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Generation Mean Analysis in Cowpea [*Vigna unguiculata* (L.) Walp.] under Flower Thrips Infestation

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Abstract

Two sets of six generations (P_1, P_2, F_1, F_2, BC_1P_1, BC_1P_2) of cowpea were developed from crosses of contrasting inbred lines VYA (susceptible) × SANZI (resistant) and LORI (susceptible) × SANZI (resistant). The aim of this study was to determine the inheritance and elucidate the genetic control of cowpea resistance to thrips. The first set (VYA × SANZI) was evaluated under natural thrips infestation in the field in a completely randomized block design with three replications. The second set (LORI × SANZI) was screened using artificial thrips infestation in the screen house. In each trial, data were recorded on 150 individual plants. These included the score of thrips damages using the scale of one to nine, number of thrips per flower, number of pods per plant, pod weight per plant and grain weight per plant. The generation mean analysis revealed that both additive and non-additive types of gene effects were significant. Dominance × dominance was the most predominant type of gene effects for thrips resistance, suggesting that breeders should delay selection to late generations to allow advancement of as many high-potential recombinants as possible during hybridization. The number of genes that control the expression of number of thrips per flower was three and ranged from three to four, for score of thrips damages. High broad sense and moderate narrow sense heritability were observed ranging from 0.53 to 0.65 and 0.14 to 0.36, respectively for all of the traits measured.

Keywords: heritability, gene effects, resistant cowpea

1. Introduction

Flower bud thrips (*Megalurothrips sjostedti* Trybom) feed on a wide range of alternative host plants belonging mostly to Fabaceae family, which complicates its management (Tamò et al., 2002). Cultural practices recommended to minimise thrips infestation include irrigation, tillage operation, planting date, crop rotation and intercropping (Asiwe, Nokoe, Jackai, & Ewete, 2005; Ngakou et al., 2008). In order to minimise yield losses associated with thrips damage in cowpea, a major component of long lasting and affordable control package would be genetic control via host plant resistance (Alabi, Odebiyi, & Tamò, 2006; Muchero, Ehlers, & Roberts, 2010). However, studies in other thrips spp. systems suggested that genetic resistance mechanisms might be highly specific to the insect species or even the developmental stages of the insect-pest (Frei, Bueno, Diaz-Montano, Gu, Cardona, & Dorn, 2004; Maharijaya et al., 2012). Variation exists for traits such as thrips damage score, number of thrips adults per flower, number of larvae per flower, number of pods per plant, pod weight per plant, and grain weight per plant among cowpea genotypes (Dormatey, Atokple, & Ishiyaku, 2015). Understanding the genetic control of these traits is necessary for the intelligent choice of breeding procedures for developing resistant or tolerant and high-yielding varieties. The individual value of different sources of resistance in a breeding programme cannot be assessed until the genetic relationships among them are better understood. The choice of an efficient breeding procedure depends on the knowledge of the genetic control system of the character to be selected (Adeyanju, Ishiyaki, Echekwu, & Olarewaju, 2012). This is because selection efficiency of a trait is mainly dependent on the magnitude of genetic variation and heritability of such

trait (Falconer & Mackay, 1996). There is no consensus from available reports on the genetic control of thrips resistance which illustrates the magnitude of the complex nature of this trait (IITA, 1993; Omo-Ikerodah, Fatokun, & Fawole, 2009; Dormatey, Atokple, & Ishiyaku, 2015). It is imperative to undertake a thoughtful study to better elucidate the genetic control of resistance to thrips. Thus, the objective of this study was to determine the mode of inheritance of resistance in cowpea to flower thrips. This information will be useful in determining selection criteria and appropriate breeding methods for durable resistance and sustainable yield in cowpea.

2. Materials and Methods

The study was carried out in the screen house at the Regional Research Centre of Maroua (10°35.060′N; 14°17.185′E) and in the field at IRAD's experimental site of Guiring (10°37.198′N; 14°22.114′E) from June to October 2016.

2.1 Plant Materials

The cowpea genotypes SANZI, LORI and VYA were used to develop two sets of six basic generations (P_1, P_2, F_1, F_2, BC_1P_1, and BC_1P_2) for generation mean analysis for score of thrips damage and number of thrips per flower (Table 1). VITA-7, a thrips susceptible genotype was obtained from the International Institute of Tropical Agriculture and planted as spreader of thrips in the field.

Table 1. Origin and description of the genotypes used in the experiment

Genotypes	Origins	Characteristics
LORI (S)	Institute of Agricultural Research for Development (IRAD), Cameroon	Large seed size, cream seed testa, very susceptible to thrips damage
VYA (S)	Institute of Agricultural Research for Development (IRAD), Cameroon	High number of seed per pod, white seed testa, very susceptible to thrips damage
SANZI (R)	Savannah Research Institute (SARI), Ghana	Medium yield, small seed size, black seed testa, resistant to thrips damage

Note. S = Thrips susceptible; R = Thrips resistant.

2.1.1 Population Development

Two sets of six basic generations each (P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2) were developed in the screen house in pots of 0.21 m in diameter and 0.25 m in depth, filled with 15 kg of sandy-loam soil collected from the field. The parental lines involved in these crosses were:

Set 1: P_1 = VYA (susceptible parent); P_2 = SANZI (resistant parent)

Set 2: P_1 = LORI (susceptible parent); P_2 = SANZI (resistant parent)

Three seeds were planted per pot and two plants were retained after thinning. There were 20 pots for each of the susceptible parents and 40 pots for the resistant parent. Two litres of tap water was applied per pot every morning between 6:00 to 7:00 a.m. during the growing cycle of the plants. No insecticide spray or fertilizer was applied. Weeds were hand removed from the pots when necessary. Light green buds from the female plants (P_1) were emasculated in the evening and pollinated next morning between 6:00 to 7:00 am with pollen from opened flowers of the male parent (P_2). The process of emasculation was carefully done with sharply pointed forceps sterilized with alcohol between crosses to prevent contamination by unwanted pollen. Each cross was tagged immediately with the names of parents that were involved in the cross and date of the cross. To maximize the number of successful crosses, they were carried out twice a day; early morning and late in the evening between 5:00 to 6:00 pm. In a situation whereby the flowers of the male were ready and the buds from the female were not ready, the paternal flowers were collected early in the morning, preserved in the fridge and then used to pollinate the maternal parent in the evening. In set 1: VYA × SANZI, 100 F_1 seeds were obtained and partitioned as follow: 10 seeds kept, 30 seeds planted and selfed to generate 120 F_2 seeds, 30 seeds planted and used in crosses to VYA to generate 120 BC_1P_1 (VYA × F_1) seeds. The last portion of 30 seeds was planted and used for crosses to SANZI and generated 120 BC_1P_2 (LORI × F_1) seeds. The different crosses were carried out simultaneously depending on the available ready flowers and buds. They formed the first six basic generations. Forty seeds of F_1 (LORI × SANZI) were generated for set two. Ten seeds were kept and three sub-portions of 10 F_1 seeds each were used to develop 40 F_2 seeds, 40 BC_1P_1 (LORI × F_1) seeds and 40 BC_1P_2 (SANZI × F_1) seeds to form the second six generations.

2.1.2 Evaluation of Populations

The same donor parent was used in both set of crosses. The evaluation was conducted in two different environments in order to assess the consistency effect of the resistant gene from the same donor parent. Set one (VYA × SANZI) was used for field experiment where the layout was a Randomized Complete Block Design (RCBD) with three replications. Each replication had one row of 10 plants for each non-segregating generations (P_1, P_2 and F_1) family and four rows of F_2, BC_1P_1 and BC_1P_2 leading to 40 plants. For the whole experiment, there were 30 plants for P_1, P_2 and F_1; and 120 plants for F_2, BC_1P_1 and BC_1P_2. In the same row, plants were separated by 0.20 m and 0.75m was allowed between the rows. VITA-7 was planted 10 days earlier surrounding the plots and between the plots after three rows each. At 35 days after planting, VITA-7 were uprooted and laid between the plots to allow thrips moving from dead plants and infest the plants being evaluated in the six generations. No pest control measure was applied.

Set two of population involving LORI × SANZI was used to establish pots experiment in the screen house in a RCBD. One hundred fifty pots of 0.21 m in diameter and 0.25 m in depth were filled with 15 kg of sandy-loam soil collected from the field and assigned as follows: 10 pots each for P_1, P_2 and F_1; 40 pots each for F_2, BC_1P_1 and BC_1P_2. One seed was planted per pot giving a total of 150 plants for this experiment. Watering was carried out as described earlier. At 35 days after planting 30 thrips were loaded per pot from flowers of VITA-7 which is a highly thrips susceptible variety earlier established in the field (Salifu & Singh, 1987; Omo-Ikerodah, Fatokun, & Fawole, 2009). The infestation was carried between at 6:00 to 7:00 a.m. for five consecutive days.

2.2 Data Collection

In both experiments, data were recorded on each individual plant, which involved: Scoring of thrips damage using a scale of 1 to 9 at 45 and 55 days after planting as described by Jackai and Singh (1988), and Cardona et al. (2002) in Table 2. Counting of number of thrips per flower was done at 45 and 55 days after planting wherby, two flowers were sampled per plant between 6:00 to 7:00 a.m. and placed into a 25 ml plastic vial with 70per cent alcohol. Thrips were counted later after dissection of flower using a binocular stereomicroscope in the lab. In addition, the following yield related traits were recorded: number of pods per plant, pod weight per plant, and grain weight per plant.The data were collected as well as any agreements and payments made to participants, agreements with the institutional review board, ethical standards met, and safety monitoring procedures.

Table 2. Rating scale for thrips damages

Score	Description of the damages
1	No browning/drying of stipules, leaf of flower buds; no bud abscission
3	Initiation of browning of the stipules, leaf or flower buds; no bud abscission
5	Distinct browning/drying of stipules and leaf or flower buds; some abscission
7	Serious bud abscission accompanied by browning/drying of stipules and buds; non-elongation of peduncles
9	Very severe bud abscission; heavy browning/drying of stipules and buds; distinct non-elongation of (most or all) peduncles

Source: Jackai and Singh (1988).

2.3 Data Analysis

Data collected were subjected to analysis of variance to check the difference among the generations in the two crosses using GenStat 12th edition. Generation mean analysis (GMA) was performed on SAS 9.4 software to determine the types of gene action controlling the inheritance of resistance to flower bud thrips using thrips damage scores and the number of thrips per flower. The mean values, standard errors and variances of the different generations were subjected to weighed least-squares analysis using the scaling test (Mather, 1949) and the joint scaling test to estimate gene effects. The additive-dominance model was adopted in the estimation of gene effects for thrips damage rating, and thrips population. The adequacy of the additive - dominance model was tested using the ABC scaling test (Mather, 1949), incorporating the weighted least square method of Hayman (1960). The significance of the scales and gene effects were tested by using the t-test (Singh & Chaudhary, 1999). Values of scaling test parameters A, B and C and their corresponding standard errors (S.E.) were calculated using the following formulae:

$$A = 2BC_1 - P_1 - F_1 \quad (1)$$

$$B = 2BC_2 - P_2 - F_1 \quad (2)$$

$$C = 4F_2 - 2F_1 - P_1 - P_2 \quad (3)$$

$$V_A = 4V_{BC1} + V_{P1} + V_{F1} \quad (4)$$

$$V_B = 4V_{BC2} + V_{P2} + V_{F1} \quad (5)$$

$$V_C = 16V_{F2} + 4V_{F1} + V_{P1} + V_{P2} \quad (6)$$

$$S.E.\ (A) = (V_A)^{1/2} \quad (7)$$

$$S.E.\ (B) = (V_B)^{1/2} \quad (8)$$

$$S.E.\ (C) = (V_C)^{1/2} \quad (9)$$

Where, A, B and C are scaling test parameters, S.E. = standard error, V = variance, P_1, P_2, F_1 are the means of parent P_1, parent P_2, their F_1, F_2 progeny, and the backcrosses of F_1 to P_1 and P_2 A, B, C, parameters were tested using appropriate t-test values as follows:

$$t(A) = A/S.E.(A) \quad (10)$$

$$t(B) = B/S.E.(B) \quad (11)$$

$$t(C) = C/S.E.(C) \quad (12)$$

The calculated values of t were compared with the tabulated values of t at 5 and 1% level of significance. In each test, the degrees of freedom were the sum of the degrees of freedom of the various generations involved (Mather, 1949). The significance of any one of these scales was an indication of the presence of non-allelic interactions (Singh & Narayanan, 1993). It is assumed that if the additive-dominance model is adequate to explain the differences among generation means, C will be equal to zero within the limits of the standard error. When the additive-dominance model proves to be inadequate to explain the variation existing among generations, the six parameters model of Hayman (1960), and Mather and Jinks (1982) incorporating mean [m], additive effect [a], dominance effect [h] and the three digenic interactive components, (additive × additive [i], additive × dominant [j] and dominant × dominant [l] was determined as follows:

$$m = F_2 \quad (13)$$

$$a = BC_1 - BC_2 \quad (14)$$

$$h = -½\ P_1 - ½\ P_2 + F_1 - 4F_2 + 2BC_1 + 2BC_2 \quad (15)$$

$$i = -4\ F_2 + 2\ BC_1 + 2BC_2 \quad (16)$$

$$j = -½\ P_1 + ½\ P_2 + BC_1 - BC_2 \quad (17)$$

$$l = P_1 + P_2 + 2F_1 + 4F_2 - 4BC_1 - 4BC_2 \quad (18)$$

The significance of the genetic effects was tested using a similar t-test as described previously. Broad and narrow sense heritability was estimated as follows:

$$H^2b = [V_{F2} - (V_{P1} + V_{P2} + V_{F1})/3]/V_{F2} \quad (19)$$

$$h^2n = [2V_{F2} - (V_{BC1P1} + V_{BC1P2})]/V_{F2} \quad (20)$$

Where, H^2b = broad sense heritability, h^2n = narrow sense heritability, V = variance for P_1, P_2, F_1, F_2, BC_1P_1 and BC_2P_2 generations.

Gene factors controlling the score of thrips damages, number of thrips per flower, number of pods per plant, pod weight per plant and grain weight per plant were estimated using the method of Burton (1951) as:

$$k = [0.25(0.75 - h + h^2)\ D^2]/(VF_2 - VF_1) \quad (21)$$

Where, k = minimum number of effective factors, VF_1 = Variance of F_1 population, VF_2 = Variance of F_2 population, P_1 = mean of parent 1, P_2 = mean of parent 2,

$$h = (F_1 - P_2)/P_1 - P_2 \quad (22)$$

$$D = P_1 - P_2 \quad (24)$$

The degree of dominance (deviation from the mid-parent value) and direction of dominance in the two sets estimated by hand in accordance with the method of Falconer and Mackay (1996) as follows:

$$D\ (\text{degree of dominance}) = d/a \quad (25)$$

Where, d = heterozygote = means of $F_1 - 1/2(P_1 + P_2)$, where mean = values of P_1, P_2 and F_1 respectively.

3. Results

3.1 Variability among Cowpea Generations

The analysis of variance showed that there were significant differences among the generations for thrips damage scores, number of thrips per flower, number of pods per plant, pod and grain weight per plant in the two sets of crosses (Table 3).

Table 3. Mean squares of the different traits for crosses LORI × SANZI and VYA × SANZI

Traits	LORI × SANZI		VYA × SANZI	
	Mean squares	F_{calc}	Mean Squares	F_{calc}
Score of thrips damage	15.36	11.12^{***}	3.15	5.66^{***}
Number of thrips per flower	187.10	2.47^{*}	47.38	4.90^{***}
Number of pod per plant	33.91	5.73^{***}	100.35	10.15^{***}
Pod weight per plant (g)	47.02	4.25^{***}	134.91	10.43^{***}
Grain weight per plant (g)	32.16	4.95^{***}	171.38	19.84^{***}

Note. $F_{cal.}$ = F Calculated at 5 degrees of freedom; *; *** = significant differences at 0.05 and 0.01 probability levels, respectively.

3.2 Mean Performance and Distribution of Six Generations

SANZI, the resistant parent, recorded the lowest score for thrips damage in the two crosses (Tables 4 and 5). The damage score ratings ranged between 2.5 and 2.7 for SANZI. Higher scores of between 4.8 and 6.0 were observed for the two susceptible parents, VYA and LORI. Similar trends were observed for the number of thrips per flower. Seven to 10 thrips per flower were recorded for SANZI while LORI and VYA showed 24 and 17 thrips per flower, respectively. In the cross LORI × SANZI, the scoring of thrips damages for the F_1 was almost the same as the resistant parent (SANZI). The F_1 showed 8 thrips per flower which was close to that recorded for SANZI in the cross VYA × SANZI. The number of thrips per flower for BC_1P_2 (10) was the same in both crosses and corresponded to the number for SANZI in the cross LORI × SANZI. The parameters recorded for yield involved the number of pods per plant, pod weight per plant and grain weight per plant. The highest performances were observed in BC_1P_1 derived from the cross involving VYA × SANZI: 20 pods per plant, 22.8 g of pod weight per plant and 18.3 g of grain weight per plant. Among the three parents involved in the crosses, SANZI had the highest number of pods per plant while the highest values for pod and grain weight per plant were observed on VYA. In Cross LORI × SANZI, the performances of F_1, F_2, BC_1P_1 and BC_1P_2 progenies were higher than the best parent (SANZI) for the three yield related traits. Partial dominance was detected for thrips damage scores and number of thrips per flower in both crosses and over dominance was detected for pod weight per plant (both crosses), number of pods per plant (VYA × SANZI) and grain weight per plant (LORI × SANZI). Negative and positive signs of degree of dominance were also observed in the two crosses.

Table 4. Generation mean performances and degree of dominance in cross of LORI × SANZI

Generations	Traits				
	Score of thrips damage	Number of thrips per flower	Number of pod per plant	Pod weight per plant (g)	Grain weight per plant (g)
P_1 = LORI	6.0	24	3	7.5	5.5
P_2 = SANZI	2.7	10	12	7.8	5.7
F_1	2.8	19	7	11.4	8.7
F_2	3.5	16	9	11.6	8.8
BC_1P_1	4.2	18	7	10.0	7.6
BC_1P_2	3.6	10	8	9.5	7.0
MP	3.4	17	8	7.7	5.6
S.E.	0.4	5.2	1.5	1.2	0.9
D	0.9	-0.3	-0.2	37.0	31.0

Note. MP = Mid-parent; S.E = standard error of means, D = degree of dominance based on Falconer and Mackay (1996).

Table 5. Generations mean performances and degree of dominance in cross of VYA × SANZI

Generation	Traits				
	Score of thrips damage	Number of thrips per flower	Number of pod per plant	Pod weight per plant (g)	Grain weight per plant (g)
P_1 = VYA	4.8	17	11	17.5	8.7
P_2 = SANZI	2.5	7	16	20.9	16.8
F_1	3.6	8	19	21.2	14.5
F_2	4.1	12	15	18.9	12.6
BC_1P_1	4.6	11	20	22.8	18.3
BC_1P_2	4.5	10	16	16.8	11.1
MP	3.7	12	14	19.2	12.8
S.E.	0.43	2.2	1.8	2.0	1.7
D	0.08	0.8	2.5	-1.2	-0.4

Note. MP = Mid-parent; S.E = standard error of means, D = degree of dominance based on Falconer and Mackay (1996).

3.3 Estimates of Genetic Components for Resistance to Flower Thrips and Yield related Traits

Significant and negative additive ×dominance [j] and dominance × dominance [l] interactions were observed for score of thrips damage in cross LORI × SANZI (Table 6). Significant additive [a], dominance [h], additive ×additive [i] and dominance × dominance [l] effects were found for the same trait in VYA × SANZI (Table 7). For number of thrips per flower, significant positive additive [a] and dominance × dominance [l] gene actions were detected in cross LORI × SANZI. For the same trait inverse trends were observed in cross of VYA × SANZI where negative additive [a] and additive × dominance [j] were found. In case of the number of pods per plant, dominance [h] and additive × dominance [j] effects were significant in both crosses. In addition, significant additive [a] and dominance × dominance [l] effects were detected in cross VYA × SANZI. For pod weight per plant significant dominance [h], additive × additive [i] and dominance × dominance [l] effects were observed in cross LORI × SANZI, while significant additive [a], additive × dominance [j] and dominance ×dominance [l] gene effects were found for the same trait in VYA × SANZI cross. In addition, the additive effects were positive in direction of the susceptible parent while the dominance was negative towards the resistant parent. Finally, non-allelic additive × additive [i] and dominance ×dominance [l] were observed for grain weight per plant in the cross of LORI × SANZI. Significant additive [a], additive × additive [i] and additive × dominance [j] gene interactions were also found for this trait in the cross of VYA × SANZI.

Table 6. Means ± standard error and genetic effects for thrips resistance and yield related traits in the cross LORI × SANZI

Components	Traits				
	Score of thrips damage	Number of thrips per flower	Number of pod per plant	Pod weight per plant (g)	Grain weight per plant (g)
[m]	3.55^{**}±1.05	16.53^{**}±2.31	8.63^{**}±2.07	11.63^{**}±2.00	8.85^{**}±0.76
[a]	-0.63±0.45	8.08^{**}±3.06	0.19±2.56	0.50±2.50	0.65±1.09
[h]	-0.32±1.36	-8.68±11.17	-5.38^{*}±2.77	-3.62^{*}±1.72	-3.12±2.49
[i]	1.37±5.04	-8.72±11.08	-4.30±9.73	-7.37^{**}±3.43	-6.22^{*}±3.53
[j]	-2.20^{*}±1.15	0.79±3.24	4.94^{*}±2.65	0.63±2.60	0.73±1.54
[l]	-2.63^{*}±1.52	19.91^{*}±11.60	2.93±13.28	6.39^{**}±3.13	5.70^{*}±3.01

Note. *; ** = Estimate significantly different from zero at P = 0.05 and 0.01 respectively, [m] = mean, [a] = additive effect [h] = dominance effect, [i] = additive × additive, [j] = additive × dominant and [l] = dominant × dominant.

Table 7. Means ± standard error and genetic effects for thrips resistance and yield related traits in the cross VYA × SANZI

Components	Trait				
	Score of thrips damage	Number of thrips per flower	Number of pod per plant	Pod weight per plant (g)	Grain weight per plant (g)
[m]	4.09** ±0.11	11.85** ±4.07	14.82** ±2.17	18.93** ±2.16	12.59** ±2.51
[a]	-0.14** ±0.63	-2.28** ±0.15	-3.75** ±0.84	6.98** ±3.06	7.06** ±0.20
[h]	1.64*±0.95	-6.41 ±23.17	17.59** ±8.84	7.35 ±10.70	12.03 ±16.92
[i]	1.76** ±0.98	-2.21 ±3.92	12.74 ±8.86	5.4 ±10.50	7.50** ±2.32
[j]	1.05 ±0.68	-5.84* ±3.10	6.35** ±0.93	5.31* ±3.09	4.54** ±1.86
[l]	-5.46** ±2.78	-1.31±9.15	-20.13** ±0.11	-5.82* ±3.42	-6.6 ±8.15

Note. *; ** = Estimate significantly different from zero at P = 0.05 and 0.01 respectively, [m] = mean, [a] = additive effect [h] = dominance effect, [i] = additive × additive, [j] = additive × dominant and [l] = dominant × dominant.

3.4 Estimates of Heritability and Number of Effective Factors

Heritability and estimates of the minimum number of genes (effective factors) controlling resistance to thrips in cowpea are shown in Table 8. In the two crosses, broad sense heritability varied from 0.61 to 0.65 for the score of thrips damage and 0.58 to 0.74 for the number of thrips per flower. Narrow sense heritability was low ranging from 0.21 to 0.25 and 0.14 to 0.17 for score of thrips damage and estimates of about three genes were found to be controlling thrips resistance related traits. For broad sense heritability of yield related traits, the highest value (0.77) was observed for pod weight per plant and the lowest value (0.53) was found for grain yield per plant. The highest value of narrow sense heritability (0.36) was obtained for number of pods per plant. The lowest narrow sense heritability (0.26) was found for pod weight per plant. Over all, the mean of number of effective genes controlling yield related traits in this study was around four.

Table 8. Heritability and minimum number of effective genes derived from two crosses

Traits	LORI × SANZI			VYA × SANZI		
	H^2b	h^2n	EF	H^2b	h^2n	EF
Score of thrips damage	0.65	0.25	3	0.61	0.21	4
Number of thrips per flower	0.58	0.14	3	0.74	0.17	3
Number of pod per plant	0.66	0.36	4	0.70	0.30	5
Pod weight per plant (g)	0.54	0.28	3	0.77	0.26	5
Grain weight per plant (g)	0.53	0.33	4	0.55	0.24	4

Note. H^2b = broad sense heritability, h^2n: narrow sense heritability, EF: minimum number of genes.

4. Discussion

In the present study the various generations differed significantly from each other for scores of thrips damage, number of thrips per flower, number of pods per plant, pod weight per plant and grain weight per plant. The existence of genetic variability indicated the possibility of response to selection for these traits. In fact, progress of any breeding programme depends upon the existence of genetic variability (Akhshi, Cheghamirza, Ahmadi, & Firouzabadi, 2014). The efficiency of selection and the expression of heterosis depend also on the magnitude of genetic effects present in the plant population (Farshadfar, Aghaie, Sharifi, & Yaghotipoor, 2008). The analysis of mean performances of six generations in the two sets of crosses indicated that SANZI was consistently the best parental line for thrips resistance with scores of damage ranging between 2.5 in the field to 2.7 in the screen house. This low levels of damage were combined with low infestation by thrips. The number of thrips per flower in SANZI ranged from 7 to 10 whereas scores of 6.0 and 4.8 were recorded for the susceptible parents and their thrips, infestations were 17 to 24 thrips per flower. These results are in agreement with the findings of Alabi, Odebiyi, and Tamò (2006) who reported that SANZI performed consistently better than the resistant control (TVu 1509). They further inferred that the presence of a unique protein band in cowpea genotype Moussa local and SANZI could be associated with flower bud thrips resistance in cowpea. Similar results have been reported

by Omo-Ikerodah, Fatokun, and Fawole (2009) and recently by Dormatey, Atokple, and Ishiyaku (2015) who observed lower scores and number of thrips per flower on SANZI. In the two crosses, the means of the parents were far apart for score of thrips, number of thrips per flower and number of pods per plant in the screen house. The same trend was observed for all the traits in the field except for score of thrips damage and pod weight per plant. The differences found in the field and screen house may illustrate the magnitude of environmental effects on most of the traits measured. Estimates of degree of dominance from mean genotypic values of traits support the hypothesis of environmental factors influence on genes controlling all the traits considered in this study. Results showed that there was incomplete dominance ($-1 < D < 0$ or $0 < D < 1$) and over dominance ($D < -1$ or $D > 1$) types of gene effects (Tables 6 and 7) as both positive and negative signs of dominance were found. This is in agreement with the findings by Lagervall (1960) who reported that negative or positive degree of dominance is common in inbred lines. He further indicated that epistasis may bias the estimate of dominance to a larger or lesser extent (Lagervall, 1961). Mid-parent values were larger than F_1 means for score of thrip damage in the two crosses and number of thrips per flower in the cross VYA × SANZI. In addition, the degree of dominance was between zero and one for these traits indicating partial dominance in the direction of the best performing parent (resistant) for these characters. The result also indicated the possibility of improving thrips resistance in cowpea. These findings are consistent with the reports of Omo-Ikerodah, Fatokun, and Fawole (2009), and Dormatey, Atokple, and Ishiyaku (2015). Regarding the yield related traits, the mid-parent values were lower than the F_1 mean for all the traits except for number of pods per plant in the cross LORI × SANZI and the degree of dominance was more than one indicating the presence of over dominance effects towards the best performing parent thus implying that selection for these characters should be delayed to later segregating generations in order to permit loss of non-additive genetic variance through inbreeding. However, our result disagrees with the findings of Adeyanju, Ishiyaki, Echekwu, and Olarewaju (2012) where additive gene effects were reported suggesting selection at early generations. The observed differences may be due to the differences in genotypes used in both studies. Estimates of genetic parameters revealed significant positive dominance [h] and negative dominance × dominance [j] for score of thrips damages in cross VYA × SANZI suggesting the presence of duplicate gene action (Adeyanju, Ishiyaki, Echekwu, & Olarewaju, 2012). The high and negative magnitude of dominance × dominance [l] gene effects in both crosses suggest the presence of dominance effects at heterozygous loci for resistant plants. Dominance × dominance [l] gene action had the highest magnitude than any other single effect for number of thrips per flower in the cross LORI × SANZI. These results suggest that selection for resistance to thrips should be undertaken in late generations and the interaction should be fixed by selection through selfing. This result is in agreement with Dormatey, Atokple, and Ishiyaku (2015) who reported that dominance and epistasis made major contributions to the inheritance of resistance to thrips. From the two crosses used in the present study, dominance × dominance [l] effects showed the highest magnitude for number of pods per plant, additive × additive [i] was the highest for pod and grain weight. All gene effects observed were associated with additional types of digenetic interaction in controlling the inheritance of the yield component traits assessed with dominance × dominance [l] being the predominant type of gene effects. These results indicate the complex nature of these traits and suggest delay in selection for number of pods per plant, pod and grain weight to improve cowpea yield. High broad-sense heritability estimates ($H^2b > 0.4$) and moderate narrow-sense heritability estimates ($0.2 < h^2n < 0.4$) were observed for all the traits except for number of thrips per flower in the cross LORI × SANZI. The results indicated that most of these traits were influenced by environment. The minimum number of effective factors (genes) controlling their inheritance varied from 3 to 5 depending on the trait, suggesting the polygenic nature of the traits measured. The results confirmed that effective progress could be made for all of the traits considered in this study through selection at late generations.

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