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Genetics of Thrips Resistance in Cowpea

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***Abstract* – Genetics of flower bud thrips (*Megalurothripssjostedti)* resistance in cowpea was studied by crossing two resistant cowpea genotypes, Sampea 8 and Sanzi, to three susceptible genotypes Ife Brown, Sampea 7 and Padi-tuya. Sufficient seeds of the parental, F$_1$, F$_2$ and backcross populations were generated and evaluated under natural thrips infestation at the Savannah Agricultural Research Institute (SARI), Nyankpala (9^0 25^{1}N: 0^0 58^{1}W), Ghana. The results confirmed Sanzi to be resistant and Sampea 8, moderately resistant, whilst Ife Brown, Sampea 7 and Padi-tuya were classified as susceptible. Maternal effects were implicated while frequency distributions of the F$_2$ and backcross generations revealed quantitative inheritance. Additive, dominance and epistatic gene effects made major contributions. The effective factors of 3 to 5 indicated an oligogenic inheritance of resistance to flower bud thrips. The study indicated that the resistance genes in Sampea 8 and Sanzi were non-allelic. Broad sense heritability estimates for number of thrips per plant, thrips damage rating and pods per peduncle ranged from 53.00 to 58.00%, 49.70 to 58.32% and 85.00 to 94.00%, respectively. Narrow sense heritability estimates for the same traits ranged from 13.00 to 28.00%, 12.69 to 20.86% and 18.00 to 41.00% respectively. Genetic advance of reduction of susceptibility from 4 to 6 thrips per plant at 10 % selection intensity was predicted. The broad and narrow sense heritability estimates with the genetic advance showed the possibility to increase and diversify resistance of cowpea to thrips by using the two resistant genotypes, Sanzi and Sampea 8.**

***Keywords* – *Vignaunguiculata* (L.) Walp., Genetic Advance, *Megalurothripssjostedti*, Gene Effects, Oligogenetic Inheritance, Allelism.**

I. INTRODUCTION

Cowpea (*Vignaunguiculata*(L.) Walp.) is one of the world's most important food legume crops and the main source of plant protein in West and Central African regions [10]. The tender leaves, immature pods, soft stems and fresh seeds are eaten as vegetables and the dry grains serve as staple food. The protein content ranges from 23-38 % in the grain and 29-43 % in the leaves [11]. In addition, cowpea contributes to the sustainability of the cropping systems and soil fertility improvements in marginal lands by providing ground cover, fixing atmospheric nitrogen and suppressing weeds. However, its production is still constrained by several yield reducing factors such as thrips species (*Thysanoptera: Thripidae*) which is the most important biotic stress that has devastating effects on cowpea in West Africa and other parts of the world [6]. The species *Megalurothripssjostedti* appears most destructive in West Africa, causing 20-80 % yield losses under severe infestation [19].

Cultural practices recommended to limit thrips infestation include irrigation, tillage operation, planting date, crop rotation and intercropping [21]. However, the incidence of multiple infestations in cereals, vegetables, and cowpea [18] preclude effective control through these methods. Insecticides use which has also been recommended for thrips has a major drawback such as rapid development of insecticide resistance in thrips populations rendering the chemical treatments ineffective [18]. In addition, these chemicals are expensive and sometimes need to be applied with special equipment that put them out of reach of the majority of resource-poor farmers. The correct usage of these chemicals to ensure effective control is another limitation.

In order to minimize 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. In that, identification and deployment of host-plant resistance in elite cultivars to manage thrips minimizes dependence on environmentally toxic chemicals that resource poor-farmers cannot afford and are not well equipped to handle [12]. However, studies in other insects systems suggest that genetic resistance mechanisms may be highly specific to the insect species or even the developmental stages of the insect pest [23].

Better understanding of the resistance mechanisms and mode of gene action determining inheritance of the different mechanisms of resistance can improve methods of screening and enhance identification and development of resistant or tolerant 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. This is useful in determining selection criteria, appropriate breeding methods for durable resistance and sustainable yield in cowpea. The study was therefore designed to validate the resistance status of the source materials, elucidate the mode of inheritance of resistance to thrips and determine the allelic relationship between the resistance sources. Host-plant resistance would also form the basis of integrated pest management.

II. MATERIALS AND METHODS

A. Development of Genetic Populations

Three thrips-susceptible genotypes; Ife brown, Sampea 7, Padi-tuya and two resistant genotypes Sanzi and Sampea 8 were crossed using the bi-parental mating design to generate six sets of F$_1$ populations. The F$_1$ populations were advanced to F$_2$ and at the same time backcrossed to their respective parents to produce BC$_1$P$_1$ and BC$_1$P$_2$ populations, respectively. For each cross, six generations, P$_1$,P$_{2,}$ F$_{1,}$ F$_{2,}$ BC$_1$P$_{1,}$ and BCP$_2$ were produced in the screen house. In order to study the allelic relationship between the resistance and susceptible sources, the two cowpea resistant genotypes, Sampea 8 and Sanzi were reciprocally crossed as well as two susceptible genotypes, Ife Brown and Padi-tuya to generate genetic populations.

B. Field Evaluations for Flower Bud Thrips Resistance

The five parentals and their genetic populations (F$_1$, F$_2$, BCP$_1$ and BCP$_2$) were planted in the experimental field of the Savanna Agricultural Research Institute, Nyankpala, northern Ghana (9^o 25' 41' N: O^{o}58' 42'W at altitude 183 m above sea level) on 14 October, 2013. The design was randomized complete block with three replications. For the parentals, each genotype was planted on a 3-row plot, 3 m long with inter-row and intra-row spacing as 0.60m and 0.20m respectively leaving one plant per hill. The genetic populations had two rows of the F$_1$s, three rows for the backcrosses and four rows of each F$_2$ generation. To ensure high selection pressure of the thrips, spreader rows of susceptible genotype, Ife Brown were planted around the experimental plot and between the rows two weeks prior to planting of the test materials. Thirty-five days after planting, the spreader row plants were uprooted and laid down between the of test plots. The plants were protected by spraying with the insecticide, Karate 2.5 EC (λ-cyhalothrin) at the rate of 2.5 g (a.i.) ha^{-1}using a CP-15 knapsack sprayer at days to 50 % podding against pod-sucking bugs (PSBs) to eliminate their confounding effects.

Data collected included, thrips damage rating, number of thrips/plant, days to 50 % flowering (DFF), number of days to 50 % maturity, number of pods/plant, number of peduncles/plant, number of seeds/plant and dried pod weight. The test materials were rated for damage on a scale of 1-9 at 35 days after planting according to [12]. Rating was based on a combination of varying intensities of browning of the stipules and flower buds, non-elongation of peduncles and flower bud abscission. Populations of thrips were estimated by randomly picking 5 flowers per plant for all generations, depending on the stage of growth. The samples were taken early in the morning, between 7–9.00 am local time during the peak of flowering. The flowers were placed in glass vials or petri-dish containing 40 % ethanol and subsequently dissected to count the number of thrips [1]. The infestations were assessed twice during the crop phenology. At maturity, all plants were harvested, hand threshed and the seeds stored in clearly labelled paper bags.

C. Statistical Analyses

The data pertaining to thrips resistance; number of thrips/plant, thrips damage rating, number of pods/peduncle, days to 50 % flowering, days to 50 % maturity, number of pods/plant and number of seeds/plant were subjected to analysis of variance using the general linear model (GLM) procedure of the Statistical Analysis System (SAS) programme. Duncan Multiple Range Test was used to separate the means where there was significant difference. Paired t-test Analysis was carried outto determine the possible reciprocal differences of the respective F_1 hybrids.

Generation Mean Analysis (GMA) was used to measure genetic parameters according to [14]. Generation mean was calculated for six generations on an individual plant basis. To determine the mode of inheritance of resistance to thrips, [5] notation was used as:

$$Y = m + \alpha a + \beta d + \alpha 2aa + 2\alpha\beta ad + \beta 2dd.$$

Where Y is the observed generation mean; m, mean; a, additive gene effects; d, dominance gene effects; aa, additive x additive epistatic gene effects; ad, additive x dominance epistatic gene effects; dd, dominance x dominance epistatic gene effects. α and β represent the coefficients for the genetic effects for the particular generation being estimated [17].

Chi-square Test was conducted to test the goodness of fit of the data to the additive dominance model by (Little and Hill, 1978)

$$\chi^2 = \sum \frac{(O-E)^2}{E}$$

Where:

O = Observed value, E = Expected value and

$\sum$ = summation

The model described by [4] was used to estimate the expected values:

Number of Effective Factors were calculated using the formula; $N = R^2 / 8(\sigma^2{}_g)$ as proposed by [15].

Where: R is range of F_2 segregates in the cross, σ_g^2 = genetic variance of the F_2 population of a cross.

Broad sense ($H_{(B)}$) and narrow sense (h) heritability estimates were obtained using the variance component methods. The F_2 variances were used to compute the broad sense heritability according to [16] as follows:

$$H_{(B)} = \frac{\sigma^2 F_2 - \sqrt{\sigma^2 P_1 x \sigma^2 P_2}}{\sigma^2 F_2} x100$$

Where $\sigma^2 F_2 = \sigma^2 G + \sigma^2 E$, $\sigma^2 P = \sigma^2 E$, $\sigma^2 P_1 = \sigma^2 E_1$, $\sigma^2 P_2 = \sigma^2 E_2$.

In these relationships: $H_{(B)}$ = broad sense heritability, $\sigma^2 F_2 =$ phenotypic variance of F_2 population of a cross, $\sigma^2 G =$ genetic variance of the F_2 population of a cross

σ^2 E = environmental variance of F_2 population of a cross.

The narrow sense heritability estimates were computed using the formulae described by Warner (1952).

$$h2 = \frac{2\sigma^2 F_2 - (\sigma^2 B_1 + \sigma^2 B_2)}{\sigma^2 F_2}$$

Where; h^2 = narrow sense heritability,

$$\sigma^2 F_2 = \tfrac{1}{2}A + \tfrac{1}{4}D + E$$

$$\sigma^2 B_1 + \sigma^2 B_2 = \tfrac{1}{2}A + \tfrac{1}{2}D + E$$

$$2\sigma^2 F_2 - \sigma^2 B_1 - \sigma^2 B_2 = A + \tfrac{1}{2} D + 2E - (\tfrac{1}{2} A + ½ D + 2E) = ½ A$$

The Genetic Advance (GA)was calculated in accordance with the method illustrated by [3] as: GA or $G_s = K * \sigma^2{}_A * h^2$

Where, K is the standardized selection differential, at 10 % selection intensity, K = 1.755

$\sigma^2{}_A$ is additive variance and h^2 is narrow sense heritability estimate.

Genotypic and phenotypic correlations were used to investigate the association between damage rating and number of thrips/plant and other agronomic characters measured in the parental genotypes and their progenies. Correlation coefficients were calculated from component of variance and covariance according to [22].

III. RESULTS

A. Validation of thrips resistance status of parental materials

The average number of seeds/plant, pods/peduncle, number of trips/plant and the thrips damage rating and mean number of pods/plant were indices of resistance status of the parental materials (Tables 1 and 2). The mean number of pods/plant showed highly significant differences (*P*> 0.01) among the parental materials (Table 1). The average number of pods/plant ranged from the lowest value of 3.41 to the highest value of 8.35 for Ife Brown and Sanzi, respectively. The average number of pods/plant was drastically reduced by flower bud thrips infestation in cowpea genotypes, Ife Brown, Sampea 7 and Padi-tuya while considerable number of pods was sustained in the genotypes, Sampea 8 and Sanzi (Table 1). These values took into consideration the elimination of confounding effects of other cowpea insect pests. Though, there were no significant differences among the parental materials for days to 50 % flowering, the days to 50 % maturity showed significant differences (Table 1).

The average number of seeds/plant, pods/peduncle, number of trips/plant and the thrips damage rating are presented in Table 2. The parental genotype, Sampea 7 had a mean of 8.30 thrips/ plant, Sanzi and Sampea 8 had mean of 3.43 and 5.80 thrips/plant, respectively. Ife Brown had a mean of 7.67 thrips damage rating, Sampea 7 and Padi-tuya had mean of 7.70 and 7.66 thrips damage rating, while Sanzi and Sampea 8 had mean of 3.00 and 5.00 thrips damage rating, respectively. The genotypes, Ife brown, Sampea 7 and Padi-tuya had means of 0.51, 0.58 and 0.59 pods per peduncle per plant respectively, while Sanzi and Sampea 8 had mean of 0.85 and 0.75 pods/peduncle. Ife Brown, Sampea 7 and Padi-tuya were susceptible and had mean of number of seeds/plant as 12.12, 11.92 and 11.89 respectively. The resistant genotypes Sanzi and Sampea 8 had mean of 21.78 and 17.80 number of seeds/plant respectively.

The means of the thrips damage rating, number of flower thrips per plant and pods per peduncle for the crosses; Sampea 8 x Sanzi (resistant x resistant) and Ife brown x Padi-tuya (susceptible x susceptible) and their generations are presented in Table 3. The means of the parents varied significantly (*P*> 0.05); Sampea 8 (5.83) and Sanzi (3.43) as well as all the generations were significantly different from each other (Table 3). The means of the F_1 generation varied with the resistant parents used. The reciprocal backcross population BCP_1 and BCP_2 were all resistant (Table 3). Most of the F_2 progenies were resistant while some were susceptible in spite of the fact that the two parents were resistant. There were some F_2segregants that were more resistant than the parents, they recorded few number thrips than both parents, which could be categorised into resistant, moderately resistant and susceptible. However, the ratio of F_2 to F_1 variance (3.71) was significant (P> 0.05) for thrips damage rating, confirming that the F_2 segregation observed was significant. The result from generation mean analysis revealed that dominance gene effects was significant for the cross Sampea 8 x Sanzi. However, the reaction of Ife brown x Padi-tuya and Padi-tuya x Ife brown showed no significant difference among all the generations (Table 3). No apparent segregation pattern was evident in their backcross and the F_2 populations.

Table 1: Mean number of days to 50 % flowering, days to 50 % maturity and average number of pods/plant of cowpea genotypes evaluated under natural infestation of thrips.

Genotype	Days to 50 %* Flowering	Days to 50 %* Maturity	Number of Pods* per Plant
Ife brown	42.33	71.33^b	3.41^c
Sampea 7	42.47	72.64^a	3.57^c
Sanzi	41. 33	61.67^d	8.35^a
Sampea 8	41.33	62.23^d	5.60^b
Padi-tuya	42.33	67.00^c	3.61^c
Grand Mean	42.2	67.2	4.91
C.V (%)	1.53	0.99	9.35
S. E±	0.28	0.42	0.22

* Means with the same alphabet in a column are not significantly different according to Duncan Multiple Range Text (DMRT).

Comparing F_1 hybrids, reciprocal differences were indicated in the cross between Sampea 8 x Sanzi (P< 0.01 and P< 0.05) for thrips damage rating, number of thrips/plant and number of pods/peduncle. The number of thrips per plant however, was not significant but the performance of the RF_1 was slightly above the F_1 (Table 4).

Table 3: Mean performance of the two resistant and the two susceptible cowpea genotypes and their progenies for allelic test

	TDR	**NTP**	**NPP**		**TDR**	**NTP**	**NPP**
Generation	**Mean***	**Mean***	**Mean***	**Generation**	**Mean***	**Mean***	**Mean***
Samp.8 (R)	5.00^b	5.83^a	0.71^f	Ife brown (S)	7.67	8.51	0.53
Sanzi (R)	3.00^d	3.43^d	0.85^b	Padi-tuya (S)	7.63	8.32	0.55
F_1	2.40^f	3.10^e	0.86^a	F_1	7.70	8.33	0.56
F_2	5.20^a	5.76^b	0.72^e	F_2	7.71	8.57	0.59
F_1x Samp.8	3.37^c	4.95^c	0.81^c	F_1 x Ife brown	7.72	8.40	0.56
F_1 x Sanzi	3.00^d	3.43^d	0.75^d	F_1 x Pad-tuya	7.72	8.40	0.58

*Means with the same alphabets in a column are not significantly different according to Duncan Multiple Range Test.
TDR = Thrips damage rating, NTP = Number of Thrips per plant, NPP = Number of pods per peduncle per plant

Table 4: Comparison of F_1 hybrids with their respective reciprocals for mean thrips damage rating, number of thrips/plant and number of pods/peduncle.

Cross^a	Mean Thrips damage rating	Mean number of thrips/plant	Mean number of pods/peduncle
Sampea 8 x Sanzi	3.72±0.4	5.9±0.28	0.70±0.03
Sanzi x Sampea 8	3.10±0.4	7.8±0.31	0.86±0.04
t-test^b	Ns	**	*

^{a}First named parent = ♀, second named parent = ♂
^{b} F_1 means compared with Reciprocal F_1 (RF_1)means
*, ** and ns-Significant at 0.05; 0.01 probability levels and non-significant by t-test

B. Progenies of Crosses

Frequency distributions for number of thrips per plant and pods per peduncle in the parental, F_1, F_2, and backcross generations are presented in Figures 1 – 8. The parents used in the study did not represent genotypic extremes for resistance and susceptibility to thrips; the mean number of thrips per plant was 3.43 for Sanzi, 8.50 for Ife brown, 8.30 for Sampea 7, 8.27 for Padi-tuya and 5.80 for Sampea 8, respectively. The observed frequency distributions of the two parents overlap for number of thrips per plant for all the crosses (Figs. 1 to 8). The mean of F_1 hybrids of all the crosses involving resistance x susceptible, were lower than that of the susceptible parents (P_2s). BCP_1 and BCP_2 plants were partially distributed across the range of both parents but were skewed towards the recurrent parents for number of thrips per plant. The phenotypic classes intermediate of the parents were also observed, the F_2 distributions occurred over the range of both parents for number of thrips/plant among the 105 plants studied. However, this result observed for number of thrips/plant was similar to that of thrips damage rating and number of pods/peduncle (Figures 1 to 8)

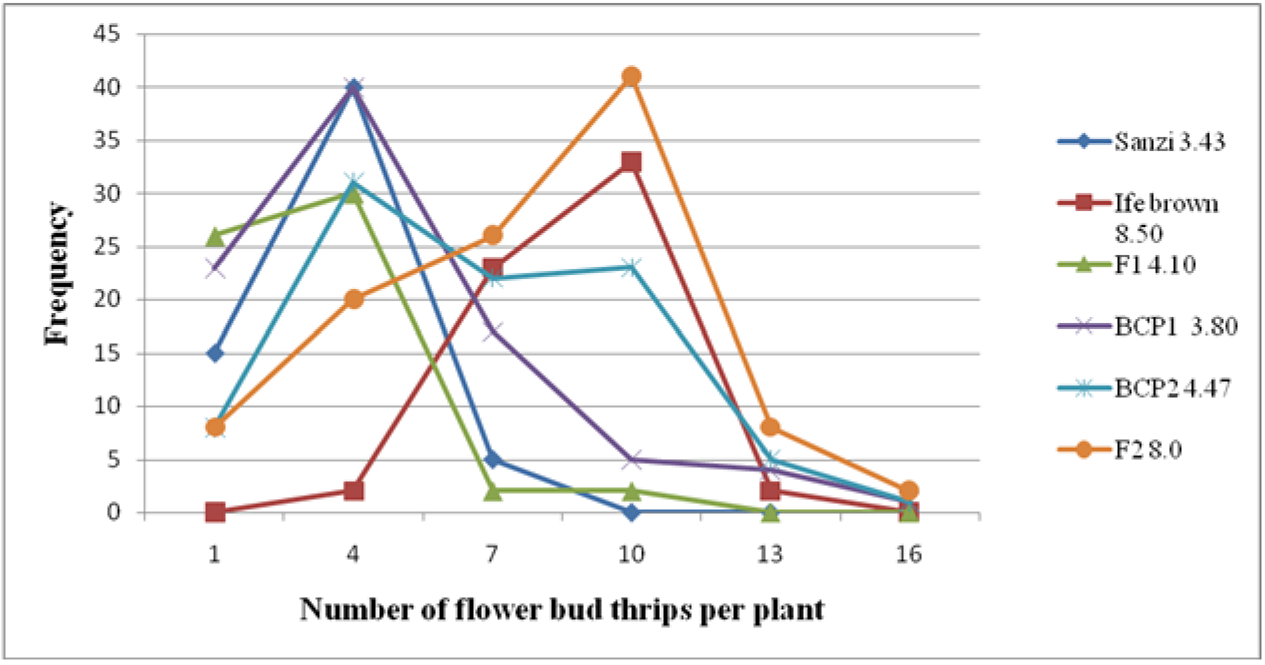

Fig.1. Frequency distribution of number of thrips/plant for parents, F_1, backcross and F_2 populations for the Sanzi x Ife Brown cross evaluated in the field.

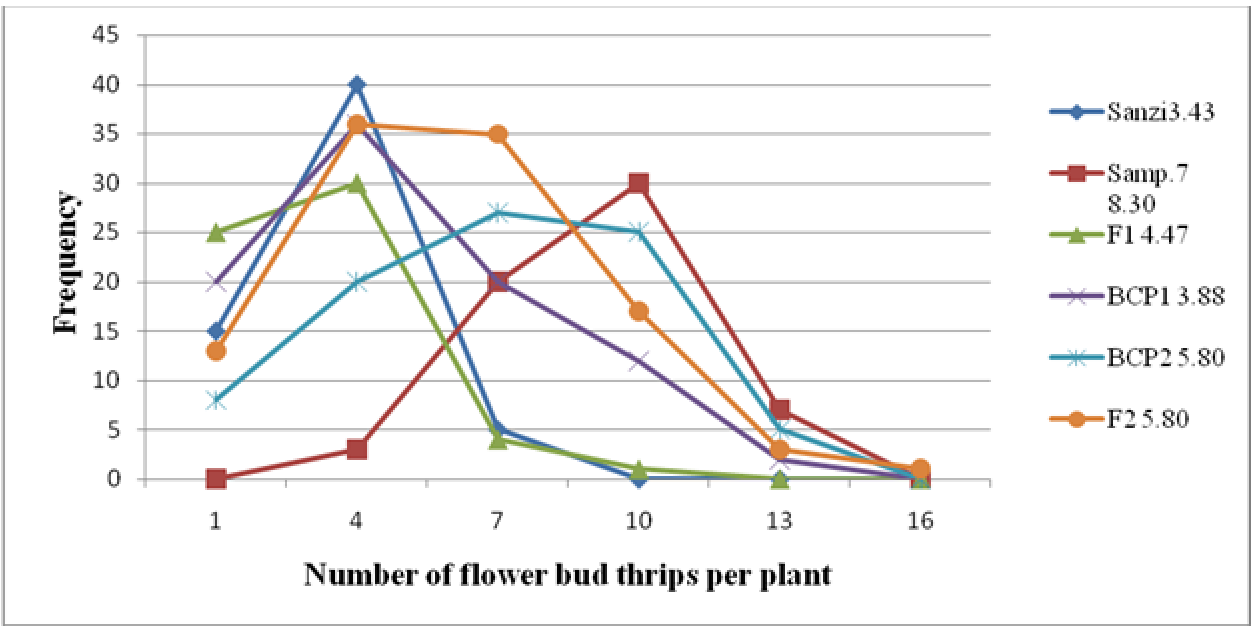

Fig.2. Frequency distribution of number of flower bud thrips per plant for parents, F_1, backcrosses and F_2 populations for the Sanzi x Sampea 7 cross evaluated in the field

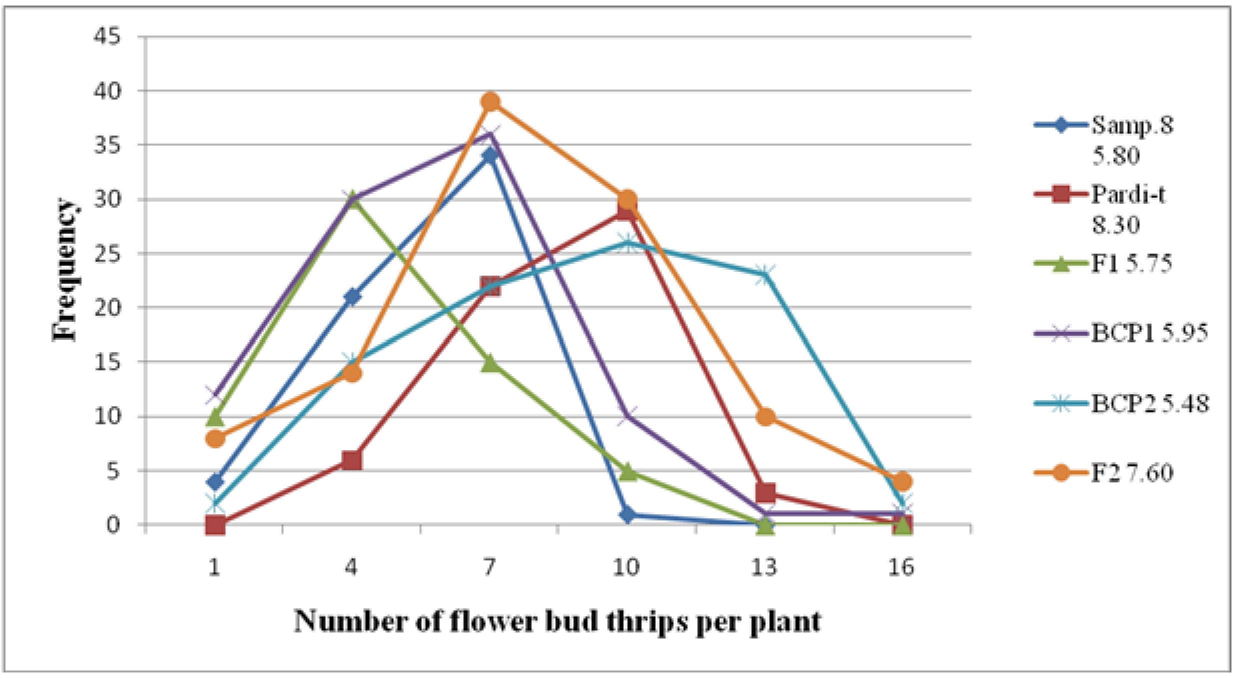

Fig.3. Frequency distribution of number of flower bud thrips per plant for parents, F_1, backcrosses and F_2 populations for the Sampea 8 x Pardi-tuya cross evaluated in the field

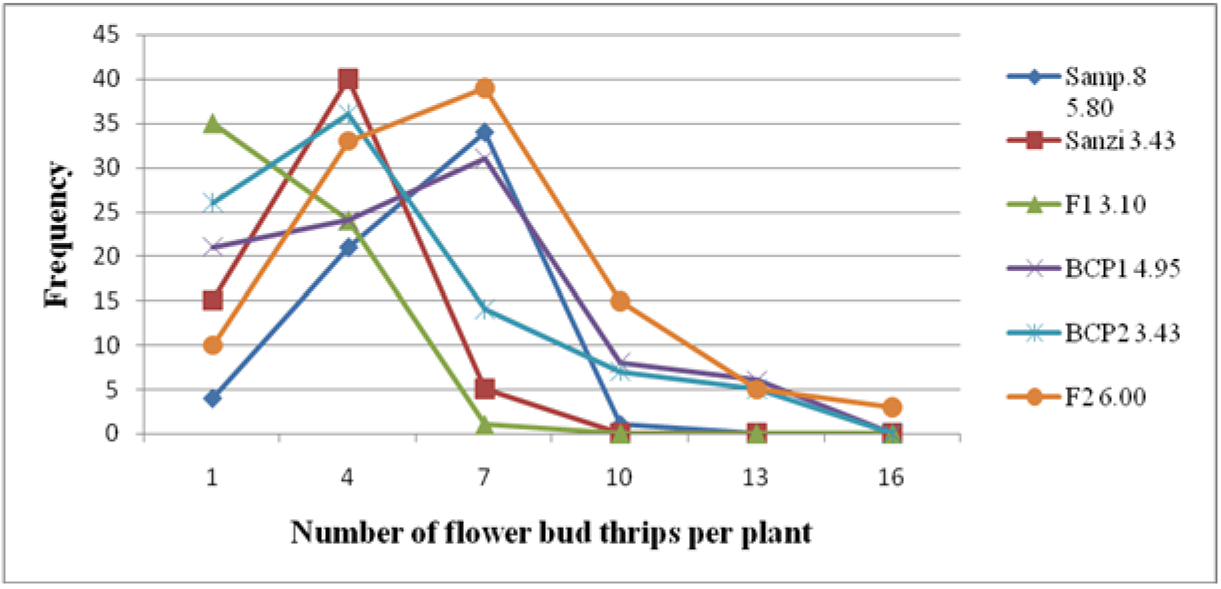

Fig.4. Frequency distribution of number of flower bud thrips per plant for parents, F_1, backcrosses and F_2 populations for the Sampea 8 x Sanzi cross evaluated in the field.

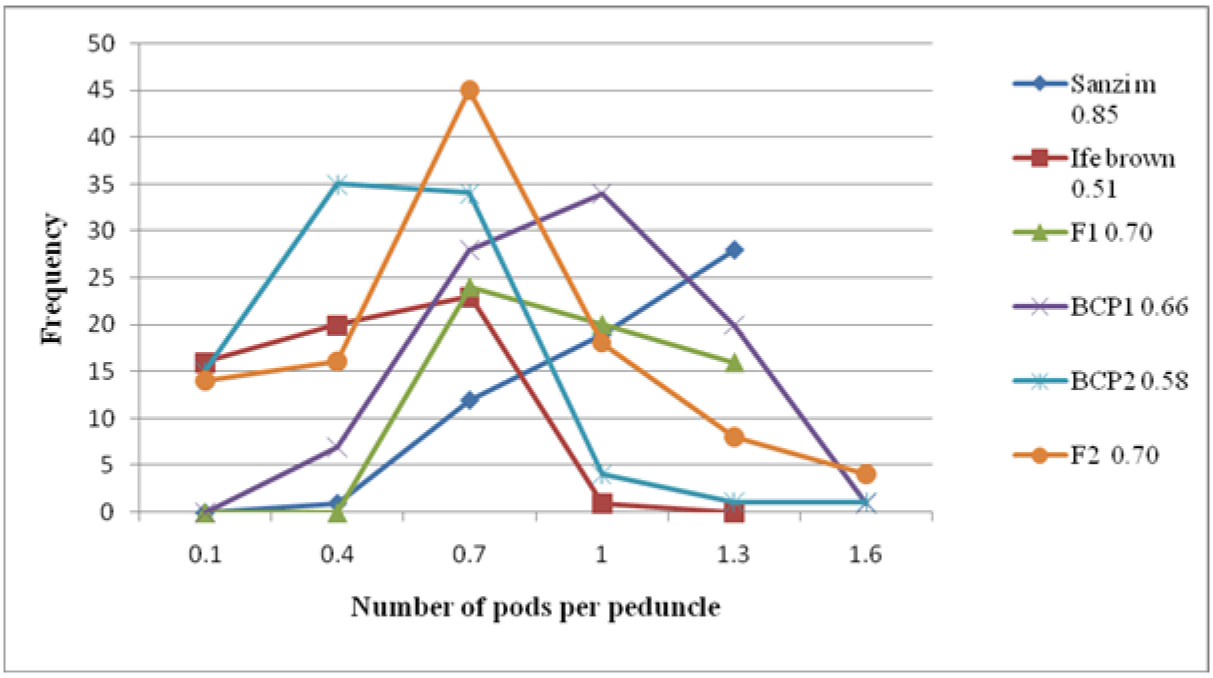

Fig.5. Frequency distribution of number of pods per peduncle per plant for parents, F_1, back crosses and F_2 populations for the Sanzi x Ife brown cross evaluated in the field

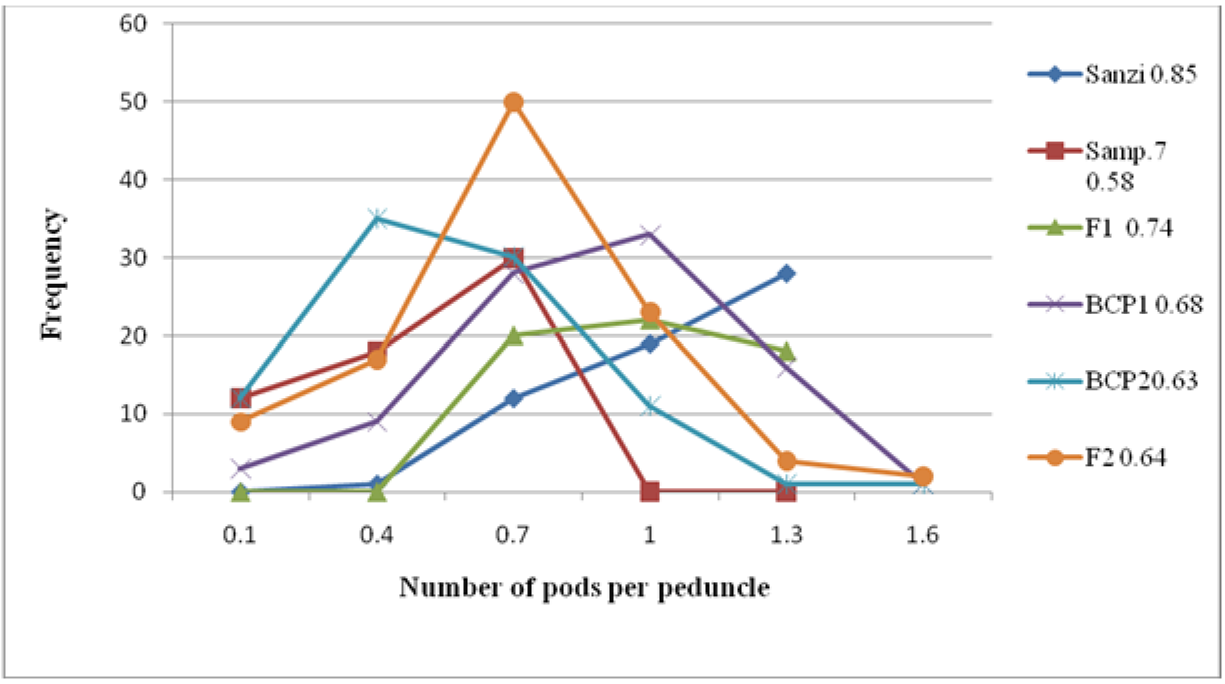

Fig.6. Frequency distribution of number of pods per peduncle for parents, F_1, backcrosses and F_2 populations for the Sanzi x Sampea 7 cross evaluated in the field.

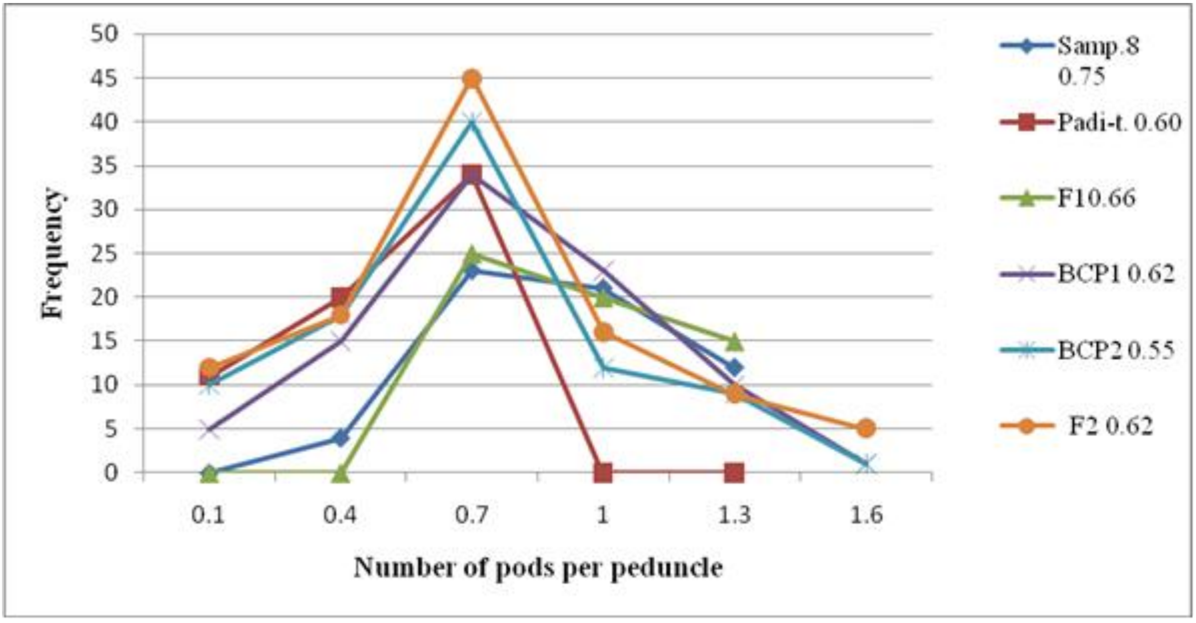

Fig.7. Frequency distribution of number of pods per peduncle for parents, F_1, backcrosses and F_2 populations for the Sampea 8 x Padi-tuya cross evaluated in the field

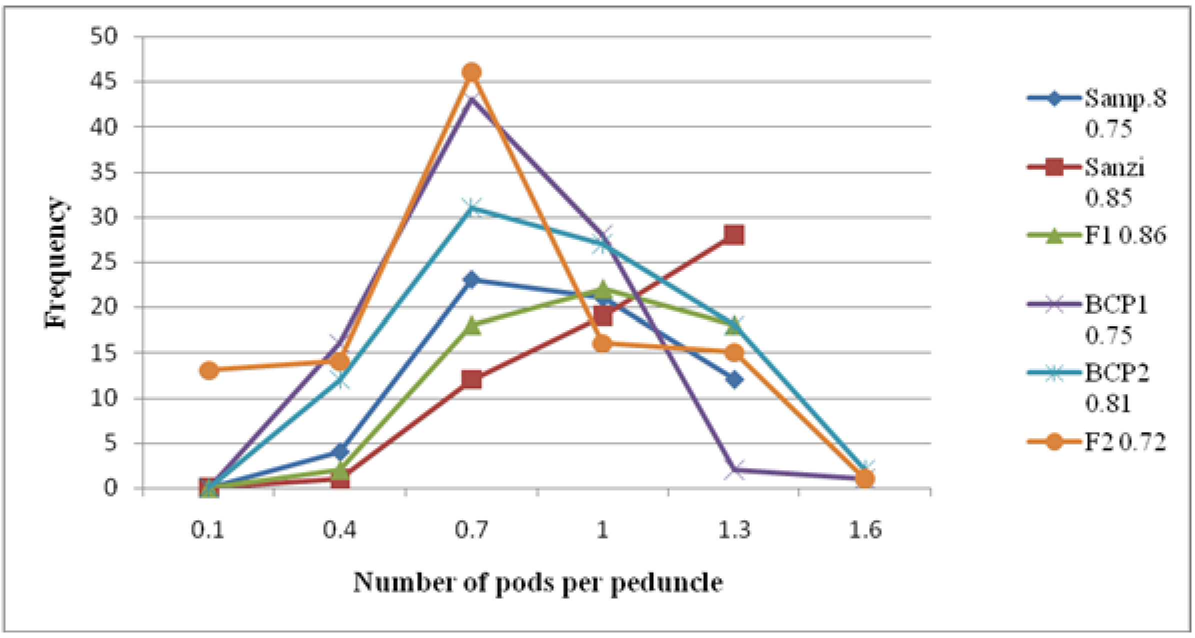

Fig.8. Frequency distribution of number of pods per peduncle per plant for parents, F_1, backcrosses and F_2 populations for the Sampea 8 x Sanzi cross evaluated in the field

C. Estimates of Gene Effects for Thrips Damage Rating, Flower Bud Thrips and Number of Pods per Peduncle

The results of generation mean analyses for the thrips damage rating, number of thrips per plant and number of pods per peduncle showed the presence of epistatic gene actions in all the crosses involving resistant x susceptible and resistant x resistant (Tables 5, 6 and 7). The estimation of the various gene effects for the six parameters revealed that additive (a) gene effect was significant in number of thrips/plant, thrips damage rating and number of pods/peduncle in all the six families of the crosses (Tables 5, 6 and 7). Except for the crosses, Sanzi x Ife brown and Sampea 8 x Sanzi, the dominance (d) gene effect was also significant in three crosses for thrips damage rating, number of thrips/plant and number of pods/peduncle. In the resistant x susceptible crosses, dominance gene effects were greater than the additive gene effects with all the three important traits studied. The dominance gene effects ranged from 2.84 to 7.05, whilst additive gene effects ranged from 1.00 to 2.35 in thrips damage rating for resistance (Tables 5, 6 and 7). In the resistant x resistant crosses, dominance gene effects made the greater contribution than additive gene effects with 6.80 to 7.29 and 0.63 to 1.85 against 1.22 to 2.60 and 0.06 to 0.17 in number of thrips per plant and number of pods per peduncle, respectively. However, both dominance and additive gene effects were in negative directions in only number of pods/peduncle. In addition, the epistatic component, additive x additive (aa), additive x dominance (ad) and dominance x dominance (dd) gene interaction effects were also vital in two of the five crosses involving the three traits studied (Tables 6, 7 and 8). The additive x additive (aa) interaction gene effects were generally important in all the traits studied among resistant x susceptible crosses except in the case of the crosses involving Sampea 8 x Padi-tuya. This ranged from 3.48 to 6.14 for thrips damage rating, 4.47 to 5.46 for number of thrips/plant and 0.21 to 0.81 for number of pods/peduncle, respectively (Table 5, 6 and 7).

Additive x dominance (ad) gene interaction effects were significant in three of the crosses except that of Sampea 8 x Padi-tuya in thrips damage rating and number of thrips per plant, but for pods per peduncle, it was significant in only one cross (Sanzi x Ife brown). Dominance x dominance interaction gene effects was significant ($P > 0.05$ and $P > 0.01$) for thrips damage rating for two crosses Sampea 8 x Sanzi and Sampea 8 x Padi-tuya as well as number of thrips/plant for Sanzi x Ife brown and Sampea 8 x Padi-tuya. But in pods/peduncle, dominance x dominance interaction gene effects was significant in three crosses, except Sampea 8 x Sanzi. In the resistant x resistant cross (Sampea 8 x Sanzi), additive, dominance, additive x additive, additive x dominance and dominance x dominance gene effects were significant ($P > 0.01$ and $P > 0.05$, respectively). But additive, dominance and additive x additive gene effects were more vital than the rest in thrips damage rating. On the other hand, all the five types of gene effects were observed to be important in two or all the characters (number of flower bud thrips per plant and number of pods per peduncle) in the crosses (Table 5, 6 and 7).

A test of goodness of fit to the additive-dominance model (Tables 8 and 9) were not significant (*P*< 0.05, χ^2 1.67, 7.4, 5.61 and 5.11, respectively) involving crosses of Sanzi x Ife brown and Sampea 8 x Padi-tuya for number of thrips/plant as well as Sanzi x Ife Brown and Sampea 8 x Sanzi for thrips damage rating and number of pods/peduncle. The nature of gene action involved in the resistance of cowpea to thrips confirmed that additive-dominance model is inadequate to explain the gene action governing the inheritance of resistance to flower bud thrips.

Table 5: Estimates of gene effects for thrips damage rating for five cowpea crosses evaluated under natural infestation of thrips in the field.

Crosses	**m**	**A**	**d**	**aa**	**ad**	**dd**
Sanzi x Ife brown	5.53 **	2.33**	3.07	4.41**	-4.07**	1.06
	±0.18	±0.03	±1.48	±0.33	±0.39	±0.91
Sanzi x Sampea 7	5.27*	2.35**	7.05*	6.14**	-3.42*	-0.98
	±0.19	±0.08	±2.73	±0.97	±0.84	±1.9
Sampea 8 x Sanzi	5.20**	1.00**	2.84**	3.48**	-1.62**	1.84**
	±0.24	±0.01	±0.43	±0.15	± 0.1	±0.32
Sampea 8 x Pardi-tuya	5.03*	1.30**	-6.57*	0.53	-0.83	5.82*
	±0.21	±0.04	±1.57	±0.61	±0.44	±1.07
Ife brown x Padi-tuya	7.73*	-0.02	1.38	-0.07	0.10	-0.51
	±0.14	± 0.05	±0.83	±0.34	±0.22	±0.51

Table 6: Estimates of gene effects for number of thrips/plant for five cowpea crosses evaluated under natural infestation of thrips in the field.

Crosses	**m**	**a**	**d**	**Aa**	**Ad**	**dd**
Sanzi x Ife brown	7.75*	2.60**	-0.29	4.47*	-6.29**	6.50*
	±0.25	±0.12	±2.71	±1.18	± 0.59	±1.68
Sanzi x Sampea 7	5.80**	2.45**	7.29**	5.46**	-1.20*	-1.89
	±0.22	±0.09	±2.04	±0.88	±0.47	±1.19
Sampea 8 x Sanzi	5.61**	1.22**	6.80*	4.98*	-5.08**	-0.91
	±0.25	±0.16	±3.01	±1.28	± 0.73	±1.91
Sampea 8 x Padi-tuya	7.59**	1.33**	-6.18	0.16	-1.44	6.76*
	±0.19	±0.17	±4.82	±2.13	±1.01	±2.89
Ife brown x Padi-tuya	8.57**	0.11	-0.29	-0.03	0.27	0.43
	±0.067	±0.06	±0.18	±0.34	±0.29	± 0.54

The upper values and their standard errors
*, ** Significant at 0.05 and 0.01 probability levels, respectively

Table 7: Estimates of gene effects for number of pods per peduncle per plant for five cowpea crosses evaluated under natural infestation of thrips in the field.

Crosses	**m**	**A**	**d**	**Aa**	**Ad**	**dd**
Sanzi x Ife brown	0.67 **	-0.17**	-1.85**	-0.81**	0.19**	1.03**
	±0.06	±0.01	±0.22	±0.09	±0.06	±0.14
Sanzi x Sampea 7	0.63**	-0.14**	-1.89**	-0.38*	0.14	0.44*
	±0.06	±0.01	±0.29	±0.12	±0.08	±0.18
Sampea 8 x Sanzi	0.73*	-0.07*	-0.12	-0.54*	-0.08	0.41
	±0.05	±0.02	±0.40	±0.18	±0.09	±0.25
Sampea 8 x Pardi-tuya	0.60*	-0.06*	-0.96*	-0.38*	-0.04	0.54 *
	±0.20	±0.02	±0.30	±0.13	±0.04	±0.19
Ife brown x Padi-tuya	0.59**	0.04*	-0.40	-0.15	-0.23	0.23
	±0.12	± 0.02	±0.27	±0.06	±0.12	±0.10

The upper values and their standard errors
*, ** Significant at 0.05 and 0.01 probability levels, respectively

Table 8 Test of goodness of fit to the additive-dominance genetic model for the crosses Sanzi x Ife brown and Sampea 8 x Padi-tuya for number of thrips per plant

Sanzi (R) x Ife Brown (S)				**Sampea 8 (R) x Padi-tuya (S)**			
Generation	Observed	Expected	χ^2	Generation	Observed	Expected	χ^2
Sanzi	3.43	2.76	0.16	Sampea 8	5.83	5.49	0.03
Ife brown	8.5	7.95	0.09	Padi-tuya	8.3	8.14	0.009
F_1	4.08	4.27	0.0028	F_1	5.75	0.63	2.48
F_2	7.83	4.81	0.70	F_2	7.59	3.72	1.39
BC_1P_1	3.79	6.11	0.14	BC_1P_1	5.33	9.23	2.82
BC_1P_2	4.47	4.59	0.58	BC_1P_2	5.92	4.38	0.67
Total			**1.67**	Total			**7.4**
Significance			$P < 0.05$	Significance			$P < 0.05$

Table 9: Test of goodness of fit to the additive-dominance genetic model for the crosses Sanzi x Ife Brown for thrips damage rating and Sampea 8 x Sanzi for number of pods/peduncle

Sanzi (R) x Ife Brown (S)				**Sampea 8 (R) x Sanzi (R)**			
Generation	Observed	Expected	χ^2	Generation	Observed	Expected	χ^2
Sanzi	3.00	2.24	0.12	Sampea 8	0.75	0.86	0.25
Ife Brown	7.67	6.90	0.14	Sanzi	0.85	0.72	0.33
F_1	2.80	7.64	1.64	F_1	0.86	0.67	0.43
F_2	5.53	4.73	1.60	F_2	0.72	0.73	0.002
BC_1P_1	4.67	4.52	0.03	BC_1P_1	0.75	0.45	2.25
BC_1P_2	3.77	4.95	2.08	BC_1P_2	0.81	0.59	1.85
Total			**5.61**	Total			**5.11**
Significance			$P< 0.05$	Significance			$P< 0.05$

IV. DISCUSSIONS

The observations from validation of resistance status of the parental materials revealed that, there was no significant difference of the number of days to 50 % flowering among the five cowpea genotypes evaluated. Therefore, the resistance in Sanzi and Sampea 8 could not be explained by thrips infestation escape due to early flowering. However, the average number of thrips/plant for each genotype showed significant difference among them. The infestation of thrips resulted in the abscission of almost all flower buds in the case of the susceptible genotypes (Ife Brown, Sampea 7 and Padi-tuya), on the other hand, many flower buds were retained and even developed pods and grains in the resistant genotypes. The average thrips damage rating scores and mean number of pods/peduncle also showed significant differences among the cowpea genotypes. Sanzi recorded less thrips damage rating of 3.00, number of thrips/plant (3.43) and number of pods/peduncle (0.85) respectively. Sanzi, a local landrace consistently, supported fewer thrips populations and lesser damage comparable to Sampea 8 which recorded thrips damage rating of 5.00, Ife brown (7.67), Sampea 7 (7.70) and Padi-tuya (7.66), the susceptible genotypes. These important parameters showed Sanzi to be resistant and Sampea 8 to be moderately resistant whilst Ife Brown, Sampea 7 and Padi-tuya were rated as susceptible. These findings corroborated some previous results [1], [2] and [20] that Sanzi was resistant tothrips in Nigeria and Ghana. The differences observed in the reciprocal crosses between Sampea 8 x Sanzi indicated the presence of cytoplasmic factors, considering average number of pods per plant, thrips damage rating and number of thrips per plant. The F_1 plants were significantly higher than the respective mid-parent values and were closer to the resistance parent, indicating dominance of resistance over susceptibility.

The frequency distributions of thrips damage rating, number of thrips/plant and pods/peduncle revealed that, the F_1 plants were significantly lower than both parents indicating an over-dominance of resistance over susceptibility. The BC_1P_1 and BC_1P_2 plants were distributed partially across the range of both parents but skewed towards the recurrent parents. The F_2 plants were distributed over the range of both parents with continuous distribution coupled with transgressive segregation, suggesting the involvement of more than two genes controlling the inheritance of resistance of flower bud thrips in cowpea. This observation was not different from the findings on inheritance of time to flowering in cowpea [11]where the F_2 plants were distributed over the range of both parents, indicating more than two genes controlling the trait. The generation means indicated that the additive-dominance model was inadequate to explain variations observed in the inheritance of resistance to thrips in cowpea. Tests of goodness of fit to the additive-dominance model were also not significant which further suggested the importance of epistasis. This was confirmed by the results of generation mean analysis [14]. Generation means analysis provided estimates of the relative magnitudes of additive, dominance and epistatic gene effects. The estimates for the various gene effects revealed that both additive and dominance gene effects, contributed significantly to the inheritance of the traits studied, with the preponderance of dominance gene effects confirming someearlier reports[20]. Thus in addition to the significance of the additive and dominance gene effect, the epistasis component, additive x additive, additive x dominance and dominance x dominance gene interaction effects were also significant in most of the crosses, suggesting the involvement of more than one gene in control of inheritance of the trait. However, both additive and dominance were highly significant in most of the crosses. Similarly, the additive x additive and additive x dominance made major contributions to resistance to flower bud thrips. These results suggested that most of the genetic variation observed can be attributed to heritable sources. These were supported by the moderately high narrow sense heritability estimated for the crosses. Broad sense heritability were relatively high among all the crosses for the three traits studied, averaging 55.13 %, 54.28 % and 81 % coupled with moderately high narrow sense heritability, averaging 20.04 %, 17.55 % and 30.25 % for number of thrips/plant, thrips damage rating and pods/peduncle, respectively. Characters with highest heritability, phenotype is a good index of genotypic merits, so that genetic gain can be made easily through selection [13]. The breeder seeks to produce an improved pure line in self-pollinated species. However, the purpose of hybridisation is to provide genetic variation for selection. Epistasis is more important than dominance to the breeder of self-pollinating species, in that dominance is broken by segregation following hybridization. Epistasis, on the other hand, does not depend on heterozygosity and can therefore permit more gene combinations than dominance. Dominance and epistasis made major contributions to the inheritance of resistance to thrips in this study.

The minimum number of effective factors segregating for resistance ranged from 3 to 5 in F_2 progenies from the crosses. The 3 to 5 gene model being proposed here means there are three to five resistance loci each contributing equally and additively in resistance to thrips. This indicated an oligogenic type of inheritance of resistance to thrips in cowpea, corroborating the earlier results [20]. On the contrary, an earlier report [9] indicated two recessive genes controlling resistance to thrips damage rating in cowpea. The earlier report differs from the present findings, probably due to the different cowpea genotypes used at different ecological areas of the studies.

For all the associations in this study, phenotypic and environmental correlations were not significant. This meant that there were strong inherent relationships among the traits measured. The result of correlation analysis in this study showed that thrips damage rating exhibited significant negative correlation with number of pods/plant, number of pods/peduncle and number of seeds/plant but was positively correlated with number of thrips/plant. The negative and highly significant genotypic correlation observed between thrips damage rating and other agronomic traits suggested that cowpea genotypes with high damage rating would suffer severe reduction in number of pods produced per plant, pods/peduncle as well as grain yield.

In the present study, the observation of heterosis in the F_1 and transgressive segregation in the F_2, of the resistant x resistant cross may be explained by postulating the presence of both resistance and susceptible factors in the two resistant parents and complementary action of these factors in their F_1 hybrids. These observations are in line with the finding of Wolf and Hallauer (1997), who reported that an epistatic genes effect could contribute to the expression of heterosis for specific hybrids. The two resistant parents Sampea 8 x Sanzi had different performances in the mean damage ratings, number of thrips/plant and pods/plant. Coupled with significant dominance towards the better of the parent, Sanzi consistently showed that some of the genes in the parents are non-allelic. The two resistant genotypes were chosen based on genetic diversity because of the functions of pedigree such that, alleles contributed by the two parents with different ancestry are more likely to vary from those parents with common ancestors. Thus Sampea 8 (IT93K-452-1) is a released variety from Institute for Agricultural Research (IAR) Samaru, Nigeria, while Sanzi is a local landrace from Ghana. Therefore, there is a high possibility that they have different pedigrees. The two resistant genotypes could be incorporated into breeding programmes, not only on the basis of resistance to thrips but also on the basis of their high yielding potentials and early maturity. These genes can therefore be transferred into high yielding cultivars of cowpea to enhance their productivity by backcross method using the resistant genotypes as females. For flower bud thrips, the resistance available in cowpea should be used with appropriate complementary agronomic practices of an integrated control package.

V. CONCLUSION

In the present study, the cowpea genotypes, Sampea 8 and Sanziwere found to be resistant to thrips. The mode of inheritance of thrips resistance was oligogenic with 3 to 5 genes being estimated. Dominance and epistasis made major contributions to the inheritance of resistance to thrips in this study. Coupled with significant dominance towards the better of the parent, Sanzi consistently showed that some of itsresistance genes were non-allelic to those of Sampea 8.Thrips damage rating exhibited significant negative correlation with number of pods/plant, number of pods/peduncle and number of seeds/plant but was positively correlated with number of thrips/plant. Backcross breeding method using the resistant genotypes as females would help develop cowpea varieties with resistance to thrips.

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