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Inheritance and combining ability estimates for cowpea resistance to bruchid (*Callosobruchus maculatus* Fab.) in Benin cowpea

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ABSTRACT

Cowpea bruchid (Callosobruchus maculatus Fab.) is the most important storage pest causing significant economic losses. Development of bruchid resistant cowpea varieties is the most sustainable strategy for controlling bruchid. However, information regarding the nature of gene action governing the resistance to bruchid is limited for cowpea genotypes in Benin. This study aimed to understand the genetic basis of cowpea resistance to C. maculatus. Eight parents were crossed in a full diallel mating design. 56 F2 progenies were tested with the eight parental genotypes in alpha lattice design with three replications in laboratory. Data were recorded on bruchid emergence (BE); weight loss (WL); median development period (MDP); Dobie susceptibility index (DSI); number of eggs laid (NEL); average number of holes (ANH); seed damage (SD). Combining ability analysis was performed using Griffin's method 1, model 1 in AGD-R software. The results showed that general combining ability (GCA) effects were highly significant ($p < 0.001$) and negative for BE, WL, DSI, NEL, ANH, and SD on the parents. Significant positive GCA effects were observed for MDP. Thus, the parents TVU13677, IT84S2246-4, WC36 and WC66*5T were the best combiners for bruchid resistant. High narrow sense heritability was observed for BE (0.75), WL (0.69), DSI (0.72), ANH (0.77) and SD (0.69). These results showed that both additive and non-additive gene action govern the resistance to bruchid in cowpea. The genotypes (TVU13677; IT84S2246-4; WC36; WC66*5T) and the resistant crosses were the promising genotypes and can be used in breeding programs seeking to develop bruchid resistant cowpea varieties.

1. Introduction

Cowpea (*Vigna unguiculata* L. Walp.) is cultivated worldwide, especially in the tropical region of Africa [1]. This crop is important in Sub-Saharan Africa [2] and is an essential component of the diet of people in West Africa since it is a principal source of proteins and various nutrients [3,4]. However, in West Africa especially in Benin, this crop is confronted to huge losses during storage where grain quantity and quality are severely reduced by a cosmopolitan insect pest of cowpea storage in this region: *Callosobruchus maculatus* (F.) (Coleoptera: Bruchinae), which is the major pest of cowpea in storage [3,4]. Cowpea seed damaged by bruchid loss nutritional quality, seed weight and viability and these seeds stack become warm leading to proliferation of mold [5]. A greater part of cowpea production in West Africa is impaired in postharvest condition when the cowpea storage is untreated [4,6]. It is also estimated that about 24% of cowpea produced each year throughout the world is damaged by cowpea bruchid with no intervention [7].

Common practices to control bruchid include the chemical insecticides or pesticides utilization, which often cause health issues to the human body and environmental hazards. It is reported that chemical tools increasingly used by farmers to control the cowpea bruchid incidences in storage have sanitary and environmental hazards and also associated with harmful effects on stakeholders [8,9]. However,

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following the increased of public perception on health and environmental safety aiming to reduce the harmful effects, the use of natural products and biopesticide plants have been encouraged [6]. Therefore, the development of the alternative methods to manage the cowpea bruchid in storage are the major priorities. Host plant resistance may be the best strategy to manage bruchid, reducing or eliminating the dependence of toxic chemicals that farmers are not well equipped to handle [10]. These authors report that cowpea varieties resistant to bruchid are the most efficient approach and ecofriendly, as they cause no harm to the humanity and besides the environment.

Breeders argued that information regarding combining ability, nature of gene action governing the inheritance of resistance to a constraint and heritability estimates are basic requirements for breeding resistant crops genotypes [11]. Combining ability and heritability estimates are specific to germplasm being tested [12]. Development of cowpea varieties resistant to bruchid requires knowledge of the nature of bruchid resistance and on the breeding value of the genotypes, providing the valuable directions in the choice of the cowpea breeding strategies. Previous inheritance studies reported on the resistance to bruchid in cowpea showed that parents TVu-2027, 2419 and IT84s-2246 were good combiners for the bruchid resistance in cowpea in Uganda [13]. Additional investigations using TVu-2027 as donor parent, showed that maternal gene effect is involved in the inheritance of bruchid resistance [14]. This work also showed the implication of a recessive gene and modifiers, and highlighted that either dominant or interactive effects were more significant than additive effects of genes [14].

However, information about combining ability and nature of gene action governing the resistance to bruchid are not available for cowpea genotypes in Benin. Thus, the use of sources of resistance to introgress resistance into susceptible landraces with desired agronomic traits through a breeding program is limited. The resistance characteristic in cowpea seed was reported to be based on the delay, stagger and low emergence levels of cowpea bruchid [15]. In cowpea, the resistance to bruchid is conferred by several factors which can act alone or in combination with others. To identify cowpea lines expressing resistance to bruchid for inheritance study, several studies have been conducted. The screening method of cowpea is usually used to identify the resistant and the moderately resistant cowpea among the cowpea lines [16,17]. Thus, to check the resistance and susceptible status of cowpea germplasm, over 8000 cowpea germplasm have been screened by Singh and Singh [18] and few additional sources have been identified.

A screening study was conducted in previous research conducted in Benin [19], and fourteen bruchid resistant accessions were identified. However, for these accessions, the lack of knowledge regarding the genetic control of resistance to cowpea bruchid is affecting further improvement of cowpea aiming the resistance to bruchid [20]. Thus, it is relevant to understand how the resistance to bruchid can be transferred through generations and the gene action controlling it. The main objective of this research was to understand the gene actions governing the resistance to bruchid and to estimate the heritability of traits associated to the resistance to bruchid among the germplasm.

2. Materials and methods

2.1. Development of genetic populations

Eight cowpea accessions including four cowpea bruchid resistant (TVU13677; IT84S2246-4; WC36; WC66*5T), and four cowpea bruchid susceptible (*Glessissaffodo*, *Kpegnikoun*, TVU946 and *Akounado*) were selected from the previous screening [19], and used as parents. Except the resistance and susceptible characteristics of parents used (Table 1), these cowpea accessions were also selected based on their adaptation to Benin agro-ecology, high yielding, and resistance to other biotic and abiotic stresses (Table 1). At flowering step, each cowpea variety was hand emasculated and was crossed in all possible combinations following full diallel mating design to generate 28 F_1, 28 reciprocals and 8 parents self-crossed. The F_1s and the reciprocal plants were selfed to generate F_2 seeds. The F_1 seeds planted were placed along their female-parents to identify true crosses (success crosses). At the end of maturity of pods, the F_2 seeds of each category (F_1 crosses and reciprocals crosses) were harvested.

Table 1
Parents characteristics.

Entry	Names	Origin	Resistance status	Agronomic characteristics
1.	TVU13677	IITA-Nigeria	Resistant	High yielding
2.	IT84S2246-4	IITA-Nigeria	Resistant	Resistant to bruchid
3.	WC36	Uganda	Resistant	High yielding, Thrips susceptible
4.	WC66*5T	Ghana	Resistant	High yielding
5.	*Glessissaffodo*	Benin-landrace	Susceptible	High yielding
6.	*Kpegnikoun*	Benin-landrace	Susceptible	High yielding
7.	TVU946	IITA-Nigeria	Susceptible	Resistant to LPB[a]
8.	*Akounado*	Benin-landrace	Susceptible	Drought resistant

[a] LPB: Legume Pod Borer.

2.2. Culturing of cowpea bruchid

Cultures of cowpea bruchid used in this experiment were established during a previous study [19]. These cultures of bruchid were maintained using a highly susceptible accession, *Tawa* (local variety) which was kept in a freezer at −20 °C for a week to eliminate eventual field infestation. One hundred (100) adults of cowpea bruchid (*C. maculatus*) were used to infest 10 Kg of *Tawa* shared into four plastic jars of 2 L. About 72 h after infestation, the one hundred adults of cowpea bruchid previously introduced in jars were removed and the infested grains were left until emergence of new adult insects. Then, each plastic content, were sieved daily to collect 24 h old insects which were used in the screening experiment.

2.3. Experimental design

2.3.1. Artificial infestation and data collection

A total of 10 randomly selected F_2 cowpea seeds per (petri-dish) were tested in a screening test. 10 F_2 seeds and the eight parents were weighed and separately put in a petri-dish (90 × 15 mm). For the infestation, a sample of 10 seeds of each of the 192 experimental types of F_2 seeds were frozen at −20 °C for 14 days to control any previous infestations (live insects or eggs) by cowpea bruchid or any other pests. Each cowpea sample in petri-dish was infested with four newly emerged bruchid: 2 males and 2 females. Each petri-dish was covered to prevent the bruchid from escaping. The adults of cowpea bruchid were allowed to mate and oviposit for 6 days on the cowpea seeds [21], after which the individuals bruchid were removed from the petri-dishes and the number of eggs laid were counted. The experiment was laid in alpha lattice design with three replications. Data were collected on the number of exit holes, number of damaged seeds, residual seed weight (g). The number of emergence days; and percentage of weight loss were computed using the method of Amusa et al. [22]. Total number of emerged adults of bruchid in each sample were counted and recorded daily until the end (no more adults emerged for three days).

- Percentage of Bruchid Emergence

$$\text{Adult emergence } (\%) = \frac{\text{Number of adults emerged}}{\text{Total number of eggs laid}} \times 100$$

- Percentage of seed damage

$$\%\ \text{Seed damage} = \frac{\text{number of damaged seed}}{\text{total number of initial seed}} \times 100$$

- Percentages of weight loss

$$\%\ \text{weight loss} = \frac{\text{initial weight} - \text{final weight}}{\text{initial weight}} \times 100$$

Dobie Susceptibility Index (DSI) was calculated for each plot using the data on total number of adult bruchid that emerged and their median development period using the formula of Dobie [23];

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

where, F_1 is the total number of emerging adults and MDP is the median development period (days).

The median development period was calculated as the number of days from the middle of oviposition (d3) to the first progeny emergence. If none emergence of insect occurred over the test period, the Dobie Susceptibility Index value is equal to zero (DSI = 0) [24].

The susceptibility index ranging from 0 to 11 were used to categorize the cowpea varieties; where; 0–3 = resistant, 4–7 = moderately resistant, 8–10 = susceptible and ≥10 = highly susceptible [23].

2.4. Data analysis

Statistical analyses on the data were performed in R version 3.6.0. One-way analysis of variance (ANOVA) was used to examine differences in the performance of cowpea genotypes according to their bruchid resistance. Fisher's LSD test was used to separate the means at 5% significant level. Pearson correlation was used to determine the relationship between the resistance parameters assessed in this study.

Diallel analysis was performed for all data using the method 1 and model 1 of Griffing [25] in Analysis of Genetic Designs in R (AGD-R) Version 3.0 [26]. This method is expected to provide unbiased estimates of population parameters [25,27,28]. For this model, genotypes (parents, F_2s, and reciprocals) were considered as a fixed effect in contrast to the replication effects which were random. The statistical model used for the analysis variance on the full diallel analysis was:

$$Y_{ijk} = \mu + g_i + g_j + S_{ij} + r_{ij} + b_k + e_{ijk},$$

where μ is the overall mean, g_i is the GCA (General Combining Ability) effect of the ith parent, g_j is the GCA effect of the jth parent, s_{ij} is the SCA (Specific Combining Ability) effect of the ijth genotype, r_{ij} is the reciprocal effect of the ijth genotype, b_k is the effect of kth block, and e_{ijkl} is the experimental error effect on the ijk^{th} observation.

2.5. Estimate of combining ability, heritability, reciprocal and maternal effects, and Bakers ratio

The effects of general combining ability (GCA) and specific combining ability (SCA) were analyzed for different parents and crosses. A fixed model was used in this analysis, because the parents were selected purposively, regarding their bruchid resistance and other agronomic traits.

Baker's ratio (X) was used to determine the importance of general combining ability (GCA) over the specific combining ability (SCA):

$$X = \frac{2\sigma^2 g}{(2\sigma^2 g + \sigma^2 s)},$$

where $\sigma^2 g$ is the GCA variance component and $\sigma^2 s$ is the SCA variance component.

This Baker's ratio suggests the relative significance of additive versus non-additive effects [29]. General combining ability (GCA) effect is higher in progeny performance prediction when the ratio closer to unity and in the cases of fixed effects analysis, the mean squares components of the parameters would be used [29]. Coefficient of genetic determination in the broad sense (CGD-BS) and narrow sense (CGD-NS), analogous of the narrow sense (h^2) and broad sense heritability (H^2), respectively were estimated:

$$\text{NS} - \text{CGD} = \frac{2\ \sigma^2 g}{(2\sigma^2 g\ + \sigma^2 s\ + \sigma^2 e)} \approx h^2;$$

$$\text{BS} - \text{CGD} = \frac{(2\ \sigma^2 g + \ \sigma^2 s)}{(2\ \sigma^2 g\ + \sigma^2 s\ + \sigma^2 e)} \approx H^2,$$

where $\sigma^2 g$, $\sigma^2 s$ and $\sigma^2 e$ are respectively GCA variance, SCA variance and error variance.

3. Results

3.1. Effects of bruchid infestation on the cowpea genotypes

The results from the analysis of variance revealed significant differences among the genotypes for all traits measured except the Number of Egg Laid (NEL). The Percentage of Weight Loss (PWL) ranged from 0.00 to 88.63% with a variation coefficient (CV) of 67.2%. Dobie Susceptibility Index (DSI) varied from 0.00 to 8.98 among the genotypes with a CV of 64.75%; the Percentage of Seed Damage PSD ranged from 0 to 100 with a CV of 64.13%; MDP varied from 0 to 61 with a CV of 54.57% and PBE ranged from 0.00 to 95.45 with a CV of 55.00% (Table 2).

Variability was also observed among the genotypes for all parameters and confirmed the difference among the cowpea genotypes tested for bruchid resistance (Table 3). Most of the bruchid susceptible crosses and parents had the highest average number of holes (ANH) *Akounado* (ANH = 32.7), *Kpegnikoun*Glessissaffodo* (ANH = 30.7); whereas the bruchid resistant parents and crosses had the lowest average number of holes (ANH): WC36 (ANH = 0), TVU13677*WC36 (ANH = 1) (Table 3).

For all cowpea genotypes studied, there were differences in the PWL and the PSD (Table 3). Bruchid susceptible crosses and parents had the highest PWL; *Glessissaffodo*Akounado* (100% damaged, 62% weight loss) and *Glessissaffodo* (96.67% damaged, 47.4% weight loss) while, bruchid resistant crosses and parents performed well; WC36 (0% damaged and 0.32% weight loss), and TVU13677*IT84S2246-4 (3.33% damaged and 8% weight loss). There were no significant differences in NEL among cowpea genotypes tested. However, among these genotypes there was numerical difference for the number of eggs laid. The quantity of eggs laid on susceptible crosses and parents was higher (*Akounado*Kpegnikoun* and *Akounado* with NEL of 41.33 and 39.67, respectively) than the resistant crosses and parents (WC36*IT84S2246-4 and WC66*5T with 0 and 10.67, respectively; (Table 3).

For percentage of bruchid emerged (PBE) and median development period (MDP) there were significant difference among crosses combinations. The bruchid susceptible genotypes had the highest PBE and the lowest MDP (*Kpegnikoun*: 89.37 PBE and 21 MDP) in opposite to the bruchid resistant genotypes with lower PBE and higher MDP (TVU13677 with 5.74 PBE and 17.67 MDP) (Table 3). It also recorded that crosses including bruchid susceptible and bruchid resistant extended the development time (*Kpegnikoun**IT84S2246-4: 53.06 PBE and 29.67), showing the resistance characteristic incorporated to the susceptible genotype.

Significant differences were observed in Dobie susceptibility index (DSI) among parameters, and the genotypes TVU13677*IT84S2246-4, WC36 and WC36*IT84S2246-4 showed the lowest DSI (0), while others genotypes showed DSI value lower than 3 and were resistant to bruchid (Table 3). The genotypes that showed DSI values lower than 3 include; *Glessissaffodo**WC36 (DSI = 2.92), and *Akounado**IT84S2246-4 (DSI = 2.09).

Table 2

Means squares for cowpea resistance parameters to *C. maculatus* on parents and F_2 progenies.

Source of variation	Df	Parameters						
		ANH	PWL	PSD	NEL	PBE	MDP	DSI
Genotypes	63	331.3***	1315.5***	3094.1***	408.6^{ns}	2623.7***	300.68***	16.63***
Residuals	128	122.2	191.6	455.2	303.2	219.5	20.11	2.19
Range		0–69	0.00–88.63	0–100	0–85	0.00–95.45	0–61	0.00–8.98
CV (%)		51.73	67.20	64.13	43.88	55.00	54.57	64.75

PBE: Percentage of Bruchid Emergence; PWL: Percentage of Weight Loss; MDP: Median Development Period; DSI: Dobie Susceptibility Index; NEL: Number of Egg Laid; ANH: Average Number of Hole; PSD: Percentage of Seed Damage; *** = $p < 0.001$; ns: no significant; df: degree of freedom.

The classification of the studied genotypes, based on the Dobie's susceptibility index revealed that 31.25% were resistant, 62.5% moderately resistant and 6.25% were susceptible (Table 3).

3.2. Analysis of variance for crosses, reciprocal, GCA and SCA

The results showed that there were significant ($P < 0.001$) differences among crosses for ANH, PWL, PSD, NEL, PBE and DSI. The GCA effects were significant for all evaluated parameters while the SCA effects were only significant for PWL, PBE, and DSI (Table 4). GCA effects contributed 100% of the crosses sum of squares for Average Number of Hole.

Percentage of weight loss (PWL) for crosses, reciprocal, and GCA were significant ($p < 0.001$) and SCA was also significant ($p < 0.01$) (Table 4). The assessment of the relevance of the genetic effects governing the PWL revealed that GCA effects contributed to 89% while SCA contributed to 11%.

The percentage of seed damaged (PSD) analysis indicated that crosses, replications and GCA were significant at 0.1% (Table 4). About the determination of the importance of genetic effects controlling the PSD, it was observed that GCA effects participated for 97%, while SCA effects participated for 3% of the crosses' sum of squares.

For the number of egg laid (NEL), the crosses, replications and GCA components were significant at 0.1% and reciprocal ($p < 0.05$) (Table 4). GCA and SCA contribution analyzing in NEL showed that only GCA effects contributed (100%) to the crosses' sum of squares.

The mean square values for the percentage of bruchid emerged (PBE) showed that crosses, replications, GCA and SCA were significant ($p < 0.001$) (Table 4). Concerning the analysis of genetic effects that govern PBE, it was perceived that GCA effects explained 88%, while SCA effects explained 12% of the crosses' sum of squares.

For the median development period (MDP), the mean square values indicated that GCA effect was significant ($p < 0.05$), and was highly significant at 0.1% (Table 4). Evaluation of genetic effects that control the MDP showed that GCA effects accounted for 100% of the crosses' sum of squares.

The mean square values for Dobie Susceptibility Index revealed that crosses and GCA effects were highly significant ($p < 0.001$). Reciprocal was significant ($p < 0.01$) and SCA effects were also significant at 5% (Table 4). The proportion of crosses sum of squares that show the importance of genetic effects in relation to the governance of Dobie Susceptibility Index was 93% for GCA effects and 7% for SCA effects.

3.3. General combining ability estimates

Estimates of general combining ability effects for the cowpea genotypes used in this study are shown in Table 5. The parents TVU13677 and IT84S2246 exhibited a highly significant and negative GCA effects ($p < 0.001$) for average number of holes. WC66*5T and WC36 also exhibited a significant and negative GCA effects for average number of hole (Table 5). A significant and positive GCA effects were exhibited by *Akounado* ($p < 0.001$), *Glessissaffodo*, TVU946 ($p < 0.01$), and *Kpegnikoun* ($p < 0.05$) for the ANH (Table 5).

The parents IT84S2246, WC66*5T, TVU13677 and WC36 presented significant ($p < 0.001$) and negative GCA effects for percentage of weight loss, while *Glessissaffodo*, *Akounado*, *Kpegnikoun* and TVU946 presented highly significant and positive GCA effects ($p < 0.001$) (Table 5). For the percentage of seed damaged the parents IT84S2246, WC66*5T, TVU13677 and WC36 displayed highly significant and negative GCA effects at 0.1%, while *Glessissaffodo*, *Akounado*, *Kpegnikoun* and TVU946 displayed highly significant and positive GCA effects ($p < 0.001$) (Table 5). TVU13677 and IT84S2246-4 produced a significant ($p < 0.01$) and negative GCA same parameter effects for number of eggs laid while *Akounado* produced a significant ($p < 0.01$) and positive GCA effects for the (Table 5).

Regarding the percentage of bruchid emerged, highly significant and negative GCA effects were observed on WC36, WC66*5T, TVU13677 and IT84S2246-4 at 0.1%, while *Akounado, Glessissaffodo, Kpegnikoun* and TVU946 exhibited highly significant and positive GCA effects at 0.1% (Table 5). Estimates of GCA effects for median development period showed that WC66*5T produced significant and positive GCA effects at 5%. Regarding Dobie Susceptibility Index, highly significant and negative GCA effects ($p < 0.001$) was produced by IT84S2246, WC66*5T, TVU13677 and WC36, while *Akounado, Glessissaffodo, Kpegnikoun* and TVU946 produced highly significant and positive GCA effects at 0.1% for the same parameter (Table 5).

3.3.1. Specific combining ability estimates for the F_2s, reciprocals and maternal effects

The specific combining ability estimates on the bruchid resistance parameters for the F_2s progenies are presented in Table 6. Significant SCA effects for percentage of weight loss (PWL) were exhibited in three crosses (WC66*5T*Glessissaffodo; WC36*Kpegnikoun; IT84S2246-4*Glessissaffodo). The lowest significant SCA value for PWL were recorded on WC66*5T*Glessissaffodo with a value of −3.28 ($P < 0.05$) and the highest were recorded on IT84S2246-4*Glessissaffodo with a value of 12.6 ($P < 0.01$) and WC36*Kpegnikoun with a value of 15.9 ($P < 0.001$).

For the percentage of seed damaged, significant SCA and positive effects ($p < 0.05$) were observed for WC66*5T*Akounado (14.3) and WC36*Kpegnikoun (18.4) (Table 6). Regarding the percentage of bruchid emerged, the significant SCA and negative effects were observed on seven crosses including TVU13677*WC66*5T (−11.4) at 5% (Table 6). For the median development period, no significant SCA effects were recorded for all crosses (Table 6). Concerning the Dobie Susceptibility Index, the significant SCA and positive effects were revealed for four crosses including WC36*Kpegnikoun (1.17) at 5% (Table 6).

For the percentage of weight loss, two parents: IT84S2246-4 (−4.6) and TVU13677 (−3.59) showed significant and negative maternal effects at 5% (Table 7). IT84S2246-4 with (−8.33) was the parent with significant and negative maternal effects ($p < 0.05$) for the percentage of seed damaged (Table 7). Estimates of maternal effects revealed that IT84S2246-4 (−6.78) showed significant ($p < 0.01$) and negative maternal effects on the percentage of bruchid emerged (Table 7). Concerning the Dobie Susceptibility Index, the parent IT84S2246-4 (−0.6) exhibited a significant and negative maternal effects (Table 7).

Estimates of reciprocal effects revealed that some crosses including Akounado*IT84S2246-4 (−6.8) and WC36*Kpegnikoun (−6.8) displayed

Table 3
Means of bruchid resistance parameters for parents and F2 progenies seeds evaluated.

Genotype	Type of cross	Cowpea seeds parameters			*C. maculatus* parameters			
		ANH	PWL	PSD	NEL	PBE	MDP	DSI
Akounado	Parent	32.7	47.7	83.33	39.67	90.37	21.67	6.83
*Akounado***Glessissaffodo*	S*S	19.7	50.5	90	24.67	89.46	23	5.81
*Akounado**IT84S2246-4	S*R	3.33	12.9	23.33	7.33	51.21	31.67	2.09
*Akounado**Kpegnikoun	S*S	33.7	69	96.67	41.33	88.63	21	7.4
*Akounado**TVU13677	S*R	9.33	21.1	43.33	19	48.83	27	3.69
*Akounado**TVU946	S*S	38.3	77.4	100	44.67	93.07	21	7.61
*Akounado**WC36	S*R	13.3	33.2	56.67	33	55.76	27	4.52
*Akounado**WC66*5T	S*R	10.3	31.3	60	19.67	72.69	23	4.52
Glessissaffodo	Parent	27	47.4	96.67	34.67	89.26	21	6.78
*Glessissaffodo**Akounado	S*S	34.7	62	100	43	93.1	21	7.45
*Glessissaffodo**IT84S2246-4	S*R	17.7	33.1	53.33	25	50.67	17.33	3.77
*Glessissaffodo**Kpegnikoun	S*S	18	54.6	83.33	25	86.65	21.67	6.07
*Glessissaffodo**TVU13677	S*R	5	23.4	40	10	65.08	31	2.52
*Glessissaffodo**TVU946	S*S	29.3	73.5	96.67	35.33	90.96	21	7
*Glessissaffodo**WC36	S*R	4.67	25.5	53.33	13.33	55.56	27	2.92
Glessissaffodo*WC66*5T	S*R	16	31.2	80	26.67	74.46	24.33	5.36
IT84S2246-4	Parent	1	4.85	6.667	8.333	5.333	17	0.39
IT84S2246-4**Akounado*	R*S	17	38.2	73.33	31.33	63.56	27.67	4.89
IT84S2246-4**Glessissaffodo*	R*S	18.3	54	73.33	29.67	76.64	25	5.44
IT84S2246-4**Kpegnikoun*	R*S	16.7	51.7	73.33	28.33	75.52	26.33	5.02
IT84S2246-4*TVU13677	R*R	1.67	5.09	10	13.67	8.29	35.33	0.49
IT84S2246-4*TVU946	R*S	10	36.4	53.33	18.67	74.64	25	4.53
IT84S2246-4*WC36	R*R	2.67	7.25	16.67	32.67	18.71	50.33	1.19
IT84S2246-4*WC66*5T	R*R	2.33	8.46	16.67	11	22.22	33.33	0.74
Kpegnikoun	Parent	20	51.9	86.67	25	89.37	21	6.14
*Kpegnikoun***Akounado*	S*S	28.7	57.2	90	37	84.64	21.67	6.72
*Kpegnikoun***Glessissaffodo*	S*S	30.7	58.8	90	38.67	90.5	21	6.57
*Kpegnikoun**IT84S2246-4	S*R	6.33	23.8	33.33	32	53.06	29.67	2.95
*Kpegnikoun**TVU13677	S*R	6.67	24.8	46.67	14.33	56.76	24.33	3.24
*Kpegnikoun**TVU946	S*S	13.3	51.1	80	21.33	77.86	23	5.18
*Kpegnikoun**WC36	S*R	28	57.6	80	48.33	65.42	25	5.92
*Kpegnikoun**WC66*5T	S*R	17	38.2	70	25	74.57	25	4.38
TVU13677	Parent	1	3.83	6.67	13.67	5.74	17.67	0.44
TVU13677**Akounado*	R*S	10	46.9	53.33	19.33	65.83	25	4.22
TVU13677**Glessissaffodo*	R*S	20.3	23.4	83.33	39	65.66	24.33	5.75
TVU13677*IT84S2246-4	R*R	0.33	8	3.33	2.333	8.33	17.67	0
TVU13677**Kpegnikoun*	R*S	11.3	30	73.33	27	57.54	23	4.85
TVU13677*TVU946	R*S	17	53.9	76.67	26.67	79.81	22.33	5.98
TVU13677*WC36	R*R	1	17.3	10	17.67	6.936	38	0.3
TVU13677*WC66*5T	R*R	1.67	4.53	13.33	21.67	12.22	34.67	0.83
TVU946	Parent	21.3	58.3	100	27.33	85.74	22.33	6.09
TVU946**Akounado*	S*S	23.3	62.8	86.67	29.33	88.59	21	6.56
TVU946**Glessissaffodo*	S*S	19.7	64.3	86.67	24.33	90.95	21	6.31
TVU946*IT84S2246-4	S*R	12	42.7	63.33	28	56.94	27.67	3.93
TVU946**Kpegnikoun*	S*S	25.3	71.1	100	34.33	85.78	21	6.98
TVU946*TVU13677	S*R	10	30.2	56.67	20	69.26	27	4.37
TVU946*WC36	S*R	16.7	26.7	66.67	46.67	49.91	27	5.04
TVU946*WC66*5T	S*R	16.3	48.4	76.67	29	68.64	21	6.06
WC36	Parent	0	0.32	0	0	0	NA	0
WC36**Akounado*	R*S	31.7	41.5	73.33	41.67	80.67	25.67	5.54
WC36**Glessissaffodo*	R*S	27	42.7	70	36	74.24	22.33	5.64
WC36*IT84S2246-4	R*R	0	0.22	0	0	0	NA	0
WC36**Kpegnikoun*	R*S	14.3	49.3	70	22	75.35	25	4.52
WC36*TVU13677	R*R	1.67	11.3	10	8.33	18.78	31.33	0.78
WC36*TVU946	R*S	9	42.5	50	16.33	62.62	24.33	4.13
WC36*WC66*5T	R*R	2.33	8.86	10	17	14.55	30.67	1.08
WC66*5T	Parent	2	4.68	13.33	10.67	28.21	49.67	0.75
WC66*5T**Akounado*	R*S	21	47.5	90	31	77.86	26.33	5.24
WC66*5T**Glessissaffodo*	R*S	14.7	29.6	66.67	25.67	71.45	25	5.04
WC66*5T*IT84S2246-4	R*R	1	6.81	6.67	9.67	10.83	36	0.32
WC66*5T**Kpegnikoun*	R*S	13.7	39.3	73.33	41	63.16	23.67	5.41
WC66*5T*TVU13677	R*R	1.33	10.6	13.33	13.67	11.78	37.33	0.57
WC66*5T*TVU946	R*S	12.3	47	60	23.67	68.15	25.67	4.9
WC66*5T*WC36	R*R	2.33	20.5	13.33	17.67	13.91	35.33	0.91
LSD (0.05)		17.86	22.35	34.47	28.13	23.93	22.30	2.39

S = susceptible, R = resistant; PBE: Percentage of Bruchid Emergence; PWL: Percentage of Weight Loss; MDP: Median Development Period; DSI: Dobie Susceptibility Index; NEL: Number of Egg Laid; ANH: Average Number of Hole; PSD: Percentage of Seed Damage; NA: Not Available.

significant ($p < 0.01$) and negative reciprocal effects for the average number of holes (Table 8). Some crosses *Akounado**IT84S2246-4 (−12.7) and *Kpegnikoun**IT84S2246-4 (−14; $P < 0.001$) and WC36*WC66*5T (−5.81; $P < 0.01$) exhibited significant and negative reciprocal effects on the percentage of weight loss (Table 8). For the percentage of seed damaged, significant and negative reciprocal effects were revealed for crosses, for instance *Akounado**IT84S2246-4 (−25) ($p < 0.001$) and WC36*TVU946 (−8.33) at 5% (Table 8).

Table 4
Analysis of variance for GCA and SCA, for crosses, reciprocal, replications and residual of parent and F2 population diallel analysis for the parameters.

Sources of variation	Df	Mean Squares						
		ANH	PWL	PSD	NEL	PBE	MDP	DSI
Replications	2	1137.92***	482.06**	2060.41***	3474.58***	785.18***	356.51***	17.18***
Crosses	63	322.26***	1088.6***	2934.42***	394.77***	2505.9***	184.84^{ns}	15.5***
GCA	7	2189.3***	9652.1***	23669.05***	1572.73***	20573.52***	381.76*	127.16***
SCA	28	52.76^{ns}	259.66**	439.8^{ns}	163.14^{ns}	535.5***	164.24^{ns}	2.64*
Reciprocal	28	145.26^{ns}	287.27***	604.76*	363.0179*	224.5^{ns}	169.58^{ns}	2.99**
Residual	112	98.215	123.31	368.37	200.5685	191.77	177.99	1.52

*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; df: degree of freedom; ns: non-significant; PBE: Percentage of Bruchid Emergence; PWL: Percentage of Weight Loss; MDP: Median Development Period; DSI: Dobie Susceptibility Index; NEL: Number of Egg Laid; ANH: Average Number of Hole; PSD: Percentage of Seed Damage.

Table 5
Estimates of general combining ability for the parameters in the parental population.

Parent	ANH	PWL	PSD	NEL	PBE	MDP	DSI
Glessissaffodo	6.62**	9.8***	21.97***	4.44^{ns}	20.52***	-2.36^{ns}	1.5***
IT84S2246-4	−7.03**	−14.14***	−24.68***	−6.76**	−21.52***	0.76^{ns}	−1.81***
Akounado	8.49***	11.4***	18.43***	6.69**	19.32***	-1.22^{ns}	1.55***
WC66*5T	−5.46***	−11.43***	−14.48***	-3.8^{ns}	−13.29***	5.99*	−1.14***
TVU946	4.47**	17.49***	21.56***	3.65^{ns}	18.94***	-2.01^{ns}	1.6***
Kpegnikoun	4.99*	13.49***	20.31***	5.69*	18.04***	-1.97^{ns}	1.39***
TVU13677	−7.78***	−15.4***	−22.60***	−7.16**	−21.18***	1.8^{ns}	−1.67***
WC36	−4.32*	−11.21***	−20.52***	-2.74^{ns}	−20.82***	-0.99^{ns}	−1.42***

*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; df: degree of freedom; ns: non-significant; PBE: Percentage of Bruchid Emergence; PWL: Percentage of Weight Loss; MDP: Median Development Period; DSI: Dobie Susceptibility Index; NEL: Number of Egg Laid; ANH: Average Number of Hole; PSD: Percentage of Seed Damage.

Table 6
Estimates of SCA for bruchid parameters in the F2 population.

FEMALE	MALE	ANH	PWL	PSD	NEL	PBE	MDP	DSI
Glessissaffodo	*Glessissaffodo*	-0.22^{ns}	-7.47^{ns}	-4.1^{ns}	1.12^{ns}	-9.63^{ns}	0.43^{ns}	-0.29^{ns}
IT84S2246-4	*Glessissaffodo*	4.42^{ns}	12.6**	9.27^{ns}	4.99^{ns}	6.8^{ns}	-2.53^{ns}	0.84^{ns}
IT84S2246-4	IT84S2246-4	1.07^{ns}	-2.16^{ns}	-0.7^{ns}	-2.8^{ns}	-9.48^{ns}	-9.82^{ns}	-0.05^{ns}
Akounado	*Glessissaffodo*	-1.93^{ns}	-0.22^{ns}	-2.2^{ns}	-1.96^{ns}	-6.4^{ns}	0.28^{ns}	-0.49^{ns}
Akounado	IT84S2246-4	-5.29^{ns}	-6.99^{ns}	-2.2^{ns}	-5.26^{ns}	1.74^{ns}	4.82^{ns}	-0.32^{ns}
Akounado	Akounado	1.69^{ns}	-10.4^{ns}	-10^{ns}	1.62^{ns}	-6.12^{ns}	-1.2^{ns}	-0.34^{ns}
WC66*5T	*Glessissaffodo*	0.19^{ns}	**−3.28***	9.06^{ns}	0.87^{ns}	7.88^{ns}	-4.26^{ns}	0.77^{ns}
WC66*5T	IT84S2246-4	0.17^{ns}	-2.07^{ns}	-5.9^{ns}	-3.76^{ns}	-6.51^{ns}	2.61^{ns}	-0.58^{ns}
WC66*5T	*Akounado*	-1.35^{ns}	4.17^{ns}	**14.3***	-2.21^{ns}	**11.4***	-5.41^{ns}	0.4^{ns}
WC66*5T	WC66*5T	-1.06^{ns}	-7.73^{ns}	-14^{ns}	-6.38^{ns}	-3.06^{ns}	12.4^{ns}	-1.03^{ns}
TVU946	*Glessissaffodo*	-0.58^{ns}	6.31^{ns}	-8.6^{ns}	-2.92^{ns}	-6.36^{ns}	0.07^{ns}	-0.52^{ns}
TVU946	IT84S2246-4	-0.43^{ns}	0.87^{ns}	4.69^{ns}	1.79^{ns}	**10.5***	2.28^{ns}	0.37^{ns}
TVU946	*Akounado*	3.88^{ns}	5.92^{ns}	-3.4^{ns}	1.99^{ns}	-5.28^{ns}	-1.07^{ns}	-0.14^{ns}
TVU946	WC66*5T	1.34^{ns}	6.34^{ns}	4.48^{ns}	1.83^{ns}	4.89^{ns}	-5.95^{ns}	**0.95***
TVU946	TVU946	-1.6^{ns}	**−12***	0.1^{ns}	-4.63^{ns}	-9.99^{ns}	1.05^{ns}	-1.18^{ns}
Kpegnikoun	*Glessissaffodo*	-1.27^{ns}	-1.88^{ns}	-12^{ns}	-2.96^{ns}	-7.83^{ns}	0.36^{ns}	-0.65^{ns}
Kpegnikoun	IT84S2246-4	-0.45^{ns}	3.14^{ns}	0.94^{ns}	6.58^{ns}	9.92^{ns}	3.91^{ns}	0.33^{ns}
Kpegnikoun	*Akounado*	3.69^{ns}	2.95^{ns}	-2.2^{ns}	2.12^{ns}	-8.57^{ns}	-0.78^{ns}	0.05^{ns}
Kpegnikoun	WC66*5T	1.82^{ns}	1.43^{ns}	9.06^{ns}	6.45^{ns}	6.27^{ns}	-4.99^{ns}	0.57^{ns}
Kpegnikoun	TVU946	-4.12^{ns}	-5.17^{ns}	-8.6^{ns}	-6.17^{ns}	**−13***	0.68^{ns}	**−0.99***
Kpegnikoun	*Kpegnikoun*	-3.97^{ns}	-10.4^{ns}	-11^{ns}	-11^{ns}	-4.55^{ns}	-0.36^{ns}	-0.72^{ns}
TVU13677	*Glessissaffodo*	-0.16^{ns}	-6.31^{ns}	5.52^{ns}	2.56^{ns}	8.19^{ns}	2.93^{ns}	0.23^{ns}
TVU13677	IT84S2246-4	1.82^{ns}	0.8^{ns}	-2.8^{ns}	-2.73^{ns}	-6.83^{ns}	-1.36^{ns}	-0.35^{ns}
TVU13677	Akounado	-5.04^{ns}	2.67^{ns}	-4.3^{ns}	-5.03^{ns}	1.35^{ns}	0.11^{ns}	0.01^{ns}
TVU13677	WC66*5T	0.76^{ns}	-0.88^{ns}	-6.4^{ns}	3.97^{ns}	**−11.4***	2.91^{ns}	-0.56^{ns}
TVU13677	TVU946	2.82^{ns}	4.69^{ns}	10.9^{ns}	2.18^{ns}	**18.9*****	-0.43^{ns}	**1.17***
TVU13677	*Kpegnikoun*	-2.2^{ns}	-5.96^{ns}	5.52^{ns}	-2.53^{ns}	2.45^{ns}	-1.47^{ns}	0.24^{ns}
TVU13677	TVU13677	2.56^{ns}	-0.65^{ns}	-4.9^{ns}	3.33^{ns}	-9.73^{ns}	-11.2^{ns}	-0.3^{ns}
WC36	*Glessissaffodo*	-0.45^{ns}	0.25^{ns}	3.44^{ns}	-1.69^{ns}	7.35^{ns}	2.72^{ns}	0.12^{ns}
WC36	IT84S2246-4	-1.31^{ns}	-6.2^{ns}	-3.2^{ns}	1.18^{ns}	-6.15^{ns}	0.09^{ns}	-0.25^{ns}
WC36	*Akounado*	4.34^{ns}	1.88^{ns}	10.3^{ns}	8.72^{ns}	**11.9***	3.24^{ns}	0.83^{ns}
WC36	WC66*5T	-1.87^{ns}	2.02^{ns}	-10^{ns}	-0.78^{ns}	-9.5^{ns}	2.7^{ns}	-0.51^{ns}
WC36	TVU946	-1.31^{ns}	-6.96^{ns}	0.52^{ns}	5.93^{ns}	0.3^{ns}	3.36^{ns}	0.33^{ns}
WC36	*Kpegnikoun*	6.5^{ns}	**15.9*****	**18.4***	7.56^{ns}	**15.3****	2.66^{ns}	**1.17***
WC36	TVU13677	-0.56^{ns}	5.65^{ns}	-3.6^{ns}	-1.76^{ns}	-2.98^{ns}	8.55^{ns}	-0.45^{ns}
WC36	WC36	-5.35^{ns}	**−12.5***	-16^{ns}	**−19.2***	**−16.2***	**−23.3****	-1.24^{ns}

*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; df: degree of freedom; ns: non-significant; PBE: Percentage of Bruchid Emergence; PWL: Percentage of Weight Loss; MDP: Median Development Period; DSI: Dobie Susceptibility Index; NEL: Number of Egg Laid; ANH: Average Number of Hole; PSD: Percentage of Seed Damage.

Table 7
Estimates of maternal effects on the parameters in the F2 population diallel analysis.

Parent	ANH	PWL	PSD	NEL	PBE	MDP	DSI
Glessissaffodo	1.56^{ns}	1.25^{ns}	3.33^{ns}	2.48^{ns}	2.65^{ns}	-0.1^{ns}	0.34^{ns}
IT84S2246-4	-1.75^{ns}	**−4.6***	**−8.33***	-3.81^{ns}	**−6.78****	-3.94^{ns}	**−0.6***
Akounado	2.4^{ns}	**3.79***	6.04^{ns}	2.69^{ns}	3.41^{ns}	-0.33^{ns}	**0.31***
WC66*5T	-0.02^{ns}	-1.9^{ns}	0.21^{ns}	-0.77^{ns}	1.39^{ns}	-1.08^{ns}	0.04^{ns}
TVU946	0.38^{ns}	2.22^{ns}	-1.25^{ns}	-1.56^{ns}	2.31^{ns}	-0.21^{ns}	0.01^{ns}
Kpegnikoun	0.15^{ns}	3.35^{ns}	5^{ns}	0.15^{ns}	1.86^{ns}	-0.5^{ns}	0.33^{ns}
TVU13677	-1.63^{ns}	**−3.59***	-5.83^{ns}	-3.42^{ns}	-1.1^{ns}	1.77^{ns}	-0.4^{ns}
WC36	-1.08^{ns}	-0.52^{ns}	0.83^{ns}	4.25^{ns}	-3.75^{ns}	**4.39***	-0.1^{ns}

*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; df: degree of freedom; ns: non-significant; PBE: Percentage of Bruchid Emergence; PWL: Percentage of Weight Loss; MDP: Median Development Period; DSI: Dobie Susceptibility Index; NEL: Number of Egg Laid; ANH: Average Number of Hole; PSD: Percentage of Seed Damage.

Table 8
Estimates of reciprocal effects on the parameters in the F2 population diallel analysis.

FEMALE	MALE	ANH	PWL	PSD	NEL	PBE	MDP	DSI
IT84S2246-4	*Glessissaffodo*	0.33^{ns}	10.46***	10**	2.33^{ns}	12.99***	3.83^{ns}	0.84**
Akounado	*Glessissaffodo*	−7.5***	−5.74**	-5^{ns}	−9.17**	-1.82^{ns}	1^{ns}	−0.8**
Akounado	IT84S2246-4	−6.8**	−12.7***	−25***	−12***	−6.18*	2^{ns}	−1.4***
WC66*5T	*Glessissaffodo*	-0.7^{ns}	-0.79^{ns}	−6.67*	-0.5^{ns}	-1.51^{ns}	0.33^{ns}	-0.2^{ns}
WC66*5T	IT84S2246-4	-0.7^{ns}	-0.82^{ns}	-5^{ns}	-0.67^{ns}	−5.69*	1.33^{ns}	-0.2^{ns}
WC66*5T	*Akounado*	5.33**	8.13***	15***	5.67*	2.59^{ns}	1.67^{ns}	0.36^{ns}
TVU946	*Glessissaffodo*	−4.8**	−4.57*	-5^{ns}	−5.5*	-0^{ns}	0^{ns}	-0.3^{ns}
TVU946	IT84S2246-4	1^{ns}	3.15^{ns}	5^{ns}	4.67*	−8.85**	1.33^{ns}	-0.3^{ns}
TVU946	*Akounado*	−7.5***	−7.35**	−6.67*	−7.67**	-2.24^{ns}	0^{ns}	−0.5*
TVU946	WC66*5T	2^{ns}	0.671^{ns}	8.33*	2.67^{ns}	0.24^{ns}	-2.3^{ns}	0.58*
Kpegnikoun	*Glessissaffodo*	6.33**	2.11^{ns}	3.33^{ns}	6.83**	1.92^{ns}	-0.3^{ns}	0.25^{ns}
Kpegnikoun	IT84S2246-4	−5.2**	−14***	−20***	1.83^{ns}	−11.2***	1.67^{ns}	−1***
Kpegnikoun	*Akounado*	-2.5^{ns}	−5.92**	-3.33^{ns}	-2.17^{ns}	-1.99^{ns}	0.33^{ns}	-0.3^{ns}
Kpegnikoun	WC66*5T	1.67^{ns}	-0.53^{ns}	-1.67^{ns}	−8**	5.71*	0.67^{ns}	**−0.5***
Kpegnikoun	TVU946	−6**	−10***	−10**	−6.5*	-3.96^{ns}	1^{ns}	−0.9**
TVU13677	*Glessissaffodo*	7.67***	-0.02^{ns}	21.7***	14.5**	0.29^{ns}	-3.3^{ns}	1.61***
TVU13677	IT84S2246-4	-0.7^{ns}	1.45^{ns}	-3.33^{ns}	−5.67*	0.02^{ns}	−8.8**	-0.2^{ns}
TVU13677	*Akounado*	0.33^{ns}	12.9***	5^{ns}	0.17^{ns}	8.50**	-1^{ns}	0.27^{ns}
TVU13677	WC66*5T	0.17^{ns}	-3.03^{ns}	0^{ns}	4^{ns}	0.22^{ns}	-1.3^{ns}	0.13^{ns}
TVU13677	TVU946	3.5*	11.84***	10**	3.33^{ns}	5.27*	-2.3^{ns}	0.8**
TVU13677	*Kpegnikoun*	2.33^{ns}	2.61^{ns}	13.3**	6.33*	0.39^{ns}	-0.7^{ns}	0.81**
WC36	*Glessissaffodo*	11.2***	8.57***	8.33*	11.3***	9.34**	-2.3^{ns}	1.36***
WC36	IT84S2246-4	−1.3***	-3.51^{ns}	−8.33*	−16.3***	−9.36**	-25^{ns}	−0.6**
WC36	*Akounado*	9.17***	4.14*	8.33*	4.33^{ns}	12.46***	-0.7^{ns}	0.51*
WC36	WC66*5T	0^{ns}	−5.81**	-1.67^{ns}	-0.33^{ns}	0.319^{ns}	-2.3^{ns}	0.09^{ns}
WC36	TVU946	−3.8*	7.88**	−8.33*	-15.2^{ns}	6.357*	-1.3^{ns}	−0.5*
WC36	*Kpegnikoun*	−6.8**	−4.16*	-5^{ns}	−13.2***	4.968*	-0^{ns}	−0.7**
WC36	TVU13677	0.33^{ns}	-2.98^{ns}	0^{ns}	−4.67*	5.924*	-3.3^{ns}	0.24^{ns}

*** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; df: degree of freedom; ns: non-significant; PBE: Percentage of Bruchid Emergence; PWL: Percentage of Weight Loss; MDP: Median Development Period; DSI: Dobie Susceptibility Index; NEL: Number of Egg Laid; ANH: Average Number of Hole; PSD: Percentage of Seed Damage.

Several crosses displayed significant and negative reciprocal effects for the number of egg laid. For example: WC36*IT84S2246-4 (−16.3) and WC36*Kpegnikoun (−13.2) ($p < 0.001$), *Kpegnikoun**WC66*5T (−8) ($p < 0.01$) (Table 8). Significant and reciprocal effects were observed for crosses among which *Kpegnikoun**IT84S2246-4 (−11.2) ($p < 0.001$) and WC36*IT84S2246-4 (−9.36) ($p < 0.01$), on the percentage of bruchid emerged (Table 8). For the median development period, significant and negative reciprocal effects were exhibited by TVU13677*IT84S2246-4 (−8.8) at 1% (Table 8). Regarding Dobie Susceptibility Index, significant and negative reciprocal effects were observed for several crosses including *Akounado**IT84S2246-4 (−1.4; $P < 0.001$), WC36**Kpegnikoun* (−0.7; $p < 0.01$) and *Kpegnikoun**WC66*5T (−0.5; $p < 0.05$) (Table 8).

3.4. Estimates of coefficients of determination

The estimates of heritability for the various traits studied are shown in Table 9. Apart from number of egg laid (0.43) and median development period (0.09), higher values (from 0.71 to 0.81) were recorded for the broad sense coefficient of genetic determination (BSCGD) for all the five other traits. The estimates of the narrow sense coefficient of genetic determination (h^2) showed values greater than 50% for five traits, 69% of h^2 were recorded for percentage of seed damaged and percentage of weight loss, 72% for Dobie susceptibility index, 75% for percentage of bruchid emerged, and 77% for the average number of hole. Baker's ratio

Table 9
Variance components for the estimation of broad sense and narrow sense heritability for C. maculatus resistance parameters measured.

Traits	Genetic Parameters					
	σ^2gca	σ^2sca	σ^2r	h2	H	BR
ANH	130.7	−22.72	23.52	0.77	0.71	0.98
PWL	595.55	68.17	81.98	0.69	0.74	0.94
PSD	1456.29	35.71	118.19	0.69	0.71	0.98
NEL	85.76	−18.71	81.22	0.48	0.43	0.95
PBE	1273.86	171.86	16.36	0.75	0.81	0.93
MDP	12.73	−6.87	−4.20	0.12	0.09	0.82
DSI	7.85	0.56	0.73	0.72	0.75	0.96

σ2gca = variance of general combining ability; σ2sca = variance of specific combining ability; σ2r = reciprocal component; h2 = narrow sense heritability = NSCGD = Narrow sense coefficient of genetic determination for a fixed model; H = broad sense heritability = BSCGD= Broad sense coefficient of genetic determination for a fixed model; BR = Baker's ratio.

values estimated for all the traits studied were greater than 50%. These Baker's ratio values varied from 0.82 to 0.98.

3.5. Association among parameters studied

Correlation analyses on the parameters tested in this study are presented in Fig. 1. Along the diagonal are presented the distributions of the variables; below the diagonal the scatter plots with the tendency curve are displayed and above the diagonal the coefficients of correlation associated with their significant levels. The correlation results revealed that average number of hole had a significant ($p < 0.001$) positive correlation with other parameter except median development period. Fig. 1 showed that, apart from MDP, PWL possessed strong positive relationship with ANH ($r = 0.87$; $p < 0.001$), PSD ($r = 0.92$: $p < 0.001$), NEL ($r = 0.70$; $p < 0.001$), PBE ($r = 0.90$; $p < 0.001$) and DSI ($r = 0.93$; $p < 0.001$) (Fig. 1). Meanwhile, PSD displayed a strong positive association ($r > 0.70$***) with all parameters excepting MDP (Fig. 1). Apart from MDP, NEL had a high significant ($p < 0.001$) and positive relationship with remaining parameters ($r > 60$) (Fig. 1) PBE had a good relationship with all other parameters except MDP, with ($r > 60$; $p < 0.001$) (Fig. 1). Similar results were displayed by PBE which had a strong positive correlation ($r > 0.60$; $p < 0.001$) with ANH, PSD, NEL, DSI and PWL. Fig. 1 also indicated that DSI has a high significant ($p < 0.001$) and positive relationship with PWL ($r = 0.93$), ANH ($r = 0.92$), PSD ($r = 0.98$), NEL ($r = 0.80$) and PBE ($r = 0.96$).

4. Discussion

4.1. Effects of bruchid infestation on the cowpea genotypes

Significant variations showed by the genotypes regarding all parameters studied (ANH, PSD, NEL, MDP, PBE, DSI and PWL) showed the existence of notable contrast among the genotypes tested, and revealing a possible different resistance among the genotypes. The differences observed among the damages caused by bruchid on the different genotypes could be due to the variability in the biochemical compounds contents in these genotypes tested. Furthermore, the differences in the development period of bruchid indicated the presence of biochemical compounds of cowpea seeds that affected the biology of the insect (antibiosis mechanism). This mechanism could be due to the presence in the seeds of biochemical compounds like vicilins (7S storage proteins) conferring the resistance to *C. maculatus* in the cowpea seeds [30,31]. These type of biochemical compounds may extend the developmental period by slowing down the larval development and giving to the bruchid the lower chance to survive in the cowpea seeds [32,33]. It has been reported that in postharvest condition when antibiosis is present as resistance mechanism, the colonized seeds affect the insect performance, specifically nutrition, survival, reproduction and development of the insect pest [15]. Variability in damages caused by *C. maculatus* has been reported in many studies using local and improved cowpea varieties and focusing on inheritance study [16,17,34].

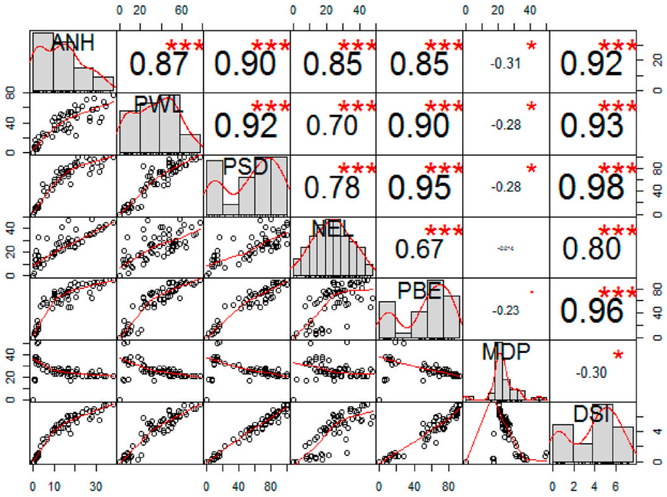

Fig. 1. Correlation matrix with scatter plots.
PBE: Percentage of Bruchid Emergence; PWL: Percentage of Weight Loss; MDP: Median Development Period; DSI: Dobie Susceptibility Index; NEL: Number of Egg Laid; ANH: Average Number of Hole; PSD: Percentage of Seed Damage; *** = $p < 0.001$; * = $p < 0.05$.

The significant means square values got for the genotypes showed that these genotypes can be distinguished into classes according to their response towards the bruchid resistance parameters. This proved the existence of bruchid resistance genes among the genotypes tested. Significant PBE is useful as it is related to the level of grain damaged. There was a significant positive correlation within these latest parameters [16]. Cowpea genotype with lower bruchid emergence is suitable for establishing bruchid resistance in cowpea. Grain damage is an important parameter associated with bruchid resistance in cowpea. Many studies have reported that grain damage was strongly positively correlated with emerged insect population and weight loss [16,35]. Thus, cowpea stored with fewer emerged insect population had reduced weight loss and small grain damage.

Other helpful parameter linked to the bruchid resistance is weight loss, since it displays clearly the economic potential of farmer [4,36]. Development of cowpea genotypes resistant to bruchid may include improving the capacity of grain to reduce weight loss. However, such improvement may also affect the nutritional and technological quality of the cowpea grains. Dobie susceptibility index is other important parameter that helps in genotypes classification regarding the bruchid resistance. Dobie susceptibility index had a strong positive relationship with other resistant parameters including bruchid emergence, weight loss and grain damage [35]. Based on the scale used, some genotypes tested (31.25%) are resistant to *C. maculatus*.

Correlation amongst bruchid resistance parameters could be used as major indicators for the improvement of cowpea resistance to bruchid. Therefore, the very high significant positive correlation observed between bruchid emergence and number of eggs laid and between bruchid emergence and average number of holes; and percentage of seed damage and percentage of weight loss was predictable, since several eggs laid and high number of holes will imply several individuals of bruchid emerged. Increased bruchid emergence will increase seed damage and weight loss [16].

Significant ($p < 0.05$) and negative correlation between Dobie susceptibility index and median development period was similar to the findings of Miesho et al. [35] who showed that longer median development period reduced the Dobie susceptibility index value. Increased time of development or longer median development period is associated to the antibiosis resistance mechanism [37]. This could justify the delaying of bruchid development in the cowpea genotypes resistant to bruchid. The strong significant and positive association observed between Dobie susceptibility index and both weight loss and seed damage showed that a higher level of percentage of seed damage and percentage of weight loss conducted to high Dobie susceptibility index.

4.2. Combining ability estimates for bruchid resistance

The estimates of combining ability are useful for the determination of the genetic potential worth of genotypes to exploit the profitable type of gene action in cowpea breeding program, focusing the resistance in cowpea. The significant differences observed among the crosses and the significant GCA and SCA effects recorded for the parameters, PBE (percentage of bruchid emerge), PSD (percentage of seed damage), DSI

(Dobie susceptibility index) and PWL (percentage weight loss) showed the genetic variability within the cowpea genotypes tested regarding their resistance to bruchid, suggesting the contribution of additive and non-additive gene actions for these parameters. Similar findings were reported by several works [13,24,38], where the GCA and SCA effects for weight loss, insect emergence, seed damage and Dobie susceptibility index were significant.

Parents with high GCA effects (negative values) would be used directly in a breeding program targeting the cowpea resistance to bruchid. In this study, GCA effects for an average number of holes showed that GCA effects for WC66*5T, TVU13677 and WC36 and IT84S2246-4 were significant and negative. Therefore, the genotypes WC66*5T, TVU13677, WC36 and IT84S2246-4 are parents that help reduce the number of holes as reported by Kananji [24]. WC66*5T, TVU13677, WC36 and IT84S2246-4 showed significant and negative GCA values for the percentage of weight loss. This showed that these genotypes will be useful in the reduction of cowpea weight loss [24].

Genotypes WC66*5T, TVU13677, WC36 and IT84S2246-4 with their significant and negative GCA values were important for reducing seed damage. TVU13677 and IT84S2246-4 exhibited significant and negative GCA values for the number of egg laid. This is desirable since these genotypes will help in the reduction of the number of the egg laid as reported by Miesho et al., [13]. WC66*5T, TVU13677, WC36 and IT84S2246-4 showed the significant and negative GCA effects for the percentage of bruchid emergence. These genotypes are beneficial regarding their capability to decrease the bruchid emergence.

WC66*5T displayed significant and positive GCA effects for the median development period, showing that the genotype WC66*5T will be useful for extending the developmental period of the weevil. This is helpful since the cowpea bruchid will take a longer period to complete his life cycle and produce fewer progeny. Amusa et al. [39], reported that when the development period of bruchid lasts longer, fewer progenies are produced. Cowpea genotypes WC66*5T, TVU13677, WC36 and IT84S2246-4 displayed significant negative GCA effects for Dobie susceptibility index. Low value of Dobie susceptibility index is an indicator of resistance to bruchid [39].

The significant SCA effects got showed the existence of the non-additive gene action [40]. High variation of SCA showed that some crosses had lower or higher levels of resistance than expected regarding the GCA values of the parents included. Therefore, the resistance to bruchid may have a complex mode of inheritance, as reported in many studies [24,29,41].

Estimates of SCA effects for percentage of weight loss revealed that genotype WC66*5T**Glessissaffodo* was the most desirable cross. This is helpful since this cross promotes the reduction of weight loss. The significant and negative SCA value for the percentage of bruchid emerged presented by the cross TVU13677*WC66*5T suggested that the cross allowed limited emergence of bruchid and make up a promised resistant variety to bruchid. The result of the contribution of GCA and SCA governing resistance parameters highlighted evidence for the existence of variation within cowpea genotypes, showing a high potential for selections targeting on improvement of the resistance to bruchid. These results corroborated the findings by Miesho et al. [13] who reported the variation among the parents and the resultant crosses based on the contribution of GCA and SCA governing the resistance parameters.

4.3. Estimates of maternal effect

In this study, few crosses were affected by maternal effects in their resistance to bruchid. For instance, TVU13677 and IT84S2246-4 exhibited significant and negative maternal effects for the percentage of weight loss. In sexual crops reproduction the maternal effect are usual, and investigation on cowpea lines can help detect the existence of difference within individuals of the reverse and forward crosses [42]. The significant maternal effects were recorded among the reciprocals, for PBE; PWL; DSI; NEL; ANH and PSD. Small ANH, lower weight loss, fewer bruchid emerge and lower DSI were exhibited on the forwards crosses, including resistant parent as female than their counter reciprocals. The direction of crossing showed maternal effects influence on PBE; PWL; DSI; NEL; ANH and PSD. These results exhibited the link between the reciprocal and the maternal effects. Some studies [13,38], have showed that the maternal effects existence were confirmed by the significant effects of reciprocals and their SCA values got.

4.4. Heritability

Estimates of narrow sense coefficient of genetic determination showed that average number of hole showed high heritability (77%) with a Baker's ratio approaching unity (0.98). This result indicated the presence of additive gene action controlling the bruchid emergence. Thus, this trait can be improved by simple recurrent selection. Narrow sense heritability estimates revealed that both percentage of weight loss and percentage of seed damage exhibited high heritability (69%). These two parameters had a Baker's ratio approaching unity with 0.94 and 0.98, respectively for percentage of weight loss and percentage of seed damage indicating the presence of additive gene action in the control of the weight loss and seed damage. These traits can be improved by simple recurrent selection. Similar results were observed on the percentage of bruchid emerge (75%) and Dobie susceptibility index (72%). Bruchid emerge and Dobie susceptibility index recorded high Baker's ratio of 0.93 and 0.96, respectively. This showed the importance of additive gene action in the resistance to bruchid for these two parameters. Simple recurrent selection can also be used for developing these traits [13]. The estimates of narrow sense coefficient of genetic determination were high for the traits presented above; suggesting that early generation selection would be expected to be effective.

Number of egg laid and median development period recorded moderately low narrow sense heritability, but their Baker's ratios were moderately high. This indicates the presence of both additive and non-additive gene action on the inheritance of cowpea resistance to bruchid and additive gene action was more important than non-additive gene action.

5. Conclusion

In the present study, significant genetic variation was revealed for PBE; PWL; MDP; DSI; NEL; ANH and PSD. Both additive and non-additive gene actions control resistance to bruchid in cowpea genotype, with additive gene effects being the most important in this study. The genotypes WC66*5T, TVU13677, WC36 and IT84S2246-4 are good transmitters of the resistance to bruchid in cowpea among the tested germplasm. Because of the maternal effects recorded, the use of resistant genotypes (WC66*5T, WC36 and IT84S2246-4) as female parent is recommended. In this experiment, antibiosis resistance mechanism has been suspected and further investigation could help to identify the biochemical compounds responsible. The resistance to bruchid in cowpea is highly a heritable trait that could be easily transmitted to the progenies in early generation selection. These genotypes will be helpful for breeders in breeding program aiming the development of genotypes capable of avoiding cowpea bruchid infestation in postharvest condition. These bruchid resistant cowpea genotypes would supply sustainable, eco-friendly and cost-effective solution to manage the stored cowpea bruchid (*C. maculatus*) in cowpea.

CRediT authorship contribution statement

Akovognon D. Kpoviessi: Methodology, Software, Data curation, Formal analysis, Writing - original draft, preparation, Writing - review & editing. **Hubert Adoukonou-Sagbadja:** Methodology, Writing - review & editing, Supervision. **Symphorien Agbahoungba:** Methodology, Data curation, Writing - original draft, Writing - review & editing, preparation Reviewing. **Eric E. Agoyi:** Methodology, Data curation, Writing - original draft, Writing - review & editing, preparation Reviewing. **Achille E. Assogbadjo:** Methodology, Writing - review & editing, Supervision, Project administration. **Daniel C. Chougourou:** Methodology, Writing - review & editing, Supervision.

Declaration of competing interest

None.

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