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RESEARCH ARTICLE

Generation means analysis in cowpea for flower bud thrips in Mali

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Abstract

Transfer of resistance gene in cowpea is under several factors making it difficult. As for cowpea flower bud thrips, two sets of crosses were done from two resistant (TVu 1509 and Sanzisabinli) and one susceptible (M'barawa) parents. The aim of this study was to determine the mode of gene action involve in flowers bud thrips (*Megalurothrips sjostedti*) resistance control into cowpea. Six generations (P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2) were evaluated using Randomized Complete Block Design under natural infestation at three locations. Data were recorded with parameters such as number of adult thrips, total number of pods per plant and damage scoring. Results revealed the involvement of fixing and non-fixing gene effects into thrips resistance control with additive (n), dominance (h) and additive x dominance (j) as the modes of gene action predominantly controlling flower bud thrips resistance in cowpea. High to moderate broad sense and narrow sense heritability were recorded with most of the traits while low narrow sense of heritability (0.22) was scored with parameter number of peduncles per plant. Polygenic resistance was involved to control thrips resistance among segregating and non-segregating populations that suggest ways to enhance cowpea landrace resistance to flower bud thrips attacks through classical breeding.

Key words: gene action, heritability, cowpea, thrips, Generation mean analysis.

Introduction

Cowpea is one of the backbones of Mali agriculture since it is used in intercropping with cereals (maize, sorghum and millet) for soil improvement and reduces weed incidence on these cereals. Previous results reported cowpea yield reduction up to 80% and complete loss on farms due to flower bud thrips (*Megalurothrips sjostedti*) attacks (Singh and Allen, 1980, Ngakou *et. al.,* 2008). Applications of chemical insecticides and bio-pesticides have been doing by farmers to minimize *M. sjostedti* damages. Incorrect amount of chemical insecticides or bio-pesticides, poor timing of spraying and lack of appropriate equipment for their application and sometime availability of them in farmers' localities are the common constraints to realize an effective control of cowpea flower bud thrips (Tanzubil, 1991). Elsewhere, majority of farmers growing cowpea cannot afford insecticides and their application equipment (Tanzubil *et. al.*, 2008). Cultural practices such as irrigation, tillage operation, planting date, crop rotation and intercropping have been doing by farmers to minimize damages from this pest (Ngakou *et. al.,* 2008). Presence of vegetable crops and more alternative hosts of flower bud thrips within cowpeas' growing areas make unsuccessful these practices (Gbaguidi *et. al.*, 2013). Over application of insecticides could lead to rapid development of thrips populations resistant to chemical treatments; elsewhere farmers and their environment are exposed to obnoxious contamination (Morse and Hoddle, 2006; Dormatey *et. al.*, 2015; Gonné *et. al.*, 2018). Because of that, efforts should be made to improve thrips resistance through introgression of resistant genes into adapted landraces (Alabi *et. al.*, 2006; Muchero *et. al.*, 2010). Therefore, farmers' production and productivity will be increased with minimal reliance on toxic insecticides through identification and growing of host-plant tolerance or resistance to manage thrips (Boukar *et. al.*, 2016). Varietal improvement is based on transmission of desirable genes. The level of gene transmission is estimated either as broad sense or narrow sense heritability. The degree of inheritance is estimated based on Generation Mean Analysis (GMA) that determines mode of gene action controlling traits. Several inheritance studies have been done on qualitative and quantitative traits in cowpea over the world. Researchers from International Institute of Tropical Agriculture (IITA) suggested flower bud thrips resistance control under two recessive genes. Continuous distribution of phenotype was observed by Jackai and Singh (1988) ranging from very susceptible to resistant suggesting that thrips resistance is quantitatively inherited. Omo-Ikerodah *et. al.*, (2009), Bediako (2012), Dormatey *et. al.*, (2015) and Symphorien *et al.* (2018) found significant epistasis gene effects governing by additive and dominance gene actions for thrips resistance control. Gonné *et al.* (2018) suggested positive dominance and negative dominance x dominance gene action for minimizing thrips damage with an effective factor ranging from 3-4 which is equaled to the same number identified by Dormatey *et al.* (2015) while 3-5 and 1-3 were the number of gene involved into thrips resistance control respectively recorded by Omo-Ikerodah *et. al.*, (2009) and Symphorien *et. al.*, (2018). To improve Malians' cowpea landraces for thrips resistance, it is necessary to study the genetic pattern that control resistance and determine the heritability. According to Kearsey and Pooni (1996), the proportion of phenotypic variation that is heritable should be known before starting breeding programme since selection efficiency of that trait is mainly dependent on the magnitude of genetic variation and heritability (Falconer and Mackey, 1996). Knowing genetic control of complex quantitative traits and

magnitude of genetic that occurs among the available germplasm are important for selection and crops' genetic improvement (Mwale *et. al.*, 2017). Generation Mean Analysis (GMA) provides information on the relative significance of additive and dominance in addition to their interaction gene effects in a population generated from two contrasting lines. It is based on the means measurement of six generations (P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2) developed from these lines (Bernardo, 2002). Generation mean calculates the pooled genetic effects across loci since the actual means of single loci are unobservable. In Mali, there is little information about the genetic control of thrips (*Megalurothrips sjostedti*) resistance in cowpea. Therefore, the main objective of current study was to determine the mode of inheritance of flower bud thrips (*Megalurothrips sjostedti*) resistance in cowpea.

Materials and Methods

Study locations

Crosses, parents and their progenies were evaluated under open field in three different environments of Mali *viz.*, Cinzana (05° 57' W; 13° 15' N) and N'Tarla (05° 42' W; 12° 35' N) Agronomic Research Stations of IER in Mali, and IITA-Cotonou Station, Benin (15 m above the sea, 06° 25' W; 02° 20' N). These environments differ in their agro climatic conditions.

Population development

Three different accessions selected for inheritance study of thrips resistance are in Table 1. Parents were planted in 10 pots (Length: 21 cm, Width: 23 cm) filled with sandy loam soil, three seeds were sown per pot and thinned into two plants and pots were watering whenever necessary. This activity was conducted under screen house at Cinzana Agronomic Research Station. Pots were hand weeded followed by Di-ammonium Phosphate (DAP) (3 g/pot) application three weeks after planting. Full insecticide application started 35 days after sowing till last pods harvesting. Procedure of Ehlers and Hall (1997) slightly modified was used to generate descendants from crosses. The two resistant genotypes (Sanzisabinli and TVu 1509) (Abudulai *et. al.*, 2006; Omo-Ikerodah *et. al.*, 2009), used as males, were crossed with susceptible genotype (M'barawa) (Doumbia *et. al.*, 2019). Crosses were done October to February early in the morning (5:30 - 7:30 a.m.). Emasculation and pollination were at the same time. Sometimes, additional crosses were effectuated in the evening if lower number of crosses was made in the morning. Forceps were used to remove carefully the stamen from female flowers which were sterilized with 70% ethanol after any emasculation. Fertilization, with male flowers, was carried out based on capping method. Each cross was tagged with the name of male parent at the first position followed by female name ended by crossing date. The number of F_1 seed created from each cross was as follows: TVu 1509 x M'bawara: 582 and Sanzisabinli x M'barawa: 439. Percentage of successful crosses was 49 calculated from number of succeeded crosses over total crosses multiplied by 100. Seeds from the first cross generations (F_1) were divided into four sets and one part was kept. Two sets were used for the backcrosses to donor and recurrent parents to generate BC_1P_1 (donor parent) and BC_1P_2 (recurrent parent). The last set was advanced to generate the second filial generation (F_2).

Table 1: Some characteristics of different cross parents

Parent	Origin	Contrasting characteristics
M'barawa	Landrace from Central region of Mali	Yellow-white flower; white seed coat; prostrate; intermediate maturing; susceptible to thrips.
Sanzisabinli	Landrace from Ghana	Violet flower, mottle brown seed coat; prostrate; extra-early maturing; resistant to thrips.
TVu 1509	IITA, improved variety	White-yellow flower; light yellow seed coat; erect; extra-early maturing; moderately resistant to thrips.

Determination of thrips resistance inheritance in cowpea: Generation Mean Analysis study

The six generations (P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2) were evaluated using Randomized Complete Block Design (RCBD) in three replications; two rows of susceptible line (Vita7) were planted as spreader rows for different experiments. They were sowed and sprayed with insecticide Lambda with a dosage 9 ml : 3 liter to control Aphis and thrips parasitoids two weeks before establishing the main experiment. For generations, two seeds were buried per hill on 2 m rows and thinned into one plant three weeks after germination. Each non-segregating population (P_1, P_2 and F_1) was planted on 2 rows whilst the segregating population BC_1P_1 and BC_1P_2 were planted on 4 rows and F_2 on 6 rows. The dimensions 0.2 m and 1 m were within and between the row distances. Di-ammonium phosphate (DAP) (17 kg) fertilizer was applied after weeding three weeks from establishing main experiment; the whole plot size was 870 m^2. Spreader rows were uprooted when the majority of plants reached 50% flowering and placed within the experimental area.

Data collection

Field data were taken on 20 individual plants from non-segregating populations (F_1 and their parents), 40 individual backcross plants (BC_1P_1 and BC_1P_2) and 60 plants for each of the F_2 generations. To assess thrips damages, the following parameters were measured from individual plants of each generation: number of peduncles per plant, number of pods per peduncle, total number of pods per plant, number of adults thrips and damage scoring. Five flowers were randomly collected from individual plants and placed them into 70% ethanol for microscopic or loupe observation; thrips damage scoring was done using protocol developed by Jackai and Singh (1988) (Table 2).

Table 2: Flower bud thrips damage scoring protocol (Jackai and Singh, 1988)

Scale	Damages Scoring	Rating Appearance
1	Very low susceptibility	No browning/drying (i.e. scaling) of stipules, leaf or flower buds; no bud abscission.
3	Low susceptibility	Initiation of browning of stipules, leaf or flower buds; no bud abscission.
5	Intermediate susceptibility	Distinct browning/drying of stipules and leaf or flower buds; some bud abscission.
7	High susceptibility	Serious bud abscission accompanied by browning/drying of stipules and buds; non-elongation of peduncles.
9	Very high susceptibility	Very severe bud abscission, heavy browning, drying of stipules and buds; distinct non-elongation of (most or all) peduncles.

Data analysis

Data from different parameters were subjected to GenStat 12th edition for analysis of variance (ANOVA) and the means from different parameter were used to draw out the Boxplot. Broad sense and narrow sense heritability were determined using Zewdie and Bosland (2003) and Warner (1952) formulas respectively as follows:

Broad sense heritability

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

Narrow sense heritability

$$(h^2_n) = [2V_{F2} - (V_{BC1P1} + V_{BC1P2})] / V_{F2}$$

Where, V = variance for P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2 generations.

Number of effective factors (genes) involved in thrips resistance for different characters was estimated based on the method of Burton (1951) as:

$$k = [0.25 (0.75 - h + h^2) D^2] / (V_{F2} - V_{F1})$$

Where: $D = P_1 - P_2$; $h = (F_1 - P_2) / P_1 - P_2$; k = minimum number of effective factors; V_{F2} = Variance of F_2 population; V_{F1} = Variance of F_1 population; P_1 = mean of parent 1; and P_2 = mean of parent 2.

The mode of inheritance of thrips resistance was estimated for each cross by generation mean analysis (P_1, P_2, F_1, F_2 BC_1P_1 and BC_1P_2) based on additive/dominance model and three parameter model (Mather and Jinks, 1982). Gene effects were estimated as:

$$m = ½ P_1 + ½ P_2 + 4F_2 - 2BC_1P_1 - 2BC_1P_2$$
$$n = ½ P_1 - ½ P_2$$
$$SE^2_{(n)} = 0.5/2SE^2_{P1} + 0.5/2SE^2_{P2}$$
$$h = 6BC_1P_1 + 6BC_1P_2 - 8F_2 - F_1 - 3/2P_1 - 3/2P_2$$
$$SE^2_{(h)} = 36SE^2_{BC1P1} + 36SE^2_{BC1P2} + 64SE^2_{F2} + SE^2_{F1} + 9/4SE^2_{P1} + 9/4SE^2_{P2}$$

Where m = mean, n = additive and h = dominance effects.

The significance of difference from three parameters model was estimated through t-test at the 0.05 and 0.01 levels of probability. Mather (1949) and Hayman (1960) methods were applied to test the adequacy of the additive – dominance model using the ABC scaling test as follows:

$$A = 2BC_1P_1 - P_1 - F_1;$$
$$V_A = 4V_{BC1P1} + V_{P1} + V_{F1};$$
$$B = 2BC_1P_2 - P_2 - F_1;$$
$$V_B = 4V_{BC1P2} + V_{P2} + V_{F1};$$
$$C = 4F_2 - 2F_1 - P_1 - P_2;$$
$$V_C = 16V_{F2} + 4V_{F1} + V_{P1} + V_{P2};$$

S.E. (A) = $(V_A)^{1/2}$ t (A) = *A/S.E.(A)*

S.E. (B) = $(V_B)^{1/2}$ t (B) = *B/S.E.(B)*

S.E. (C) = $(VC)^{1/2}$ t(C) = *C/S.E.(C)*

Where A, B and C are scaling test parameters, S.E. = Standard error; V = variances of the six generations: P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2.

Comparison was done between the calculated t values and the tabulated t values at 0.05 and 0.01 levels of significances. The sum of the degrees of freedom of different generations involved in each test was considered as the degree of freedom of the parameter (Mather, 1949). From this three parameter model, presence of non-allelic interactions is determined by the any significance of A, B and C. The value of C will be equaled to zero if additive-dominance model is enough to explain the differences among generation means. The six parameter model of Hayman (1958), Mather and Jinks (1972) was used in case of inadequacy of the additive-dominance model (three parameter model) to clarify the variation present among generations by incorporating mean (m), additive

effect (n), dominance effect (h) and the three digenic interaction components additive x additive (i), dominance x dominance (l) and additive x dominance (J) as follows:

$$m = F_2;$$
$$n = BC_1P_1 - BC_1P_2;$$
$$h = - ½ P_1 - ½ P_2 + F_1 - 4F_2 + 2BC_1P_1 + 2BC_1P_2;$$
$$i = - 4F_2 + 2BC_1P_1 + 2BC_1P_2;$$
$$j = - ½ P_1 + ½ P_2 + BC_1P_1 + BC_1P_2; l = P_1 + P_2 + 2F_1 + 4F_2 - 4BC_1P_1 - 4BC_1P_2.$$

Genetic effect significance was tested using the same t-test as for the ABC scaling test. Estimation of degree of dominance (deviation from the mid-parent value) and direction of dominance for resistant control and their related traits were calculated with hand in accordance with the method of Falconer and Mackay (1996) as follows:

D (degree of dominance) = d/a

Where:

d = heterozygote = means of F_1- ½ (P_1+P_2); a = ½ (P_1 + P_2)

Mid-parent (MP) genotypic value was calculated as:

Mp: V_{P1}+V_{P2} / 2

Results and discussion

Variation among cowpea generations

Generations used in this study showed highly significant differences in all traits assessed with greater mean value recorded for total number of pods per plant and the lowest with number of pods per peduncle from cross Sanzi x M'barawa (Table 3).No significant difference was observed among generations with numbers of peduncles per plant, pods per peduncle and adults thrips with TVu 1509 x M'barawa. Damage scoring and total number of pods per plant scored respectively highly significant and significant differences between generations for the same cross.

Table 3: Mean squares of generations derived from two crosses

	Sanzi x M'barawa	TVu 1509 x M'barawa
Traits	**Generations**	**Generations**
Number of peduncle/plant	517.29**	63.7^{ns}
Number of pods/peduncle	2.84**	1.92^{ns}
Total number of pods/plant	409.06**	193.75*
Number of adults thrips	191.28**	29.82^{ns}
Damage scoring	28.71**	26.43**

Where, *, ** ns: significant, highly significant and no significant at 5% level, respectively.

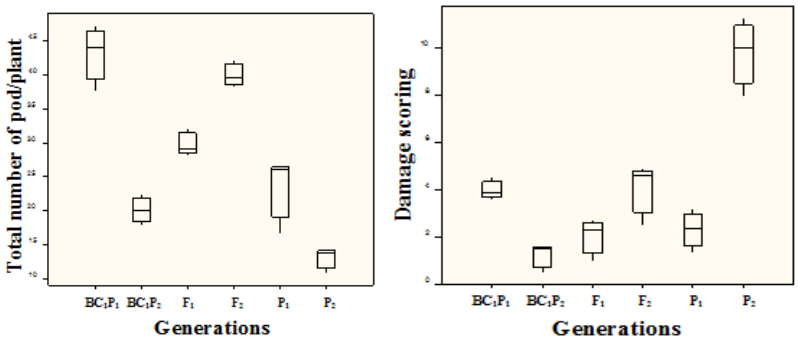
Different generations were more resistant than the susceptible parent for both crosses. Major variability was observed across the three locations since highly significant difference was recorded from progenies and their parents Sanzi and M'barawa for all parameters whereas significant and highly significant were observed with progenies from TVu 1509 and M'barawa based on some parameters. The difference between the two crosses could be related to more involvement of additive-dominance and dominance variances into resistance control of number of adults thrips and thrips incidence on progenies from Sanzi and M'barawa enforcing resistances' level.

Differentiation between cowpea progenies and parents

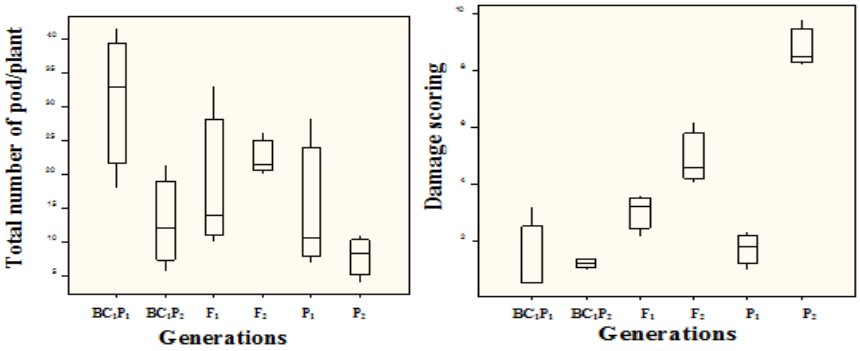
Distinguishing feature was noticed in term of generations' repartition (Fig.1). Most

generations from Sanzi x M'barawa were closed to the resistant parent for damage scoring traits; F_1 and BC_1P_2 lightly overlapped Sanzi (resistant parent) whereas more segregation was observed with BC_1P_1 and F_2 populations. The yield in terms of total number of pods per plant for F_1, F_2, and BC_1P_1 extended beyond that of resistant parent whilst BC_1P_2 was neared of the resistant parent. Variability was observed for all generations compared to the parents TVu 1509 and M'barawa. Progenies BC_1P_1, F_1 and F_2 skewed toward the resistant parent TVu 1509 (P_1) with transgressive segregation since some progenies overlapped TVu 1509 in term of total number of pods per plant. The two backcrosses were closed to TVu 1509 with some progenies from BC_1P_1 more resistant than the resistant parent. F_1 and F_2 generations were between the cross parents with some closeness of F_1 progenies to TVu 1509. Dominance and over-dominance actions skewed generations towards resistant parents Sanzi and TVu 1509. Some progenies overlapped that of the resistant parents Sanzi TVu 1509 in terms of yield but BC_1P_2 progenies were within the range of TVu 1509 and M'barawa suggesting over-dominance recessive genes for TVu 1509. This could be subjected to the higher combined variance values from additive-dominance and dominance for total number of pods per plant that where greater than environmental variance in addition to dominance of Sanzi and TVu 1509 gene effects over the susceptible recessive for the expression of resistance for these traits. The closeness of the four segregating generations to the resistant parents with some individuals of BC_1P_2 and F_1 recording less damage than Sanzi with damage scoring parameter could be linked to the implication of higher environmental variance and higher degree of dominance positively affecting additive-dominance and dominance effect. These may lead to transgressive segregation with some of the segregating and non-segregating populations towards Sanzi and TVu 1509 for total number of pods per plant. Negative dominance and additive-dominance variances interacted for expressing recessive gene effects from TVu 1509 which increased number of adults thrips with F_1 progenies compared to the mid-parent. The results from actual investigation corroborated with the finding of Ishiyaku *et al.* (2005) reporting generations overlapping the range of parents through inheritance assessment about flowering time in cowpea. Umar (2014) found zinc concentration of the four developed generations beyond the low and high zinc parents. Estimate of dominance to a larger or lesser extent could be related to epistasis genes (Lagervall, 1961). Actual results were in agreement with the funding by Lagervall (1960) outlining negative and positive degree of dominances common in inbreed lines, it was also supported by Gonné *et al.* (2018).. The current funding differed from results of Welsh (1981) that found no expression of recessive genes over dominance in the F_1 generation based on Mendelian genetics. This difference could be due to the study materials used and different environments affecting the genetic makeup of generations. Progenies from Sanzi x M'barawa performed better than those from TVu 1509 x M'barawa. Contrasting between the two resistance gene donors could be linked to more involvement of dominance gene effect with Sanzi. This result confirmed the finding from Alabi *et al.* (2006) and Gonné *et al.* (2018) studies reporting Sanzi more performing than TVu 1509. The first authors explained this based on the association of unique band in cowpea genotype Moussa local and Sanzi which could be the same between Sanzi and M'barawa enforcing the resistant level with progenies.

Fig.1: Distribution of study's parameters with generations derived from crosses



Sanzi x M'barawa



TVu 1509 x M'barawa

Where, BC_1P_1: backcross to parent1; BC_1P_2**:** backcross to parent2; F_1**:** first filial generation; F_2**:** second filial generation; P_1**:** parent1 (Sanzi; TVu 1509); P_2**:** parent2 (M'barawa).

Yielding ability of different generations from crosses under thrips infestation

Progenies F_1 and BC_1P_2 from cross Sanzi x M'barawa performed better than resistant parent in terms of thrips damage scoring and total number of pods per plant (Table 4). BC_1P_1 had the highest values for number of peduncles per plant (43.0), number of pods per peduncle (4) and total number of pods per plant (43.0). Most variability was seen between generations with number of peduncles per plant and number of adults thrips having, respectively, 27.0 and 25.3 as CV%. Progeny had more peduncles per plant, pods per peduncle and total number of pods per plant than the resistant parent. The F_1 progenies performed better than the mid-parent value for most traits except for number of adults thrips and damage scoring. The susceptible parent (M'barawa) had the lowest number of pods per peduncle (1) and highest number of adults thrips (25.0) and damage scoring (9). Mean of damage scoring was 4 with 17.7 as CV%; progenies of BC_1P_1 and BC_1P_2 from cross TVu 1509 x M'barawa scored the same damage (2) as resistant parent (P_1) (Table 5). The highest damage scoring and number of adults thrips were recorded from F_2 population. The resistant parent TVu 1509 performed better than BC_1P_2 in terms of total number of pods per plant. The F_1 had more thrips than the mid-parent value and mid-parent was less tolerant than the F_1 in terms of thrips damage scoring. The greatest coefficient of variation (40.1%) was for total number of pods per plant with 18 as mean value. The F_1 performed better than the mid-parent with most parameters from both crosses

indicating dominance of resistance over susceptibility which was in line with study done by Dormatey *et al.* (2015) and Gonné *et al.* (2018). Elsewhere, F_1 had higher number of adults thrips than MP with TVu 1509 x M'barawa meaning the implication of recessive gene (s) into resistance control taking more time before expressing.

Table 4: Mean performances of families and Mid-parent values derived from Sanzi x M'barawa

	Traits				
Generations	**NPLP**	**NPPL**	**TNPP**	**NAT**	**DS**
P_1	16.3	2.7	23.2	5.4	2.0
P_2	10.0	1.0	13.0	25.0	9.0
F_1	22.0	3.0	30.0	4.0	2.0
BC_1P_1	43.0	4.0	43.0	11.0	4.0
F_2	28.0	3.0	40.0	18.0	4.0
BC_1P_2	37.0	4.0	38.0	8.0	2.0
MP	**15.2**	**2**	**15.8**	**11.1**	**6.0**
Mean	25	3	28	12	4
CV%	27.0	3.9	9.5	25.3	11.7
SE	6.8	0.1	2.7	3.0	0.5

Table 5: Mean performances of family and Mid-parent derived from TVu 1509 x M'barawa

	Traits				
Generation	**NPLP**	**NPPL**	**TNPP**	**NAT**	**DS**
P_1	11.6	2.7	15.3	10.3	2.0
P_2	17.2	1.2	7.8	11.8	8.9
F_1	17.0	3.0	19.0	14.0	3.0
BC_1P_1	18.0	4.0	31.0	8.0	2.0
F_2	12.0	3.0	23.0	15.0	5.0
BC_1P_2	24.0	3.0	13.0	7.0	2.0
MP	**14.4**	**2.0**	**11.5**	**11.4**	**5.0**
Mean	17	3	18	11	4
CV%	40.1	19.7	41.2	17.4	17.7
SE	6.7	0.6	7.5	1.9	0.6

Where, CV%: coefficient of variation; DS: damage scoring; MP: mid-parent; NPLP**:** number of peduncles per plant; NPPL**:** number of pods per peduncle; TNPP**:** total number of pods per plant; NTA**:** number of adults thrips; P1**:** resistant; P_2**:** susceptible parent; F_1: first filial generation; F_2**:** second filial generation; BC_1P_1**:** backcross to parent1; BC_1P_2**:** backcross to parent2; SE**:** standard error.

Estimation of genotypic differences among generations

Number of effective factors controlling thrips resistance in cowpea were estimated from 3 (number of peduncle per plant and number of pods per peduncle) to 5 (number of adults thrips

and damage scoring) for cross Sanzi x M'barawa (Table 6). Negative dominance was seen for number of adults thrips (-72.7) and damage scoring (-66.8) with the highest value for number of pods per plant. Broad sense heritability was ranking from 0.87% for damage scoring to 0.57% for number of pods per peduncle. The number of adults thrips had the lowest narrow sense heritability (41%) and highest for damage scoring (60%). The inverse was realized with progenies from TVu 1509 x M'barawa with damage scoring and number of pods per peduncle recording the lowest effective factor (3) and the highest (5) for number of peduncles per plant and total number of pods per plant. The highest degree of dominance (64.80) was scored under total number of pods per plant and damage scoring was the only one to get negative degree of dominance (-43.18) and the heritability for this parameter was 0.76 and 0.42 corresponding to broad and narrow senses. Number of adults thrips per plant had the highest narrow sense (0.52) and the lowest narrow sense (0.22) and broad sense (0.48) attributed to number of peduncles per plant. The maximum value of broad sense was recorded with damage scoring (0.76). The higher broad and moderate narrow sense heritability were estimated for most of the traits showing the possibility to increase flower bud thrips resistance in cowpea by gathering genes from sources of resistance. Some of actual results supported the previous works but others don't. This finding does not agree with results from Bediako (2012) who reported low broad sense heritability for flower bud thrips resistance in cowpea. The discrepancies between the two studies could be linked to the different cowpea genotypes used for progenies development and environmental factors contributing to gene expression since current study was carried out at three different agro-ecological zones. Moreover, this result supported previous assessment done by Omo-Ikerodah *et. al.*, (2009) and Gonné *et. al.*, (2018) indicating higher broad sense heritability for flower bud thrips resistance into cowpea. The same trend was observed by Umar (2014) for iron and zinc concentrations into cowpea. Reports from study for thrips resistance indicated low to moderate narrow sense heritability (Omo-Ikerodah *et al.*, 2009) and low heritability (Bediako, 2012; Dormatey *et. al.*, 2015). The causes of this difference could be mostly related to different genotypes and environmental factors (soil texture, rainfall and soil chemical composition) that may favor expression of resistant gene effects. Elsewhere, greater additive x dominance and dominance x dominance gene effects from previous studies may decrease narrow sense heritability level. Current study indicated the presence of overestimated broad sense heritability with TVu 1509 x M'barawa. Since heritability expression is based on additive and dominance variances associated with epistasis, their high magnitudes may cause the expression of heritability more than 1. Coates and White (1998) mentioned epistasis and environmental effects as the cause of exaggerated heritability. Atemkeng-Nkoumki (2015) recorded overestimated of broad and narrow sense heritability for shoot N. The high heritabilities in actual work are linked to the additive variance components. The same tendency was observed in chickpea under saline and control environment by Samineni *et al.* (2011). Number of effective factors for all crosses was from 3 to 5 with consistence for number of peduncles per plant (3) with both crosses. The same minimum number of genes was 3 for controlling thrips adults and damage level whilst 5 was the maximum effective factors for number of total pods per plant. These results were in the same line with previous works done on *Megalurothrips sjostedti* resistance since Omo-Ikerodah *et. al.*, (2009) recorded 3 to 5, Dormatey *et. al.*,. (2015) 3 to

5.73 and Gonné *et. al.*, (2018) 3 to 5 as the numbers of effective factors. Elsewhere, Gonné *et. al.*, (2018) recorded 3 to 4 as number of effective factor from Lori x Sanzi and the difference from current study could be due to genotypes used for the development of generations and environmental factors where some assessment of previous study was done under screen house. Effective factors for others traits in cowpea were identified with 0.8 as average gene number to control nitrogen fixation (Atemkeng-Nkoumki, 2015), 0.2 and 1 for zinc and iron concentrations (Umar, 2014). Environmental factors such as rainfall, soil characteristics and plant species are more involved into genes inheritance thereof low genes implication into nitrogen fixation, zinc and iron character inheritance could be negatively affected by soil texture and chemical composition. Figure 2 indicates contribution of each component to thrips resistance transfer into cowpea from different crosses. Additive variance (VA) was important for resistance transfer for number of adults thrips whereas dominance variance (VD) was most important for number of peduncles per plant and number of pods per plant with progenies from Sanzi x M'barawa. Environmental variance (VE) was observed for all traits with higher level for total number of pods per plant and the same trend was observed with additive-dominance variance (VAD) with greater values attributed to the identical traits as VE. Some negative values were observed for number of peduncles per plant and pods per peduncle for VA, number of adults thrips and damage scoring for VD.

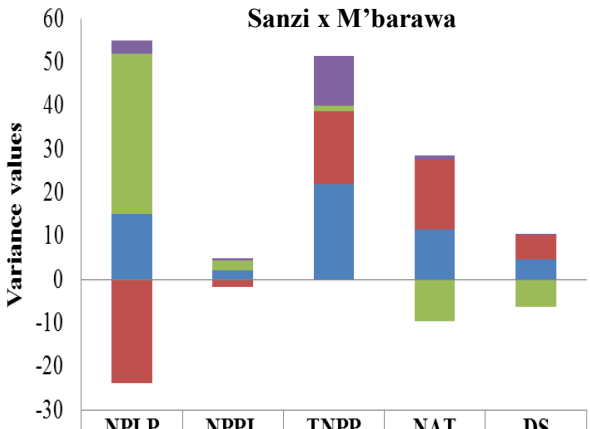
Table 6: Vital genotypic involved to the resistance transfer

	Estimates							
	Sanzi x M'barawa				**TVu 1509 x M'barawa**			
Parameters	**H^2_b**	**h^2_n**	**d/a*100**	**EF**	**H^2_b**	**h^2_n**	**d/a*100**	**EF**
Number of peduncles per plant	0.69	0.42	83.7	3	0.48	0.22	18.0	5
Number of pods per peduncle	0.57	0.44	85.4	3	0.68	0.48	51.1	3
Total number of pods per plant	0.66	0.49	65.3	4	0.63	0.43	64.8	5
Number of adults thrips	0.67	0.41	-72.7	5	-	0.52	23.2	4
Damage scoring	0.87	0.60	-66.8	5	0.76	0.42	- 43.2	3

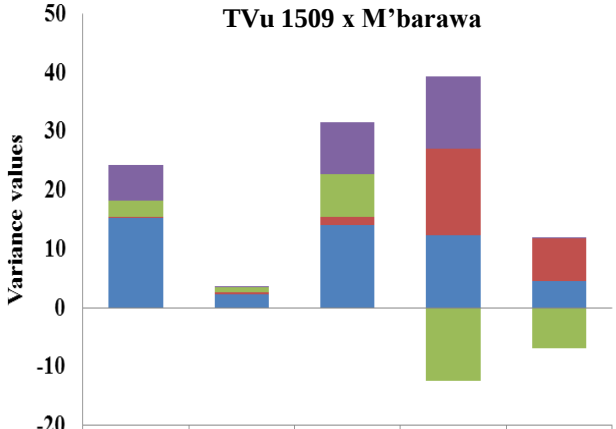
Where, H^2_b**:** broad sense heritability; h^2_n: narrow sense heritability; d/a**:** degree of dominance; EF**:** number of effective factors

As for TVu 1509 x M'barawa, negative dominance variance (VD) was registered for number of adults thrips and damage scoring. Environmental variance (VE) was more important for number of peduncles per plant, number of pods per peduncle and total number of pods per plant. The major effects controlling the number of adults thrips were additive (VA) and negative dominant (VD) while additive-dominance variance (VAD) and environmental variance (VE) were more important for resistant transfer for total number of pods per plant and number of peduncles per plant. Dominance variance (VD) and environmental variance (VE) were more involved into the rising of the number of pods per peduncle under thrips attacks. For actual work, number of gene for parameter total number of pods per plant and number of adults thrips were constantly high for crosses. This could be due to the high contribution of additive and additive-dominance variances that were positive.

Fig.2: Contribution of estimated additive-dominance, dominance, additive and environmental components to thrips resistance in cowpea from crosses



	NPLP	NPPL	TNPP	NAT	DS
VAD	3.00	0.50	11.41	0.96	0.03
VD	36.90	2.35	1.18	-9.74	-6.23
VA	-23.97	-1.86	16.81	15.99	5.55
VE	15.07	2.08	22.01	11.53	4.68

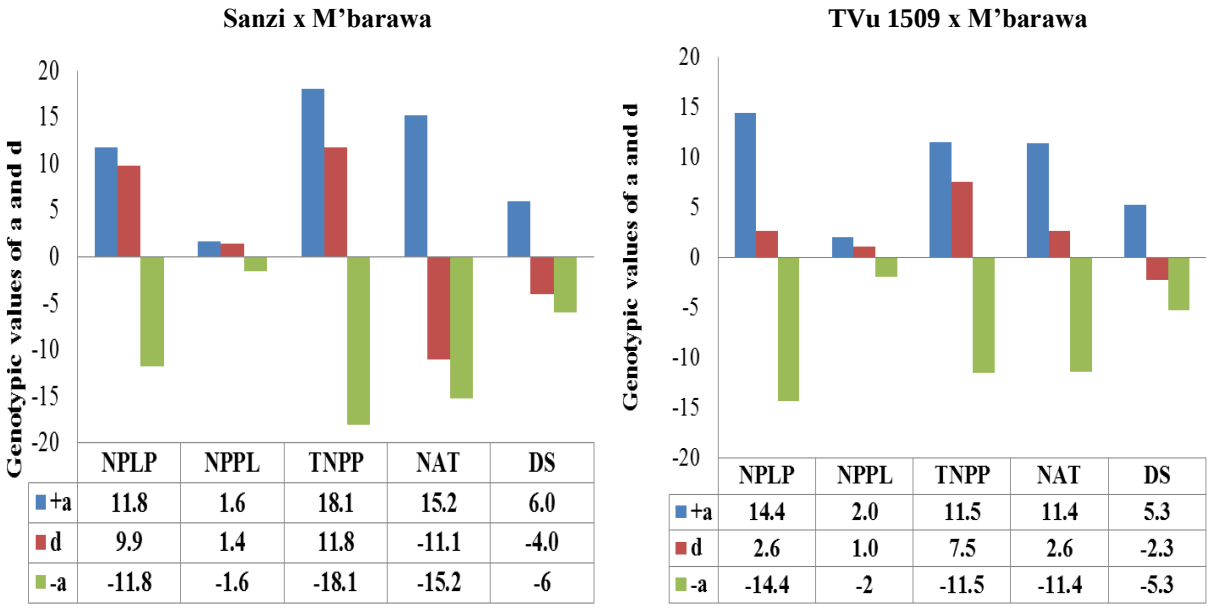


	NPLP	NPPL	TNPP	NAT	DS
VAD	6.06	0.13	8.87	12.40	0.10
VD	2.73	0.93	7.19	-12.47	-6.88
VA	0.12	0.25	1.47	14.67	7.32
VE	15.27	2.32	14.02	12.30	4.52

Where, DS**:** damage scoring; NPLP**:** number of peduncles per plant; NPPL**:** number of pods per peduncle; NAT**:** number of adults thrips; TNPP**:** total number of pods per plant; VA**:** additive variance; VAD: additive-dominance variance**;** VD**:** dominance variance; VE**:** environmental variance.

No over-dominance was observed with different genotypic components (a and d) from both crosses (Figure 3). Parameters of number of adults thrips and damage scoring registered negative values for genotypic d with progenies developed from Sanzi and M'barawa (Figure 3). Moreover, number of peduncle per plant had the highest genotypic value of a (14.4) followed by total number of pods per plant (11.5) and number of adults thrips (11.4) when TVu 1509 was used as donor of resistance gene to reduce thrips incidences. The converse was true for genotypic value of d with total number of pods per plants taking the lead (7.5) and negative genotypic value of d (-2.3) for damage scoring. Genetic components of variances suggested both additive variance (a) and dominance variance (d) to be implicated into resistance control for most traits from both crosses with additive component (a) more predominant than dominance component (d) which was opposite to the result from Olajide and Ilori (2017) indicating more implication of dominance genotypic component for drought resistance control in cowpea. The difference between the two results may be linked to crosses parent in addition to environmental factors that are more involved in insects' density stability.

Fig. 3: Level of contribution of genotypic components a and d for resistance transfers into progeny from crosses



Where, NB: + a: positive genotypic component a; -a: negative genotypic component a; d: genotypic component d; DS: damage scoring; NPLP: number of peduncle per plant; NPPL: number of pods per peduncle; NAT: number of adults thrips; TNPP: total number of pods per plant.

Estimates of main and epistasis gene effects involved in thrips resistance control in generations

For the individual scaling test, highly significant differences were with A from all traits; B with number of peduncles per plant, number of pods per peduncle and damage scoring; C with total number of pods per plant and number of adults thrips assessed from progenies of Sanzi x M'barawa (Table7). Highly significant difference was seen among generations with the mean (m) for whole parameters. The estimated dominance x dominance (l) effect was negative and higher than dominance effect for number of peduncles per plant. The non-epistasis genes (dominance, h) and epistasis genes (additive x additive, i) were implicated in the resistant control for number of pods per plant with additive x additive (i) effects being larger. Additive (n) and additive x dominance (j) effects were recorded as being responsible for thrips resistance with the total number of pods per plant and highest degree of involvement was from the additive (n) side. Negative dominance (h) and positive additive x dominance (j) effects were perceived as having the ability to reduce effects from number of adults thrips. Epistasis (dominance x dominance, l) gene effects were controlling thrips damage.

Table 7: Estimation of gene effects for thrips resistance and related traits from Sanzi x M'barawa

	NPLP		NPPL		TNPP		NAT		DS			
Gene effects estimated from three parameter model												
		t_c		t_c		t_c		t_c		t_c	$t_{0.05}$	$t_{0.01}$
m	-36.64**	**2.83**	-1.75**	**0.20**	51.70*	**2.51**	47.19*	**2.04**	11.63*	**2.24**	1.98	2.61
n	0.04^{ns}	**0.04**	40.85*	**24.48**	12.08**	**8.29**	-19.78**	**12.94**	-3.74**	**0.7.76**	2.10	2.88
h	200.28**	**2.64**	12.64^{ns}	**0.42**	4.91^{ns}	**0.04**	-74.61^{ns}	**0.49**	-20.88^{ns}	**0.42**	1.98	2.61
Individual scaling												
A	53.00^{ns}	**1.70**	4.29**	**3.50**	32.98**	**3.68**	11.91^{ns}	**1.60**	3.71**	**3.10**	2.00	2.66
B	41.06**	**4.10**	11.99**	**4.67**	-2.49^{ns}	**0.58**	-11.50^{ns}	**1.41**	-9.36**	**3.83**	2.00	2.66
C	46.12^{ns}	**0.96**	0.79^{ns}	**0.16**	64.11**	**4.08**	32.39**	**2.94**	0.31^{ns}	**0.03**	1.99	2.65
Epistasis effects estimated from six parameter model												
m	17.58**	**3.32**	2.57**	**2.80**	40.0**	**6.32**	17.8**	**4.22**	4.00**	**3.00**	2.02	2.70
n	6.01^{ns}	**0.67**	24.00^{ns}	**1.28**	22.8**	**2.87**	1.9^{ns}	**0.43**	0.05^{ns}	**0.03**	1.99	2.64
h	57.80*	**2.05**	46.09*	**2.00**	-21.8^{ns}	**0.72**	-43.0*	**2.22**	-15.13^{ns}	**1.70**	1.98	2.61
i	47.94^{ns}	**1.73**	73.71*	**2.45**	-33.6^{ns}	**1.13**	-32.0^{ns}	**1.68**	-11.10^{ns}	**1.29**	1.98	2.62
j	5.79^{ns}	**0.62**	0.39^{ns}	**0.14**	17.7*	**2.09**	11.7*	**2.24**	3.79^{ns}	**1.62**	1.98	2.63
l	-141.03**	**3.29**	-8.48^{ns}	**0.65**	3.1^{ns}	**0.07**	31.6^{ns}	**1.24**	22.25*	**2.00**	1.98	2.61

Table 8 contains information about different gene effects for thrips resistance control from cross parents TVu 1509 (resistant) and M'barawa (susceptible) and their progenies. Epistasis gene involvements were noticed with two factors for the majority of parameters. Significant level with C was observed for number of pods per peduncle and negative significance of B for number of adults thrips. Non-digenic gene effects were implicated into resistant control for all traits measured. Additive (n) and additive x dominance (j) gene effects were discovered to be responsible for thrips resistant control for number of peduncles per plant with more involvement of epistasis. The same type of gene effects conferred resistance to cowpea for number of pods per peduncle and total number of pods per plant, additive (n) effects were more important than additive x dominance (j) genes effects for both parameters. Non-fixing gene effect, dominance x dominance (l), was the only mode of gene actions for thrips resistance control with number of adults thrips and damage scoring. Gene actions in the inheritance of flower bud thrips resistance estimated the effects of additive and dominance genes additional to their interactions for most parameters. Population means were directed by the sign of epistasis genes that were associated with gene dispersion inside crosses with additive x additive (i) and additive x dominance (j) gene effects (Mather and Jinks, 1982). Dominance effect signs explain the contribution of each parent for the dominance of a particular effect. Dominance and additive effects were equal for three traits of the crosses with expressing of non-fixing gene effects. This was in agreement with previous results on thrips inheritance in cowpea (Omo-Ikerodah *et. al.*, 2009; Dormatey *et. al.*, 2015; Gonné *et. al.*, 2018).

Table 8: Estimation of gene effect for thrips resistance and related traits from TVu 1509 x M'barawa

	NPLP		NPPL		TNPP		NAT		DS			
	Gene effects estimated from three parameter model											
		t_c		t_c		t_c		t_c		t_c	$t_{0.05}$	$t_{0.01}$
m	14.81**	**6.69**	0.49**	**4.04**	14.46*	**2.32**	39.76*	**2.11**	19.92*	**2.38**	1.98	2.61
n	-0.43^{ns}	**0.20**	0.76*	**2.76**	3.74**	**3.01**	0.76*	**2.27**	-3.58*	**28.40**	2.10	2.88
h	11.23**	**3.03**	7.64^{ns}	**0.12**	28.30^{ns}	**0.09**	-75.33**	**2.62**	-42.92^{ns}	**0.93**	1.98	2.61
Individual scaling												
A	19.43**	**3.73**	1.36^{ns}	**0.39**	27.35^{ns}	**1.31**	-7.16^{ns}	**0.75**	-7.76**	**3.00**	2.00	2.66
B	-10.25^{ns}	**0.59**	2.37^{ns}	**1.51**	-0.66**	**2.04**	-11.58*	**2.21**	-9.46**	**11.93**	2.00	2.66
C	9.83*	**2.19**	2.23*	**2.27**	29.62**	**2.98**	7.72^{ns}	**0.39**	0.49^{ns}	**0.07**	1.99	2.65
Epistasis effects estimated from six parameter model												
m	18.12**	**4.26**	3.50**	**2.87**	22.67**	**4.76**	14.50**	**3.81**	4.96*	**2.23**	2.02	2.70
n	12.12*	**2.02**	21.25**	**2.70**	17.75**	**2.68**	0.01^{ns}	**0.01**	0.20^{ns}	**0.12**	1.99	2.64
h	2.36^{ns}	**0.11**	0.52^{ns}	**0.06**	4.54^{ns}	**0.19**	-26.70^{ns}	**1.52**	-16.92^{ns}	**1.73**	1.98	2.61
i	-0.24^{ns}	**-0.01**	-0.50^{ns}	**0.05**	-2.93^{ns}	**0.13**	-29.34^{ns}	**1.73**	-14.64^{ns}	**1.55**	1.98	2.62
j	14.97*	**2.27**	19.51*	**2.28**	14.01*	**1.99**	0.43^{ns}	**0.10**	3.78^{ns}	**1.65**	1.98	2.63
l	-9.19^{ns}	**-0.30**	-3.03^{ns}	**0.23**	-23.76^{ns}	**0.70**	51.63*	**2.22**	26.00*	**2.17**	1.98	2.61

Where, *, **, ns: significant, highly significant and none significant respectively at 5% and 1% level; DS**:** damage scoring; NPLP**:** number of peduncles per plant; NPPL**:** number of pods per peduncle; NAT**:** number of adults thrips; TNPP**:** total number of pods per plant; t_c: t calculate; $t_{0.05}$ and $t_{0.01}$= t table values at 5% and 1% level of significance, respectively.

Comparing crosses, additive effects were more important than dominance with TVu 1509 x M'barawa whilst dominance was the most fixing gene effects for thrips resistance control with Sanzi x M'barawa. The resistance was governed either by positive dominance (h) and negative dominance x dominance (l), positive dominance (h) and positive additive x additive (i), higher positive additive (n) and positive additive x dominance (l) or only positive dominance x dominance (l). The opposition position of dominance (h) and dominance x dominance (l) gene effects indicates duplicate gene effects that would reduce performance slowing down the level of selection for the actual trait. Elsewhere, the present results agree with those from Adeyanju *et. al.*, (2012) for pod weight from cowpea lines developed for dual purpose traits. Association of dominance x dominance (l) was detected as the type of gene effect controlling thrips damage with crosses. Duplicate positive dominance and negative dominance x dominance (l) (Sanzi x M'barawa) and complementary gene actions of positive additive (n) and positive additive x dominance (j) (TVU 1509 x M'barawa) were involved as the type of gene effects for number of peduncle per plant. The presence of positive dominance (h) and higher negative dominance x dominance suggest implication of dominance effects at heterozygous loci. This differs with results from Dormatey *et. al.*, (2015) reported negative dominance (h) and positive dominance x dominance for the same parameter which distinguishing feature may be related to different genetic makeup for resistance transfer. Most of the parameters were under complementary gene action with progenies from cross between

TVu 1509 x M'barawa including dominance (h) and additive x dominance (j) interacting for resistance under number of adults thrips with progenies from Sanzi x M'barawa and also epistasis gene effects for thrips damage control with both crosses. Contribution of these genes increased the yield of BC_1P_1, BC_1P_2 and some $F_{2's}$ from crosses which confirmed the previous finding from Acquaah (2009) who reported involvement of additive gene effects for thrips resistance control in cowpea. Number of adults thrips was under dispersion gene effects of negative dominance (h) and positive additive x dominance (l), contribution of additive (n) and higher negative value of dominance (h) towards the susceptible parent hence dominance allelic interaction. The gene actions from current study confirmed results from passed studies done by Omo-Ikerodah *et. al.*, (2009) and Gonné *et al.* (2018). Fixing and non-fixing genes were involved into cowpea seed weight character inheritance with more additives (n) and additive x dominance (j) gene effects (Egbadzor *et. al.*, 2013).

In conclusion considerable variation in terms of thrips resistance was observed from crosses of resistance and susceptible parents. Variability among non-fixing generations and differentiation from their parents implied the presence of genetic variability that could be exploited for cowpea improvement for thrips damages resistance in Mali. The current study revealed segregation and over-dominance from some generations in addition to more involvement of epistasis gene actions in cowpea indicating that thrips resistance is under polygenic control. This could therefore make important contribution to the transfer of flower bud thrips resistance in cowpea. Based on that, selection at late stages would allow the recombination of desirable genes. High heritability indicates the possibility to increase resistance of cowpea to thrips through introgression of genes from sources of resistance.

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