s-2246	WC69	-2.34***	3.59***	-3.23***
IT84s-2246	MU9	1.73***	1.66*	4.14***
IT84s-2246	SECOW5T	-4.49***	1.06ns	15.29***
IT84s-2246	IT90K-76	-3.73***	1.142ns	-1.44ns
IT84s-2246	IT97k-499-35	0.46ns	4.70***	6.14***
IT84s-2246	TVu-2027	-2.42***	0.36ns	2.16*
IT84s-2246	2419	4.79***	-1.95*	-11.25***
IT84s-2246	IT84s-2246	6.49***	-3.93***	-6.07***

***, ** and ns; significant at $P \leq 0.0001$, $P \leq 0.001$, $P \leq 0.05$ and non-significant, respectively.

Table 7. Estimates of maternal effect of parents on median development period, adult bruchid emergence and number of eggs laid by the bruchid in the F_2 population diallel analysis.

Parent	MDP	NEI	NE
SECOW2W	-1.14***	3.61***	5.26***
WC69	-1.54***	0.13ns	-1.30***
MU9	-1.94***	6.70***	6.96***
SECOW5T	-2.01***	-0.68*	2.19***
IT90K-76	0.39*	-0.17ns	-0.5ns
IT97k-499-35	-0.68*	-0.65*	-3.07***
TVu-2027	3.45***	-2.89***	-3.83***
2419	3.19***	-3.19***	-4.48***
IT84s-2246	0.28 ns	-2.87***	-1.22***

0.01) maternal effects on median development period (Table 7).

Meanwhile, SECOW2W, MU9, TVu-2027, 2419 and IT84s-2246; and IT97k-499-35 and SECOW5T showed reciprocal effects on number of emerged insects at $P \leq 0.001$ and $P \leq 0.01$, respectively. Similarly, all genotypes, except IT90K-76, showed significant ($P \leq 0.001$) maternal effect on number of eggs laid by bruchid.

Most crosses showed significant ($P \leq 0.001$) reciprocal differences for number of eggs, number of emerged insects and median development period (Table 8).

Overall, 31 reciprocal crosses showed difference in median development period and number of eggs, and 35 reciprocal crosses for number of emerged insects. Low reciprocal combining ability (reciprocal effect) for median development period was also recorded from crosses IT84S-2246 \times MU9 (-9.08), 2419 \times IT97K-499-35 (-8.58) and from crosses 2419 \times SECOW2W (-7.83). Crosses

2419 \times IT97K-499-35 (9.33), IT84S-2246 \times IT97K-499-35 (2.92) showed the highest reciprocal combining ability for median development period. Likewise, the lowest reciprocal combining ability for number of emerged insects was recorded from IT90K-76 \times SECOW2W (-9.5), MU9 \times SECOW2W (-8.67) and IT97K-499-35 \times WC69 (-3.67), indicating the presence of maternal or cytoplasmic gene effects in the inheritance of resistance to the bruchid.

DISCUSSION

Phenotypic variability

The study demonstrated the existence of phenotypic differences among the parents and segregating F_2 generations for resistance to bruchid which could be

Table 8. Reciprocal effects for median development period, adult bruchid emergence and number of eggs laid by the bruchid in the F₂ population diallel analysis.

Female	Male	MDP	NEI	NE
WC69	SECOW2W	0.92***	4.17***	1.00ns
MU9	SECOW2W	0.33ns	-8.67***	-5.17ns
MU9	WC69	-0.58***	-2.83***	0.00***
SECOW5T	SECOW2W	0.54***	-1.54***	-0.50ns
SECOW5T	WC69	0.083ns	1.83***	-1.17***
SECOW5T	MU9	1.92***	8.33***	6.83***
IT90K-76	SECOW2W	-2.17***	8.17***	10.50***
IT90K-76	WC69	-0.83***	-9.50***	-20.67***
IT90K-76	MU9	0.33ns	8.17***	17.67***
IT90K-76	SECOW5T	-0.92***	1.67***	11.50***
Female	Male	MDP	NEI	NE
IT97k-499-35	SECOW2W	0.17***	8.83***	18.33***
IT97k-499-35	WC69	-1.08***	-3.67***	-2.83***
IT97k-499-35	MU9	-1.33***	7.50***	10.33***
IT97k-499-35	SECOW5T	-2.25***	-0.17***	6.17***
IT97k-499-35	IT90K-76	0.67***	4.33***	10.50***
TVu-2027	SECOW2W	-5.17***	6.17***	6.00***
TVu-2027	WC69	-3.33***	10.33***	14.50***
TVu-2027	MU9	-3.00***	2.33***	-3.67***
TVu-2027	SECOW5T	-5.33***	0.50***	7.00***
TVu-2027	IT90K-76	2.00***	2.33***	9.00***
TVu-2027	IT97k-499-35	-4.00***	2.50***	7.33***
2419	SECOW2W	-6.08***	10.50***	12.83***
2419	WC69	-7.83***	-3.50***	-9.00***
2419	MU9	-6.50***	16.00***	28.83***
2419	SECOW5T	-6.58***	2.83***	9.67***
2419	IT90K-76	-2.42***	-0.67*	-5.83***
2419	IT97k-499-35	-8.58***	6.50***	0.67ns
2419	TVu-2027	9.33***	-3.00***	3.17***
IT84s-2246	Secow2W	1.17***	4.83***	4.33***
IT84s-2246	WC69	0.67***	12.67***	8.50***
IT84s-2246	MU9	-9.08***	6.50***	-2.50***
IT84s-2246	SECOW5T	-0.50*	-2.33***	-9.50***
IT84s-2246	IT90K-76	-0.33ns	1.00***	0.83*
IT84s-2246	IT97k-499-35	2.67***	2.00***	6.83***
IT84s-2246	TVu-2027	2.92***	1.17**	2.50***
IT84s-2246	2419	0.00ns	0.00ns	0.00ns

useful to select the best parent or cross for production or further breeding. For instance, there was a wide variation among genotypes for susceptibility index, a measure of resistance to bruchid damage (Dobie, 1974), and other traits (Table 1). Zero DSI and 44 days of MDP were recorded from genotypes IT84S-2246, IT84S-2246 × 2419, 2419 × IT84S-2246, TVu-2027, TVu-2027 × 2419 and TVu-2027 × IT97K-499-35 (Table 2), suggesting that these genotypes were resistant. These results are in line with previous finding which suggested that resistant cowpea genotypes often show reduced insects emergence and delayed insect development (Amusa et

al., 2017; Miesho et al., 2018). On the contrary, the highest number of insects was recorded from WC69 (8.46), suggesting susceptibility. Similar results were obtained by Amusa et al. (2017) and Miesho et al. (2018).

Genotypic variability

The genetics of insect development period (MDP), insect emergence (NIE) and number of eggs (NE) laid by bruchid were evaluated for the parents and the segregating F₂ population. Number of emerged insect and

bruchid development period which were strongly correlated to Dobie susceptibility index (DSI) were considered as the most important parameters to measure bruchid resistance in the tested cowpea genotypes (Redden and McGuire, 1983; Jackai and Asante, 2003; Miesho et al., 2018).

General and specific combining ability effects

The study demonstrated the existence of genetic variability among the tested genotypes in their resistance to bruchid. The GCA and SCA analysis revealed significant differences ($P < 0.001$) among genotypes for number of eggs, insect emergence and median development period (Table 4), suggesting the importance of additive and non-additive gene effects in determining the inheritance of resistance to cowpea bruchid. Dobie (1981) and Redden (1983) also reported significant GCA and SCA effects for insect emergence and median development period. A 6x 6 diallel analyses in common bean revealed significant GCA and SCA effects in the study of heritability of resistance genes to *Acanthoscelides obtectus* (Kananji, 2007). Similarly, Mwila (2013) using North Carolina Design II involving crosses among two resistant and six susceptible bean lines to *C. maculatus* also reported similar GCA and SCA effect results.

The results also showed that the inheritance of number of eggs, number of insect emergence, and median development period traits were predominantly controlled by additive gene actions (Table 4). GCA effects accounted for 52.42% (number of eggs), 64.34% (insect emergence) and 51.51% (median development period) of the sum of squares for the crosses and large (>50%) GCA/SCA ratios indicated the predominance of the additive gene action to the inheritance of resistance to bruchid (Baker, 1978). Negative combining ability values for NE and NEI, and positive values for MDP are an indicator of resistance to bruchid. Thus, genotypes that presented negative GCA values for number of eggs were TVu-2027 (-15.06), IT84s-2246 (-14.34), 2419 (-9.16), IT90K-76 (-7.80) and IT97k-499-35 (-7.71); while genotypes 2419 (-10.55), TVu-2027 (-10.03), IT84s-2246 (-8.57), IT90K-76 (-7.64) and IT97k-499-35 (-7.20) presented negative GCA values for insect emergence (Table 5). Likewise, genotypes that presented the highest positive general combining ability for MDP were 2419 (6.19), TVu-2027 (4.98) and IT84s-2246 (4.49). The negative GCA values of number of eggs and emerged insects and positive GCA values of median development period indicated that the parents contributed to reduced number of eggs, number of emerged insects and contributed to delayed insect emergence; thereby provide a positive contribution to resistance and therefore could be selected as a good parent for breeding resistance to bruchid. Kananji (2007) and Mwila (2013) reported similar

results on the resistance of beans to *A. obtectus* and *C. maculatus*, respectively. Parents 2419, TVu-2027 and IT84s-2246 were identified as promising general combiners for resistance to bruchid. These genotypes revealed low seed damage, insect emergence, and weight loss; and high percentage pest tolerance and elongated insect emergence period (Table 2). Similarly, the specific combining ability effects were used to identify specific crosses with desirable traits (Acquaah, 2007). Accordingly, crosses IT84s-2246 × 2419, 2419 × MU9, TVu-2027 × SECOW2W, and 2419 × IT90K-76, 2419 × WC69, 2419 × SECOW5T and 2419 × SECOW2W which revealed lowest number of eggs and insect emergence and elongated insect development period were the best specific crosses for bruchid resistance (Table 6). The selection of parents based on data obtained from combining ability and understanding the genetic parameters controlling trait inheritance ensures the efficiency of breeding program (Sleper and Poehlman, 2006; Sharma et al., 2015).

Maternal effect

The majority of the crosses were affected by maternal genes in their resistance to bruchid (Table 7). Maternal effects are common in sexually reproducing crops, and these can be detected by investigating the existence of difference between individuals of the forward and reverse crosses (Eizadshenass, 2013). The maternal effects were significant among the reciprocals for number of eggs, insect emergence and median development period. Fewer numbers of eggs, insect emergence and extended insect development period were observed on the forward crosses involving the resistance parent as female than their counter reciprocals and the direction of crossing revealed an influence of maternal effects on the number of eggs, insect emergence and insect development period. The existence of maternal effect was also confirmed by the significant effects of reciprocal crosses and their varied SCA effects (Tables 4 and 8). Similar results were reported by Redden (1983) and Adjadi et al. (1985) in cowpea; and mungbean (Somta et al., 2007).

Heritability and gene action

Bruchid resistance traits had low magnitude of dominance variances, revealing higher estimates of broad and narrow-sense heritability. Narrow sense heritability of 64.12, 77.69 and 80.99% were recorded for number of eggs, emerged insects and median development period, respectively (Table 4). This implied that the heritability of the traits from the parents was highly predictable, thus explaining the very high values obtained for the narrow sense heritability. The results provide evidence for the presence of additive and non-additive gene effect on the

inheritance of cowpea resistance to bruchid. High heritability estimates indicated higher frequency of genes controlling the traits (Ma-Teresa et al., 1994) and expression of the reliability with which phenotypic value guides the breeding value. In the improvement of self-pollinated plants such as cowpea, additive variation is of great importance and makes it possible to successfully select better individuals in segregating populations (Warner, 1952). For this reason, backcross, pedigree, single-seed descent or gametic selection methods are recommended for advancing the segregating populations as proposed by Bernado (2003).

Conclusion and recommendation

Significant GCA, SCA and maternal effects; high levels of broad and narrow sense heritability were detected; and high GCA/SCA (>50%) ratios to all the traits revealed the predominance of additive gene action. Due to maternal effects; it is advisable to use the resistant line as female parent. The GCA results indicated parents 2419, TVu-2027 and IT84s-2246 as the best general combiners for better resistance to bruchid. The SCA results indicated IT84s-2246 × 2419, 2419 × MU9, TVu-2027 × SECOW2W, 2419 × IT90K-76, 2419 × WC69, 2419 × SECOW5T and 2419 × SECOW2W as the best crosses for direct production.

CONFLICT OF INTERESTS

The authors declare that they have no conflict of interest.

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