GENETICS OF YIELD AND YIELD COMPONENTS IN COWPEA, *VIGNA UNGUICULATA* (L.) WALP., AND INHERITANCE OF RESISTANCE TO COWPEA APHID, *APHIS CRACCIVORA* KOCH.

BY

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1985.

DECLARATION

(a) This thesis is my original work and has not been presented for a degree in any other University.

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THIS THESIS HAS BEEN ACCEPTED FOR THE DEGREE OF M.Sc. 1985 AND A COPY MAY BE PLACED IN THE UNIVERSITY LIBRARY.

This thesis is dedicated to my father Michael Oyeyo and my mother Florah Odero.

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ABSTRACT

Cowpea (Vigna unguiculata (L.) Walp) is grown in Kenya as a grain legume and a vegetable crop. The local cultivation is mainly of landraces with minimal genetic improvement on yield and its components. Cowpea research in Kenya is aimed at improving yield, earliness and,disease and insect resistance. The cowpea aphid, Aphis craccivora Koch, is a pest of cowpea that is growing rapidly in importance. Its destruction is more serious in the semi-arid areas.

Separate trials were conducted for genetic studies of grain yield and its components, 100-seed weight, number of seeds per pod, pod length,peduncle length, number of pods per plant, peduncles per plant and pods per peduncle, and earliness characters, days to first flowering and days to maturity, and for inheritance of resistance to A. craccivora.

A 5 x 5 diallel consisting of three local varieties, ICV 1, ICV 6 and ICV 10; one irradiated mutant, ICV11 and one exotic variety, TVU310 was used to evaluate for combining ability and heterosis for grain yield and its components. The diallel analysis of Griffing (1956b) method 2 model 1 was adopted in estimating the combining abilities. A single row plot of each of the 10 F_1s and 5 parents were planted in a randomised complete block

design with four replications in the field in March 1985 at the International Centre of Insect Physiology and Ecology (ICIPE), Mbita Point Field Station, South Nyanza. Data were collected on five randomly selected plants per plot.

Combining ability analysis showed the importance of both additive and non-additive gene action for the variability in grain yield per plant, 100-seed weight, peduncle length, number of pods per plant and peduncles per plant, though the magnitude of additive gene variance was greater in the case of 100-seed weight and peduncle length. Number of seeds per pod, pod length, pods per peduncle, days to first flowering and days to maturity were predominantly under additive gene action. The exotic variety, TVU310 was found to exhibit positive GCA in more characters than the other varieties and also involved in good specific combinations. Heterosis was observed for grain yield per plant, number of pods per plant and peduncles per plant. The per se performance of the parents was considered an adequate measure of the GCA values of the varieties.

Phenotypic and genotyptic correlation coefficients were calculated from variance and covariance analyses for all possible combinations of characters. The phenotypic and genotypic correlations agreed closely in most

comparisons. Important positive correlations were observed between grain yield per plant and number of seeds per pod, pod length, pods per plant and peduncles per plant. 100-seed weight was positively correlated with seeds per pod, pod length and peduncles per plant but negatively with peduncle length and pods per peduncle. Very high correlation was noted between number of seeds per pod and pod length, pods per plant and peduncles per plant, and between days to first flowering and days to maturity. Negative correlations were present between pods per peduncle and days to first flowering and days to maturity, and between peduncle length and days to first flowering and days to maturity.

Path-coefficient analysis technique was employed to establish the relative importance of grain yield characters as determiners of grain yield per plant. Direct effects of number of seeds per pod and pods per plant were considerable. Indirect effect of pod length on yield *via* seeds per pod was positive and considerable. The three characters, number of seeds per pod, pods per plant and pod length were observed as reliable components of yield for a cowpea improvement programme.

For the study of inheritance of resistance to the cowpea aphid, *A. craccivora*, five sets of crosses, I CV1 x

TVU310, ICV1 x ICV11, ICV10 x ICV11, ICV 11 x TVU310 and 1CV10 x TVU310 were utilized. The experiment was conducted in the screenhouse. Three-day old seedlings of parents, F_1s, F_2s and backcross (where applicable) were infested with 10 adult aphids per seedling. Seedling reaction 10 days after infestation, i.e., survival (resistance) or death (susceptibility) of the parents, F_1s, F_2s and backcross populations indicated resistance to be dominant over susceptibility, and that resistance was conferred by a single gene. However, the resistance genes in these parents were different. One dominant gene Ac_1 was identified in both ICV10 and TVU310 varieties and the other gene Ac_2 in the mutant variety, ICV11. The two dominant genes were non-allelic located in the same chromosome distant apart or in different chromosomes. The two genes may be duplicate confering the same level of resistance as any combination or with cummulative effects. The resistance in any of the three parents could be transferred to a susceptible, locally adapted cultivar by use of the back-cross pedigree method.

CHAPTER 1

INTRODUCTION

Cowpea (*Vigna unguiculata* (L.) Walp) is considered one of the most popular grain legumes of Africa. Sellschop (1962) rated it third after peanut (*Arachis hypogea* L.) and bambarra groundnuts (*Vaandzeia subterranea* L.). Cowpea is important as a relatively cheap and readily available source of protein. The protein percentage in the grains varies between 20% and 28% (Sellschop, 1962; Johnson and Raymond, 1964; Godfrey-Sam-Aggrey *et al.*, 1976). The cowpea seed protein is, however, lacking in the essential sulphur-containing amino acids, methionine and cysteine (Ogunmodede and Oyenugu, 1970) which are supplemented in a cereal meal. Cowpea thrive on marginal soils, smother weeds and reduce soil erosion at the same time supplementing soil nitrogen through fixation of atmospheric nitrogen.

Large scale production of cowpea is found in Australia, the United States of America, Central and South America mainly for fodder and as a cover crop for green manure (Summerfield *et al.*, 1974). In Asia and Africa, the production is mainly for human consumption. The West African countries of Nigeria, Niger, Mali, Chad, Sierra Leone and Senegal have approximately 4.8 million

hectares under cowpea while in East Africa, Tanzania, Kenya and Uganda have one million hectares (Singh, 1979). In Kenya, cowpea is next in importance to the common bean (Phaseolus vulgaris L.) in the medium potential areas while in the marginal rainfall areas, cowpea is the most important grain legume. The Ministry of Agriculture Annual Report (1981a) estimated 106,000 hectares to be under cowpea cultivation in Kenya. The Eastern Province has 85% of the total area while Coast, Western, Nyanza and Central Provinces share the remaining 15%. Cowpea consumption is quite diverse; young tender leaves and pods are eaten as a spinach, green seeds as pounded stew and dried grains as a pulse (Acland, 1971).

The yields of cowpea grain are usually very low. The cultivation is mostly in the marginal areas with rainfall ranging from 500 mm to 800 mm annually. The crop is also grown in mixed croppings with the other staples, maize, sorghum and millet (Muruli et al., 1980) as the principle food crops. The constraints to increased production are therefore poor crop husbandry, diseases and insect pests (Raheja, 1976; Goldsworthy and Redden, 1982). The cultivars found in Africa are mostly landraces adapted to the environmental and cultural

conditions. West Africa has the greatest genetic diversity in cowpea and improvement of the crop is undertaken at the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria. However, minimal genetic improvement of yield and its components has been done. Pathak and Ollela (1985) have developed a number of cowpea varieties from selections of local Kenyan landraces at the International Centre of Insect Physiology and Ecology (ICIPE), Mbita Point Field Station, South Nyanza. The National Dryland Farming Research Station, Katumani and the Crop Science Department, University of Nairobi are also involved in cowpea improvement work in Kenya. However, the information regarding the genetic architecture of yield traits in this crop is scanty. For genetic improvement in an adapted crop like cowpea, an understanding of the mode of inheritance of the yield components, the correlation among them and the association between each component and yield, is necessary for the intelligent choice of breeding procedures for evolving high yielding varieties.

Heavy losses of grain yield in cowpea result from insect pest damage. In Kenya, the major pests of cowpea include the legume pod-borer (Maruca testulalis),

thrips (Megalurothrips rjostedti Tryhom), pod-sucking bug (Clavigralla gibosa), the leafhopper (Empoasca spp.) the aphids (Aphis craccivora Koch.) and stored grain pest, the bruchid (Callosobruchus maculatus). The ICIPE has put more emphasis on M. testulalis and A. craccivora as target pests of cowpea. The increasing economic importance of A. craccivora was noted by Singh and Van Emden (1979). Damage by the aphids can be more severe in the marginal rainfall areas. Here, the dry spells are best for aphid multiplication while the low rainfall cannot suffice to wash the aphids off the plants. The cowpea aphid also transmits numerous viral diseases to a range of host plants (Dubey and Nene, 1974). The most serious in cowpea is the cowpea aphid-borne mosaic virus (CAMV). The control measures for the aphids include: use of insecticides (chemical control) and use of resistant cultivars.

Insecticides are expensive and frequent applications present residual problems in the environment. The insects may also develop resistance to the chemical. For a crop like cowpea, with a low cash value per hectare, use of resistant varieties offers the best and most economical method for aphid control. The understanding of the inheritance of resistance to A. craccivora should give the basis for incorporating

resistance into agronomically desirable lines and cultivars. In Kenya, where 80% of the land is marginal (Anon, 1984), drought resistant crops like cowpea should be encouraged.

Therefore, the objectives of the present investigation were:

(i) To study the genetics of yield and its components in cowpea.

(ii) To determine the inheritance of cowpea resistance to the cowpea aphid (A. craccivora) and

(iii) To suggest suitable breeding procedures for cowpea improvement.

CHAPTER 2

REVIEW OF LITERATURE

2.1. The Use of Diallel Analysis for Combining Ability

Several methods have been developed for analysing data from a set of parental and all possible single-cross combinations. The diallel analysis is useful to plant breeders in understanding the nature of gene action involved in determining the quantitative traits. Diallel analysis has been used primarily to provide information on genetic variance estimates and to estimate general and specific combining ability effects of parents and their crosses.

The use of single-cross has been popular since Sprague and Tatum (1942) utilized it in investigating gene action in a set of crosses among maize inbred lines. The statistical analysis of a diallel cross was described by Yates (1947). Since 1954 diallel analyses and their genetic interpretations have been described in several reports. Jinks (1954) developed a method of analysing quantitative data from a diallel cross and applied it in a diallel cross involving Nicotiana rustica inbreds. Hayman (1954b) utilized flowering time data from the same crosses to apply a genetic algebra to the diallel theory and investigated

more complex genetical systems. He showed how to measure additive and dominance variation, describing the relative dominance properties of the parental lines and detection of non-allelic genic interactions. The Hayman (1954b) approach has been used by many workers to estimate genetic components. Aksel and Johnson (1963) illustrated, with a worked example, its use in estimating genetic components for the character kernels per head in barley. Dickson (1967) utilized the approach in investigating the genic control of various economic traits in beans (Phaseolus vulgaris). In genetic studies of quantitative characters in peas, Pisum sativum, Snoad and Arthur (1973) employed the Hayman approach of analyzing diallel crosses.

The use of diallel analysis in estimating genetic variances and combining abilities has been introduced and discussed by several workers including Kempthorne (1956), Griffing (1956a, 1956b), Gardner and Eberhart (1966) and Simmonds (1979). The ideas on combining ability were first suggested by Sprague and Tatum (1942) in the evaluation of inbred lines of maize. They defined the term general combining ability (GCA) to designate the average performance of a line in hybrid combinations while specific combining ability (SCA) was

used to mean those cases in which certain combinations do relatively better or worse than would be expected of the average performance of the lines involved.

Griffing (1956b) has given four methods of diallel analysis depending on the material included in the analysis. He has also described the methods of analysis for combining ability considering Eisenhart's Model I (fixed effects) and Model II (random effects). According to Baker (1978), in an analysis based on a fixed model, the concern is with comparisons of combining abilities of the actual parents used in the experiments and identification of superior combinations. For analysis based on a random model, inferences are made about the population from which the parents were sampled from estimates of components of variance. Gardner and Eberhart (1966) suggested that since plant breeders and geneticists are usually interested in genetic information about a particular set of parents, the fixed model should therefore be used in most cases.

The mathematical model given by Griffing (1956b) for method 2 model 1 using the parents and F_1s but excluding reciprocals is as follows:-

$m_{ij} = \mu + g_i + g_{ij} + s_{ij}$ for single cross progeny

where,

m_{ij} = the value of the response level of the ij^{th} cross.

μ = the population mean

g_i and g_j = the GCA effects of the i^{th} and j^{th} parent respectively.

S_{ij} = the SCA effect for the cross between the i^{th} and j^{th} parents.

Griffing's model has been criticized by Gardner and Eberhart (1966) that it gives only a limited information on the parents and the crosses. He does not subdivide heterosis which he calls specific combining ability. In the proposed model, Gardner and Eberhart (1966) separate the parents and the hybrids.

Baker (1978) gave statistical relationships between Griffing's (1956b) method 2 and method 4 with analysis, II and III of Gardner and Eberhart (1966). All these methods, including the analysis proposed by Hayman (1954 a), after modification by Jones (1965), could be utilized for analyzing the same data.

Sokol and Baker (1977) emphasize the fact that similar information is obtained from all these methods. There can therefore, according to Baker (1978),

be no inherent disadvantage or advantage to any of the methods.

There are assumptions about the parental materials which are important for the valid genetic interpretation of data from a diallel set of experiments. The assumptions have been discussed by several workers since Hayman (1954b) proposed them:

(i) Normal diploid segregation.

(ii) No difference between reciprocal crosses, that is, no maternal effects. This assumption is important when excluding reciprocals in a diallel cross. Utilized by Kempthorne and Curnow (1961) in a partial diallel cross.

(iii) Independent action of non-allelic genes, that is, no non-allelic interaction.

(iv) No multiple allelism.

(v) Homozygous parents. Valid for self-pollinating crops.

(vi) Genes independently distributed between parents.

In his discussion, Hayman (1954b) showed that assumption (iv) no multiple allelism is not important until the F_2. According to Gilbert (1958)' assumption (i) of diploid segregation is "usually perfectly justified". When dealing with diploid species then the assumption is

automatically accepted. Some polyploids have also been reported as behaving as diploids (Sokol and Baker, 1977). The assumption of no non-allelic interaction (no epistasis) has been discussed in detail by Baker (1978) who suggests that it is necessary to assume absence of epistasis when interpreting a diallel. Gilbert (1958) suggested that gene interaction cannot be avoided at the biochemical level and the assumption of no epistacy should therefore be only empirical. Kempthorne (1956) developed an analysis of diallel crosses based on a genetic model and included arbitrary epistasis. The assumption of homozygous parents as already mentioned is assured in cases of self-pollinated crops. Kempthorne (1956) also suggested that the assumption of homozygous parents is not essential, its necessity being only that the parents have same coefficient of inbreeding. Kempthorne (1956) and Nassar (1965) in evaluating the assumptions concluded that the assumption of independent distribution of genes in the parents is unattainable. Failure of the assumption may be by linkage or from the effects of sample size when sampling the parents. There are conflicting reports as to whether or not failure of this assumption can bias the estimating of GCA and SCA components of variance. However, the assumption, according to Sokol and Baker (1977) is necessary for

simplifying the estimates for genetical interpretation. Nassar (1965) had concluded that failure of the assumption did not cause a bias in estimates of GCA and SCA variance components. Kempthorne (1956) replaced the assumption of no multiple allelism (Hayman, 1954b) with the assumption of arbitrary number of alleles at each locus.

In the diallel mating systems the genetic parameters of interest are the additive and non-additive genetic components of the parent population genotypic variance. These are estimated from the experimental material in terms of general and specific combining ability variances. The relationship between the two sets of parameters have been discussed by Griffing (1956 a) who assumed a partitionable population phenotypic variance into various genotypic and environmental components:

$$\sigma^2_P = \sigma^2_G + \sigma^2_E \text{ and since } \sigma^2_G = \sigma^2_A + \sigma^2_{NA}$$

$$\text{then } \sigma^2_P = \sigma^2_A + \sigma^2_{NA} + \sigma^2_E$$

where, σ^2_P = Population phenotypic variance

σ^2_G = Population genotypic variance

σ^2_A = Additive genetic variance

σ^2_{NA} = non-additive genetic variance

σ^2_E = Environmental effect variance

σ^2_{NA} can be partitioned further into dominance and epistatic variance: $\sigma^2_D + \sigma^2_{AA} + \sigma^2_{AD} + \sigma^2_{DD}$

where, σ^2_D = dominance variance

σ^2_{AA} = additive x additive epistatic variance

σ^2_{AD} = additive x dominance epistatic variance

σ^2_{DD} = Dominance x dominance epistatic variance

The population genotypic variance can be partitioned in terms of the combining ability variances (Griffing, 1956a) with an arbitrary number of loci and alleles as follows:

$$2\,\sigma^2_{gca} = \sigma^2_A + \tfrac{1}{2}\,\sigma^2_{AA} + \tfrac{1}{4}\,\sigma^2_{AAA} + \text{etc.}$$

$$\sigma^2_{sca} = \sigma^2_D + \tfrac{1}{2}\,\sigma^2_{AA} + \sigma^2_{AD} + \sigma^2_{DD} + \tfrac{3}{4}\,\sigma^2_{AAA} + \sigma^2_{AAD} + \sigma^2_{AAD} + \sigma^2_{DDD} + \text{etc}$$

$$\sigma^2_G = \sigma^2_A + \sigma^2_D + \sigma^2_{AA} + \sigma^2_{AD} + \sigma^2_{DD} + \sigma^2_{AAA} + \sigma^2_{AAD} + \sigma^2_{ADD} + \sigma^2_{DDD} + \text{etc}$$

This shows that the total genetic variance is equal to twice the GCA component of variance (σ^2_g x 2) plus the SCA component of variance (σ^2_s). Based on this relationship, Baker (1978) suggested that the ratio $2\sigma^2_g/(2\sigma^2_g + \sigma^2_s)$ would define the relative importance of GCA and SCA in

determining progeny performance in a model with random effects. The closer the ratio is to unity, the greater the predictability based on GCA alone. In an analysis based on a fixed model, then equivalent average squares of the fixed gca and sca effects are used (Baker, 1978):

$$2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$$

where

$\bar{g}^2$ and $\bar{s}^2$ are the averages of the squares of the fixed GCA and SCA effects, respectively, which is

$$\bar{g}^2 = \frac{\Sigma g_i^2}{p - 1}; \quad \bar{s}^2 = \frac{\Sigma s_{ij}}{p(p - 1)}$$

From the aforegoing discussion it can be seen that the diallel cross technique is a useful tool in gaining a better understanding of the nature of gene action involved in determining quantitative traits which are complex in inheritance. Evaluation for combining ability may facilitate the selection of selection methods that could produce a greater number of outstanding offsprings.

2.2. Genetics of Yield and its Components in Cowpea

Yield is a complex character and is considered as an interaction product of many factors which influence jointly or singly (Whitehouse et al., 1958; Grafius, 1959). Hence, the prime requirement of breeding for improved yield is to understand the component traits. Several quantitative analyses have been carried out on yield and its components in cowpea and other grain legumes. Aryeetey and Laing (1973) suggested that for an intelligent choice of breeding procedures an understanding of the mode of inheritance of the yield components, their combining abilities and association between each component and yield is necessary.

2.2.1. Grain yield per plant

Genetics of grain yield and its component characters in grain legumes has been studied by several workers like Singh and Mehndiratta (1969, 1970), Singh and Jain (1972), Aryeetey and Laing (1973) Kheradnam et al. (1975), Lal et al. (1975), Tikka et al. (1980) and Imrie and Bray (1983) in cowpea; Gritton (1975), Singh et al.(1980), Kumar and Agrawal (1981) and Chandel (1983) in peas (Pisum sativum (L.) Sengugpta and Kataria (1971) in

soybean (Glycine max (L.) Merr.). They utilized yield components to successfully predict yield on single plant basis.

In a study of heterosis and combining ability in cowpeas, Singh and Jain (1972) observed that both the general combining ability (GCA) and specific combining ability (SCA) effects were important for grain yield. This indicated that yield is under the control of both additive and non-additive gene action. Lal et al. (1975) reported the importance of additive genetic variance in the inheritance of yield. Recently Imrie and Bray (1983) noted in their investigations that GCA variance for grain yield/plant was significant but not the SCA variance, an indication of the important role played by additive gene variance in the variation of yield per se in cowpea. They also reported a considerable heritability for grain yield. The inheritance of pea grain yield and its components was studied by Krarup and Davis (1970) in a six-parent diallel cross and found the mean square for SCA as important for grain yield, indicating the preponderance of non-additive gene action. Gritton (1975) reported both GCA and SCA as important in the variation of grain yield, indicating the importance of both additive and non-additive gene action for grain yield in peas. However, in that study, the SCA component was

larger than the GCA component. Gritton (1975) also noted a striking heterotic effect for seed yield. Both additive and non-additive gene action were found to control the grain yield per plant in the study of Singh et al. (1980) in peas. Kumar and Agrawal (1981) emphasised non-additive genetic component to be in preponderance for grain yield/plant.

2.2.2. Seed size (100-seed weight)

The studies on the genetics of seed size in cowpea by Brittingham (1950), Sene (1968) and Aryeetey and Laing (1973) do not agree. Brightingham (1950) reported that the F_1 exceeded the larger parent and the value of the smaller parent was not recovered in the F_2 population of 218 plants. These results indicated heterosis in seed size and transgressive segregation. Sene (1968) obtained an estimated 6 pairs of genes controlling seed size with a heritability of 71% in the narrow sense and 80% in the broad sense. He concluded that selection in the F_2 plants was effective. Aryeetey and Laing (1973) reported partial dominance for small seeds and ten pairs of genes as controlling seed size. They reported 37.4% narrow sense and 63% broad sense heritabilities for seed size. Leleji (1975) agreed with Aryeetey and Laing (1973) that small seeds appeared

to be partially dominant. Leleji (1975) also reported transgressive segregation for small seeds and 49% to 82% broad sense heritability. He agreed with Sene (1968) that selection for seed size can be effective starting from the F_2 generation. Bliss et al. (1973) also reported very high heritability for seed weight.

In combining ability studies, Singh and Jain (1972) on cowpea reported both GCA and SCA as being important for seed weight, indicating the importance of both additive and non-additive gene action though GCA variance was higher than SCA variance. Lal et al.(1975) found significant GCA and SCA variances but mean squares for GCA was larger than SCA indicating the additive gene action as more important in the inheritance of the character, seed weight. Similarly, Imrie and Bray (1983) reported significant GCA and SCA variances for 1000-seed weight with higher additive variance and high heritability. They concluded that seed weight would respond to selection. In peas, Krarup and Davis (1970) reported GCA as important for average seed weight. Gritton (1975) found GCA and SCA as important for average seed weight. Similar results were observed by Singh et al. (1980) and Kumar and Agrawal (1981) in studies of seed index as 25-seed weight. In both cases GCA mean square was higher than SCA mean square. This indicated the

preponderance of additive gene action for the character seed size. Mak and Yap (1980) in a genetic investigation of the seed protein and agronomic characters in the long bean (Vigna sesquipedalis Fruw.) found additive variance to be more important than dominance variance for seed weight which appeared to be controlled by partial dominance.

2.2.3. Number of seeds per pod

In genetic studies of cowpea, Singh and Jain (1972) observed significant SCA variance and non-significant GCA variance and concluded that in the particular population, the yield component was under non-additive gene action. Aryeetey and Laing (1973) reported heritability estimates of 19.8% and 28.2% for narrow and broad sense, respectively. The low heritability for the component character indicated non-additive gene action as more important. Contradictory results were reported by Lal et al. (1975) who found significant GCA component variance and control of number of seeds/pod to be under additive gene action. However, recently Imrie and Bray (1983) reported the character to be under non-additive gene action. Supporting Singh and Jain (1972) and Aryeetey and Laing (1973), Mak and Yap (1980) on long

bean (Vigna sesquipedallis) reported dominance variance as more important than additive variance for seeds/pod. In peas, (Pisum sativum), Gritton (1975) and later Kumar and Agrawal (1981) reported additive action as controlling the number of seeds per pod.

2.2.4. Pod length

Singh and Jain (1972) reported both GCA and SCA variances as important for pod length variability. Aryeetey and Laing (1973) calculated high heritability of 60.3% for pod length, indicating predominance of additive gene action. Lal et al. (1975) observed in their investigations that pod length had higher and significant GCA indicating the importance of additive genetic variance. Leleji (1975) reported short pods as being partially dominant over long pods. Estimates for broad sense heritability ranged from 46% to 67%. Kumar and Agrawal (1981) attributed pod length genetic control in peas to additive gene action.

2.2.5. Number of pods per plant

Aryeetey and Laing (1973) obtained an estimate of 19.8% for narrow sense heritability for pod number/plant. The low heritability value could be an indication of the

non-additive genetic variance being more important. They also found a consistent correlation with yield but, because of its low heritability, could not be used as a preliminary selection criterion for yield. Lal et. al. (1975) reported higher GCA variance than SCA variance for pods/plant indicating the importance of additive genetic variance in the inheritance of this character. Imrie and Bray (1983) found an almost equal contribution by non-additive and additive variances, showing both gene action as important. However, Gritton (1975) working on peas, reported a larger SCA variance than GCA variance for pods/plant, though both were significant, while Kumar and Agrawal (1981) observed only additive gene action for the number of pods/plant.

2.2.6. Number of peduncles per plant

In a study of combining ability in cowpea Lal et al. (1975) reported that the component clusters per plant (peduncles/plant) had higher GCA variance as compared to the SCA variance indicating the importance of additive gene variance in the inheritance of this yield component. Imrie and Bray (1983) reported the number of peduncles to be under non-additive gene action in cowpea.

2.2.7. Number of pods per peduncle

Lal et al. (1975) also studied the character pods/cluster (pods/peduncle) and found the GCA: SCA variance ratio indicated the total genetic variation to be mainly under additive gene action. The SCA and GCA variances were, however, both highly significant.

2.2.8. Number of days to first flowering

Studies of flowering time have been carried out more in peas. Watts et al. (1970) found flowering period to be under the control of an additive system with dominance for the late flowering characteristic. From that study it appeared possible to make some gain in earliness by selection. Snoad and Arthur (1973) looked at days to first flower and concluded that the character was under both major and polygenic systems. The genetic system was of an additive nature; dominance and interaction being of minor importance. They concluded that on the basis of their materials, pure lines would be the best breeding approach. Similar results were reported by Gritton (1975), who concluded that an additive genetic system was very important in determining the number of days to bloom. However, not all the variation was attributable to additivity as specific effects were

also significant. In cowpea, Imrie and Bray (1983) reported equal contributions of additive and non-additive variances for the character days to first flower. Mak and Yap (1980) in long bean reported early flowering date to be controlled by partial dominance.

2.2.9. Number of days to maturity

Measuring pod maturity in cowpea as days from date of seeding to date when at least five pods were completely yellow, Brittingham (1950) suggested that the cummulative action of the genes for pod maturity does not follow an arithmetic progression. The nature of distribution was found to have no genetic significance. Lal et al. (1975) reported the importance of additive genetic variance in the inheritance of the character maturity period in cowpea.

2.3. Correlations and Path-Coefficient Analysis

2.3.1. Correlations among yield components

The correlation studies carried out by Aryeetey and Laing (1973) indicated that genotypic correlations between all the four characters, viz, pods/plant, pod length, seeds/pod and 100-seed weight were significantly correlated. Seed yield per plant was negatively and highly correlated to pod length while the other characters

showed positive association with yield. The data by Aryeetey and Laing (1973) on genetic correlations is as below:

	Pod length	Seeds/ pod	100-seed weight	Seed yield
Pods/plant	0.67	-0.77	-0.76	0.89**
Pod length		0.97**	0.95**	-0.90**
Seeds/pod			-0.98**	0.97**
100-seed wt.				0.97**

Yield components could be most effective in breeding for higher yield/plant if they were correlated phenotypically and physiologically with each other, or at least unrelated. Unfortunately studies on correlations have revealed negative correlations among some of the important characters of yield. Such negative correlations indicate that improvement in one character would lead to a decrease in one or more of the other components. In a trial of 39 cowpea varieties, Doku (1970) found seed yield per plant to be highly and positively correlated with number of pods per plant, while other yield components were not correlated to seed yield. In the study, Doku (1970) excluded the character, number of seeds/ pod. From the studies by Doku (1970) and Aryeetey and

Laing (1973) it would appear that the character pods/plant is the yield component whose association with yield was consistent. Similar results were observed by Tikka et al. (1980) who reported grain yield to be significantly and positively correlated with pods/plant, pod length. seeds/pod and 100-seed weight. The correlation between pods/plant and seeds/pod was positive and signifant. Similarly pod length had a positive correlation with seeds/pod and 100-seed weight. Days to flowering were positively correlated with days to maturity. In a recent study, Imrie and Bray (1983) obtained positive genotypic correlation between grain yield and seed size. They also reported a desirable negative correlation between flowering time and yield indicating a potential for response to selection. In earlier studies in soybean, Johnson et al. (1955) found positive genotypic correlation of yield with maturity. Johnson et al. (1955) observed positive genotypic association of high yield and high seed weight and lateness in maturity. Anand and Torrie (1963) also on soybean, reported number of pods/plant to be positively associated with grain yield but negatively with seed weight. In the garden pea, Singh et al. (1980)

reported positive correlation between grain yield/plant and seed index (seed weight). Kaul and Garg (1982) observed positive correlations for grain yield with pods/plant and seeds/pod. Chandel (1983) also reported pod length and seeds/pod significantly correlated at phenotypic level. Bhaskaraiah et al. (1980) concluded from results on cowpea that both pods/plant and 100-seed weight are important contributors of yield. However, Sengupta and Kataria (1971), in path analysis studies of soybean, had observed non-significant correlations between grain yield and days to flowering or 100-seed weight. The results also revealed that pods/plant and clusters/plant (peduncles/plant) had strong correlation with each other and were responsible for the number of seeds produced per plant. They had an explanation for the non-significant correlation of 100-seed weight with yield; since the total food material synthesised by the leaves and transported to the seeds is constant for the plant, possibly, the same gets distributed in cases of larger number of seeds resulting in smaller size of seeds having no direct effect on yield (Sengupta and Kataria, 1971). A knowledge of the inter-relationships among yield characters is necessary if selection for the simultaneous

improvement of these traits is to be most effective.

2.3.2. Path-coefficient analysis

The path coefficient is simply a standardized partial regression coefficient (Dewey and Lu, 1959) and as such measures the direct influence of one variable upon another and permits for the separation of correlation coefficient into direct and indirect effects. The use of the method requires a cause and effect situation among the variables and the experimenter must assign direction in the causal system based upon a priori gounds or experimental evidence (Dewey and Lu, 1959). Many characters of yield are correlated because of mutual association, positive or negative, with other characters (Chandel, 1983). As more variables are considered in the correlation analysis, these indirect associations become more complex, less obvious, and somewhat perplexing. At this point the path-coefficient analysis provides an effective means of disentangling direct and indirect causes of association. Thus, path coefficient analysis permits a critical examination of the specific forces acting to produce a given correlation and measures the relative importance of each causal factor (Dewey and Lu, 1959). The path coefficient, being directional,

can be positive or negative and may be greater or less than unity (Dewey and Lu, 1959). However, Li (1956) considered it as a special type of a multivariate analysis.

Path analysis studies have been undertaken by various workers. In cowpea, Singh and Mehndiratta (1969) reported that number of pods/plant, seeds/pod and 100-seed weight showed appreciable direct effects on grain yield. They concluded that correlation studies alone may not give complete information except when in conjunction with path coefficient studies giving the cause and effect relationship. Tikka et al. (1980) observed positive direct effects on grain yield exhibited by the number of seeds/pod, pods/plant and 100-seed weight. The pod length, which had significant positive correlation with yield manifested negative direct effect. They also reported the indirect effects of pod length through seeds/pod and 100-seed weight to have been responsible for its positive correlation with yield. In peas, Chandel and Joshi (1976) demonstrated that number of seeds/pod, pods/plant and seed weight exerted a direct positive effect of high order on yield. Chandel (1983) reported the direct effect of number of peduncles as not consistent in peas, as it was positive in one year and negative in the other.

Days to flower and pod length showed negative direct and indirect effects on yield. He, therefore, suggested these attributes might be much less reliable in pea variety improvement programmes. Chandel (1983) found that pods/plant had strong direct and indirect effects on seed yield. The direct contribution of seeds/pod and 100-seed weight to grain yield was small, but the indirect effects *via* pod number was appreciable.

2.4. Cowpea Aphids, *Aphis craccivora* Koch

2.4.1. Distribution and Crop Losses

The distribution of the cowpea aphid, *Aphis craccivora* Koch, has been reported as wide, running across all the cowpea growing areas of the world (Singh and van Emden, 1979). It is the main aphid pest of grain legumes. The aphid is reported as a major pest of green gram (*Phaseolus aureus* Roxb.) in the Phillipines (Bernado, 1969) and in Japan and Taiwan (Kegasawa *et al.*, 1972). It is also a pest of cowpea in India (Dhanorkar and Daware, 1980). It infests cowpea in Nigeria (Booker, 1965), and in Tobago and Trinidad (Lawrence, 1980). It is an important pest at the cowpea flowering stage in Kenya (Muruli *et al.*, 1980) and is known to achieve its

peak population density at the pod formation stage in Assam (Saharia, 1980).

Damage caused by the aphid is due to the depletion of the assimilates by removal of sap through sucking. This results in increased respiration rate in the plant (van Emden, 1973) which, according to Singh and van Emden (1979) could be a saliva effect from the aphid. The aphids infest the crop at the seedling stage and feed on the stem and leaves (Singh, 1979). Infestation can continue through the growth phases of the plant eventually attacking the pods. The growing point of the seedling is severely affected (Chari et al., 1976) resulting in stunting of the plant. Heavy aphid populations may result in the death of the plant. Heavy losses also occur when inflorescence and pods are affected by A. craccivora (Chari et al., 1976). Working on feeding preferences of Aphis fabae (Scopoli), Kennedy and Booth (1951) reported two important stimuli after aphids have arrived at a plant, flavour and nutrition. The plant with the best compromise between the two factors will be colonized. Two pairs of slender chitinous bristles with stylets penetrate and saliva is ejected during the cell penetration (Auclair, 1963). Jordeus-Rottger (1979) suggested that the

selection of a host plant by the black bean aphid, Aphis fabae may be influenced by one or more simple phenolics which act as feeding stimulants.

The critical periods when insect control is most important in cowpea, according to Raheja (1976) are during flowering and pod formation. Pest infestation at these stages may result in at least 70% yield losses. Singh and Allen (1980) provide the only estimates of yield losses due to A. craccivora infestation in cowpea as 20% to 40% in Asia and upto 35% in Africa. Yield loss estimates due to other aphid species attacking other crops are also found in the literature. Working on peas (Pisum sativum L.) and field beans (Vicia faba) infested with the pea aphid (Acythosiphon pisum) in the German Democratic Republic, Hinz and Daebler (1984) reported yield loss estimates at different infestation stages. Pea plants infested at the five-leaf stage, with the aphid population reaching 155-175 aphids/plant, resulted in upto 30% reduction in yield. Infestation at the beginning of flowering resulted in 52% to 64% reduction in seed yield. Infestation during flowering or seed-setting resulted in 35% to 42% seed yield loss. Everly (1960) reported reduction in maize yield of upto 40% after attack by the corn leaf aphid,

Rhopalosiphum maidis (Fitch). According to McColloch (1921), Pinter (1951) and Everly (1960) the corn leaf aphid reduces the yield in two main ways: (a) Interfering with tassel development and pollen shedding and (b) feeding on leaves, silks and kernels.

Aphids are reported to be the most important vectors of plant viruses (Russell, 1981). The diseases cause reductions in the yields of the affected plants. The cowpea aphid acts as a vector of numerous viral diseases transmitted to a range of host crop plants (Dubey and Nene, 1974; Rossel, 1977). A. craccivora has been reported as a transmitor, among others of the bean leaf roll virus (Kaiser and Danesh, 1971), groundnut rossette virus (Storey and Ryland, 1955) and tobacco yellow vein virus (Adams and Hull, 1972). In cowpea the transmission of cowpea aphid-borne mosaic virus (CAMV) has been considered as most important (Singh, 1979; Ladipo and Allen, 1979). The CAMV was reported as having caused complete crop losses of irrigated cowpea crop in Northern Nigeria (Raheja and Leleji, 1974). Earlier, McColloch (1921) suggested that the corn leaf-aphid (R. maidis) may attract fungal growth on infested maize due to their honeydew production. The honeydew production by A. craccivora

could also encourage fungal growth resulting in more crop losses. Kaiser and Mossahebi (1975) reported yield losses of 15% due to CAMV infection.

2.5. Control of the Cowpea Aphids

The following managment practices have been reported by Youdeowei and Service (1983) as being in use in tropical Africa for the control of aphid pests:

(a) Early planting to give the plants time to establish themselves before the aphid infestation begins;

(b) Closer spacing to reduce aphid populations and incidence of aphid-transmitted diseases;

(c) Destruction of volunteer plants and weeds by ploughing before the rains arrive;

(d) At aphid infestation levels in excess of 10%, 1-2 sprays of the organophosphate insecticides dimethoate (600 g a.i./ha)or diazinon (600 g a.i./ha) applied at 2 weekly intervals;

(e) Use of resistant crop varieties.

2.5.1. Natural enemies:

Factors that can reduce the number of aphids in a population are of interest as natural ways of control.

Studies have attributed significant aphid mortality to natural enemies like predators, parasitoids and pathogens (Hagen and van den Bosch, 1968). Normally predators especially coccinelid beetles keep the population under control in Nigeria (Singh and Taylor, 1978). In India, Saxena et al. (1970) observed a large number of larvae and adults of Coccinella septempunctata (Coccinellidae) and Syrphid larvae (Ischiodon scutellaris) preying upon large populations of A. craccivora in green gram fields. Recently, Walker et al. (1984) observed that natural enemies did not control the potato aphid (Macrosiphum euphorbiae) populations in tomato fields. The check in aphid populations by natural enemies was indicated in experiments by Don-Pedro (1980) in a cowpea plot in Nigeria. He observed a secondary outbreak of A. craccivora in a plot of late cowpea that had been treated with DDT. There was no comparable outbreak of aphids in plots treated with tetrachlorvinphos. This indicated that DDT killed the natural enemies of the aphids but had no effect on the aphids.

Rainfall, in combination with high winds have been reported as major factors in the mortality of potato aphids in tomato fields (Walker et al. 1984).

Otherwise, during dry seasons aphids develop large populations which result in reproductive rate decrease and production of winged aphids (alates) increases (Hughes, 1963; Way and Banks, 1967; Gutierez et al., 1971).

2.5.2. Chemical control method

Chemical control using insecticides has been found as an effective method of controlling cowpea pests including A. craccivora. The yield losses atrributed to various pests by several workers (e.g. Singh and Allen, 1980) strongly suggest that in many areas, cowpea production cannot be profitable without some form of chemical control. The economic impact of chemical control in cowpea production is therefore undisputable and, in their review, Singh and van Emden (1979) have adequately addressed on the subject.

Several chemicals of differing formulations have been recommended to adequately control the aphids in the field (Anonymous, 1981b). According to Singh and Taylor (1978), A. craccivora on cowpea fields at

Ibadan, Nigeria could be easily controlled using phosphamidon, dimethoate and ɣ-BHC at the rate of 400 g per hectare. Among the recommendations by the Centre on Overseas Pest Research, London (Anonymous, 1981) is menazon which is applied as a soil trench at planting time or as a seed dressing before planting. Reddy et al. (1984) tested different insecticides under laboratory conditions for relative toxicity to A. craccivora reared on Dolichos lablab (Lablab purpureus). They reported that dust formulations of methyl parathion (Parathion methyl), fenitrothion and quinalphos were more toxic to A. craccivora than the standard endosulfan. Carbaryl proved to be the least toxic compound in their testing of ten insecticides.

In Kenya yields in farmer's fields under intercropping are extremely low ranging from 80 kgs to 150 kgs of dry seed per hectare (Khamala, 1978). Studies in Nigeria (Taylor and Ezedinma, 1964) have shown that high yields can be obtained under effective pest management. High yields have also been obtained using crop protection techniques (Eicher and Baker, 1982) and improved varieties in monocultures of high plant densities. Trials by Taylor (1968) indicated

complete chemical control measures to be highly economical resulting in yield increases of upto ten-fold. Low seed-yield of below 400 kg per hectare have otherwise been reported for Nigeria (Taylor and Ezedinma, 1964).

Systemic insecticides applied during planting can prevent the spread of the virus within a field but not between fields (Storch, 1981). Sassen (1983) showed that pyrethroids decreased the probing time of the green peach aphid, Myzus persicae (Sulzer), so extensively thus reducing PLRV transmission heavily. Deltamethrin, by its effect on the probing behaviour of the aphid, could control the spread of non-persistent plant viruses (Gibson et al., 1982 and Rice et al. 1983). In a recent study, Boiteau et al. (1985) reported surviving winged green peach aphids, M. persicae after exposure to aldicarb-treated potato plants could not be expected to be efficient virus vectors. This was caused by reduced flying and probing abilities. Similar results were obtained with the potato aphid, Macrosiphum euphorbiae.

Generally, the peasant farmer does not spray his crop. Insect control is left to chance and providence. In Kenya use of insecticides to control the aphids in

cowpea fields is not a common practice. Despite the apparent miracles pesticides are capable of performing, there are serious limitations to their effective usage at the farmer level. The vast majority of farmers still do,not have regular access to insecticides, and if they do they generally cannot afford. There is also the dangers of misuse thus increasing environmental pollution, incidence of pest resistance and human poisoning.

2.5.3. Host plant resistance

The solution to the vicious cycle of pesticide use by peasant farmers rests in the development of resistant cowpea varieties that would reduce, if not eliminate, the number of spraying regimes. It is not in every instance that a high level of resistance is obtainable or even necessary. In some cases low to moderate levels have been found most desirable especially when found with other desirable characteristics like high yielding potential and consumer acceptability. The control of A. craccivora and leaf hoppers, Empoasca sp., in cowpea can be achieved solely by the use of resistant varieties (Jackai and Singh, 1983).

Screening work in Nigeria (Singh, 1979) and in Southeast India (Chari et al., 1976) has identified several sources of resistance to Aphis craccivora and

extensive use of these resistant sources has been made in breeding programs. These include varieties such as TVU 410, TVU $408P_2$, and VITA-1, all materials of the International Institute of Tropical Agriculture (IITA) (Singh, 1979). Recently, Pathak (1983) reported high level of resistance in two cowpea cultivars, ICV11 and ICV12 obtained through induced mutations. Resistance to the cowpea aphid infestation was observed by Atiri et al. (1984) as not providing automatic resistance to the viral infection. However, cowpea cultivars possessing resistance to CAMV and multiple resistance to other viruses have been identified (Singh, 1979) and a few cultivars have shown apparent resistance to both the cowpea aphid and CAMV. According to Swenson and Hagedoru (1974) and cited by Atiri et al. (1984), the most important factor is that the resistance to the aphid would be expected to resist infection from a complex of the aphid-transmitted viruses other than to a specific virus like the CAMV. Malinga (1978) evaluated the IITA cowpea cultivars TVU $408P_2$ and TVU 410 which were found resistant to A. craccivora in Nigeria and found them resistant under Kenya conditions.

2.6. The Mechanism of Resistance

Painter (1951) in defining host plant resistance classified the resistance to insects into three main types: non-preference, antibiosis and tolerance. Insects are more reluctant to colonize non-preferred plants. Antibiosis has the effects of retarding the growth rate and decreasing the rate of reproduction of individual insect pests. Tolerant plants can withstand infestation levels at which a susceptible plant would be severely damaged.

Kennedy et al. (1961) observed most aphids to be attracted to leaves reflecting within 500 nm to 600 nm range (yellow-green). Alatae aphids were attracted to leaves reflecting about 500 nm and seemed to be attracted to plants in a physiologically suitable stage of growth. In other colour preference tests, Cartier and Auclair (1964) reported of biotypes of pea aphid which preferred orange or yellow, or both. Sticky exudates from glandular hairs have also been reported to confer resistance by entangling the aphids in the foliage in some wild potato species (Gibson 1971, 1974).

In an early study Emery (1946) attributed plant resistance in the alfalfa plant, to pea aphids, to an acid condition that was associated with environmental

factors. The resistance to the pea aphid in peas was associated with higher sugar: Nitrogen ratios by Maltais and Auclair (1957). The resistance has also been associated with lower concentrations of amino acids at growth stages corresponding to pea aphid infestation (Auclair et al., 1957) and a deep green colour in early stages of growth with increased antibiosis at higher temperatures (Cartier, 1963). Pederson et al. (1976), after selecting six alfalfa lines for high and low saponin, found that high siponin content was associated with pea aphid resistance. They, however, found no evidence that breeding for pea aphid resistance changed the foliage saponic content, and was lowered in the roots. Sugars and certain amino acids have been found to be important stimulants for the maintenance of feeding of several insects (Beck, 1965). Auclair (1963) and Maxwell et al. (1972) reported susceptible cultivars of pea to be higher in amino acids than resistant cultivars.

The mechanism of the resistance in cowpea to A. craccivora has been identified as being antibiosis and tolerance by Singh (1977) at IITA and as being antibiosis in India (Chari et al. 1976). Painter (1951) considered antibiosis as most desirable and a permanent

basis of resistance.

2.7. The Inheritance of Resistance to Aphids

The genetics of resistance to many pests has been found to be complex (Russell, 1981) and considerable disagreements have arisen over the number of genes involved in insect resistance. Inheritance studies in major crops have indicated that most resistance traits are governed qualitatively by dominant genes, others by recessive genes, while others indicate quantitative (polygenic) inheritance (Gallun and Khush, 1981).

The genetics of resistance in cowpea against A. craccivora has been scarcely studied. Two studies have been reported on the genetics so far in the available literature. At IITA (Anonymous, 1982) in five crosses of resistant and susceptible cultivars, it was reported that resistance to the aphid was dominant in comparison to susceptibility. The F_2 population resulted in a segregation ratio of three resistant to one susceptible. This implied a monogenic inheritance under a single pair of gene control. Confirmation using F_3 generation was to follow. Similar results were reported at ICIPE (Pathak, 1984, 1985).

When resistance depends on a single dominant gene, the breeding advantage is clear. At least 50% of the progeny of a cross between susceptible and resistant parent can be expected to be resistant. Difficulties may increase when more genes are involved. Gallun (1972), Dahms (1972), Maxwell et al. (1972) and Knight and Alston (1974) have reviewed the genetics of resistance to several aphids on different crops. The inheritance of resistance to melon aphid (Aphis gosypii) in a muskmelon line was identified as being due to a single dominant gene for resistance and designated as Ag by Kishaba et al. (1971) and Bohn et al. (1973). Glover and Stanford (1966) studied the inheritance of resistance to pea aphid (Acyrthosiphon pisum) in Alfalfa and reported one dominant gene as confering resistance. Several biotypes of the insect were also reported. Breeding for insect resistance could be complicated if many biotypes exist. For example, three biotypes of cowpea aphids have been identified (IITA Research Highlights, 1981). A craccivora populations from different regions of Nigeria, when compared, indicated the presence of an additional biotype which, based on host reactions, were identified as biotypes A and B. When these were tested in Upper Volta, the differential reaction of the lines indicated the

presence of a third biotype K. cowpea cultivars TVU 36, TVU 2896 and TVU 3000 were resistant to all the three biotypes.

Manglitz and Gorz (1968) studied the genetics of resistance to sweetclover aphid (Theriaphis riehmi) in sweetclover and inferred that a single dominant gene was responsible and a complimentary gene appeared to be present in some resistant clovers.

CHAPTER 3

MATERIALS AND METHODS

The trials were laid out at the International Centre of Insect Physiology and Ecology (ICIPE) Mbita Point Field Station, South Nyanza, about 43 km from Homa Bay Town; Centre coordinates 34° 10'E, 0° 25' S, at an altitude of 1240 metres above sea level. The soils are black cotton. The pH falls in the medium alkaline range (7.7 - 8.9). The organic carbon ranged from 0.5 - 1.0%.

3.1. Materials

The parental materials for this study consisted of five cowpea varieties, namely, ICV 1, ICV 6, ICV 10, ICV 11 and TVU 310. Their brief descriptions are as below:-

ICV 1: This is an improved variety developed through selection from local landraces at ICIPE. It has a spreading growth habit, an early maturing grain type. It is resistant to all common diseases and pests of cowpea except the cowpea aphids and powdery mildew.

ICV 6: This variety is a selection from South Nyanza. It has a semi-erect growth habit, and is

utilized as a dual purpose for both grain and leaves. It is susceptible to various cowpea diseases and pests including the cowpea aphid.

ICV 10: This is a selection of a landrace from Eastern Kenya and has a semi-erect growth habit and resistant to cowpea aphids. It is utilized as a grain type.

ICV 11: This is a mutant of the ICV 1. It has a semi-erect growth habit and highly resistant to the cowpea aphids. It is also called Mutant 1.

TVU 310: This is an introduction from the IITA. Nigeria. It has a semi-erect growth habit and is resistant to the cowpea aphids. It is utilized as a grain type.

(a) All possible crosses, excluding reciprocals were made among the five parental varieties. Crossing was done on potted plants in an insect-proof screenhouse at ICIPE Mbita Point Field Station. A total of ten F_1 crosses were obtained. This diallel set (10 F_1s and 5 parents) was used to study the inheritance of yield and its components.

(b) The following sets of crosses among susceptible(s) and resistant (R) varieties were prepared to study

the inheritance of resistance to cowpea aphids.

	Cross		Progeny
(i)	ICV 1(S) x TVU 310(R)	:	F_1, F_2
(ii)	ICV 1(S) x ICV 11 (R)	:	F_1, F_2 and BC_1 (ICV 1 x F_1)
(iii)	ICV 10(R) x ICV 11 (R)	:	F_1, F_2
(iv)	ICV 11(R) x TVU 310(R)	:	F_1, F_2
(v)	ICV 10(R) x TVU 310 (R)	:	F_1, F_2.

3.2. Methods

(a) Genetics of Yield and component characters

Fifteen entries (10F_1's and 5 parents) were planted in a randomized complete block design with four replications at ICIPE Mbita Point Field Station on 26th March 1985. The trial consisted of single row plots of fifteen plants spaced at 75 cm between rows and 20 cm within rows. Interblock spacing of 2 m was maintained with guard rows at the ends of each block. Usual agronomic practices were adopted with complete pest management. The experimental plot was irrigated immediately after planting to ensure uniform germination.

Data were recorded on five randomly selected plants from a row, leaving guard plants at both ends of the row, for the following traits:

1. Grain yield per plant (g)
2. 100-seed weight (g): A random sample of 100 seeds per plant.
3. Number of seeds per pod: Average of five pods per plant.
4. Pod length (cm): Average of five pods per plant.
5. Peduncle length (cm): Average of five peduncles per plant.
6. Number of pods per plant
7. Number of peduncles per plant
8. Number of pods per peduncle.
9. Days to First flowering: Days taken from the date of seeding to the date on which the first flower opened.
10. Days to Maturity: Days taken from the date of seeding to the date when at least five pods were completely yellow.

Data for the last two characters were recorded during the growth period while the first eight observations were taken at harvesting time and later. Data based on mean of five plants were used in the analyses.

Statistical analysis

In this experiment analysis of variance for a randomised complete block design with b replicates (blocks) and t treatments (entries) was applied. The

analysis consisted of the following entries:

(i) p parents; the i^{th} parent (i = 1, 2...,p) is coded as (ii)

(ii) $\frac{P(p-1)}{2}$ F_1 crosses; the crosses between the i^{th} female and the j^{th} male ($i \neq j$) is coded as (ij).

Thus the total number of treatments as determined by the half diallel cross in which the parents are included was

$$t = \frac{P(p + 1)}{2}$$

The model for the analysis of variance was

$$Y_{ijk} = b_k + m_{ij} + e_{ijk}$$

with the restriction

$$\sum_{k=1}^{b} b_k = 0$$

where Y_{ijk} = the value of the response variable of the $(ij)^{th}$ cross if i<j or i^{th} parent if i=j in the k^{th} replicate (block),

b_k = the effect of the k^{th} replicate (block),

m_{ij} = the effect of the $(ij)^{th}$ genotype if i<j or i^{th} parent if i = j,

e_{ijk} = the error effect

Based on the above model the analysis of variance (ANOVA) table for the randomized complete block design was as below:

Source	d.f.	S.S.	M.S.
Total	bt-1	$\sum_{i \leq j} \sum_{k} y^2_{ijk} - \frac{(\Sigma\Sigma Y_{ijk})^2}{bt}$	
Replicates	b-1	$\frac{1}{t} \Sigma Y^2_{++k} - \frac{(\Sigma\Sigma Y_{ijk})^2}{bt}$	$\frac{SS_t}{df_t}$
Treatments	t-1	$\frac{1}{b} \Sigma Y^2_{ij+} - \frac{(\Sigma\Sigma Y_{ijk})^2}{bt}$	$\frac{SS_b}{df_b}$
Error	(b-1)(t-1)	By substraction from totals	$\frac{S.S._e}{df_e}$

The treatment mean square (M.S.) was tested against error MS to determine the level of significance. The test for differences among treatments was made by the following F-test:

$$F\left[(t-1), (b-1)(t-1)\right] = M_t/M_e$$

Where (t-1) and (b-1) (t-1) are the degrees of freedom associated with the numerator and denominator of the F ratio and M_t and M_e are the treatment and error mean squares respectively.

Combining ability analysis

The mean values, M_{ij}'s ($i \leq j$) for each genotype over all the replicates for the diallel set was given as below.

	1	2	-	-	P
1	m_{11}	m_{12}	-	-	m_{1P}
2		m_{22}	-	-	m_{2P}
-			-	-	-
-					-
P					M_{mm}

The combining ability analysis was carried out on the half diallel table above using method 2 model I of Griffing (1956 b). The model is:

$m_{ij} = \mu + gca_i + gca_j + sca_{ij}$ for $i \leq j$; the assumption of no reciprocal effects is accepted, and the restrictions are:

$\Sigma_i gca_i = 0$ and $\Sigma_i sca_{ij} + sca_{ii} = 0$ for each i.

where,

μ = the population mean of all the crosses and parents in the diallel set.

gca_i and gca_j = general combining abilities of parents i and j.

sca_{ij} = specific combining ability of $(ij)^{th}$ cross.

sca_{ii} = arbitrary specific effect of a parent when crossed with itself (selfs).

The diallel analysis of variance (ANOVA) table was arranged as below:

Source	d.f.	S.S.	M.S.	EMS
gca	p-1	S_g	Mg	$\sigma_e^2+(P+2)\left(\frac{1}{p-1}\right)\Sigma g_i^2$
sca	p(p-1)/2	S_s	Ms	$\sigma_e^2+\frac{2}{p(p-1)}\sum\sum_{ij} S_{ij}^2$
Error	(b-1)(t-1)	S_e	mė	$\hat{\sigma}_e^2$

Where,

$$S_g = \frac{1}{p+2}\left[\sum_i (Y_i + Y_{ii})^2 - \frac{4}{p} Y_{..}^2\right]$$

$$S_s = \sum\sum_{i\leq j} Y_{ij}^2 - \frac{1}{p+2}\sum(Y_{i.} + Y_{ii})^2 + \frac{2}{(p+1)(p+2)} Y_{..}^2$$

S_e = Dividing the error sum of square obtained earlier from analysis of variance by number of replicates.

The following F ratios were used to test for gca and sca effects. To test for differences among gca effects $F[(p-1), m] = mg/mė$ was used, and to test for differences among sca effects

$F[p(p-1)/2, m] = \frac{Ms}{Mė}$ was used. The subscripts

represent the numerator and denominator of the F ratio.

GCA and SCA effects: The effects in the model were estimated as follows:

$$\mu = \frac{2}{p(p+1)} Y..$$

$$gca_i = \frac{1}{P+2} (Y_{i.} + Y_{ii}) - \frac{2}{p} Y..$$

$$sca_{ij} = Y_{ij} - \frac{1}{p+2} (Y_{i.} + Y_{ii} + Y_{j.} + Y_{jj}) + \frac{2}{(P+1)(p+2)} Y$$

The relative importance of general combining ability (gca) and specific combining ability (sca) was calculated by the ratio $\bar{2}_g^2/(\bar{2}_g^2 + \bar{s}^2)$ discussed by Baker (1978) for a fixed effects model, where $\bar{2}_g^2$ and $\bar{s}^2$ are the averages of the squares of the fixed gca and sca effects, respectively, which is

$$\bar{g}^2 = \frac{\Sigma g_i^2}{p-1}; \quad \bar{s}^2 = \frac{\Sigma s_{ij}^2}{p(p-1)}$$

Expected means: The estimated expected cross means for the crosses were calculated following the illustration of Simmonds (1979), assuming the absence of S_{ij} by

$$\mu + g_i + g_j \text{ for } i < j.$$

The expected cross means and observed cross means were plotted and a line with slope of 1, passing through the origin drawn. Scatter of points around this line indicated the relative importance of additive (gca) and

non-additive (sca) gene variances. The square of the correlation coefficient between expected and observed means (r^2) also gave the relative importance of additive gene variance as compared to non-additive gene variance

Correlations and path analysis

Phenotypic, genotypic and error variances and covariances were obtained from the variance for each character and covariance for each pair of characters. The phenotypic and genotypic correlations were worked out following Singh and Chaudhary (1979). Path coefficients were obtained from genotypic correlations by the formula suggested by Dewey and Lu (1959), by solving a set of simultaneous equations.

Heterosis

Heterosis or hybrid vigour, as usually defined as the deviation of the F_1 from mid parent, was mathematically calculated by the formula

$$\bar{F}1 - \frac{\bar{p}_1 + \bar{p}_2}{2} \quad \text{where,}$$

$$\bar{F}_1 - \frac{\bar{p}_1 + \bar{p}_2}{2} \quad \text{where,}$$

$\bar{F}_1$ is the mean value of the F_1 hybrid

$\bar{p}_1$ and $\bar{p}_2$ are the means of the respective parents in a cross.

The standard error of difference for comparing the different heterotic values were calculated as

$$S.E.D. = \sqrt{\left(\frac{M_e}{b} \times \frac{3}{2}\right)}$$

Where,

M_e = Pooled error mean square of parents and F_1s

b = number of replications

Heterotic values were tested using the t-test. The degree of heterosis was expressed as percentage as below,

$$\text{Percentage Heterosis} = \frac{\text{Heterotic value}}{\text{Mid-parent value}} \times 100$$

(b) Inheritance of resistance to cowpea aphids

The four sets containing each of the four generations (P_1, P_2, F_1 and F_2) and one set containing of five generations (P_1, P_2, F_1, F_2 and BC_1) were planted in the screenhouse on well prepared soil beds. Nitrogenous fertilizer at the rate of 20 kg N/ha was applied before planting. The experimental materials were planted on 14th May 1985 on well irrigated plot to ensure uniform germination. One row each of parents, F_1s and eight rows each of F_2's were planted. Each row had 25 plants spaced at 20 cm

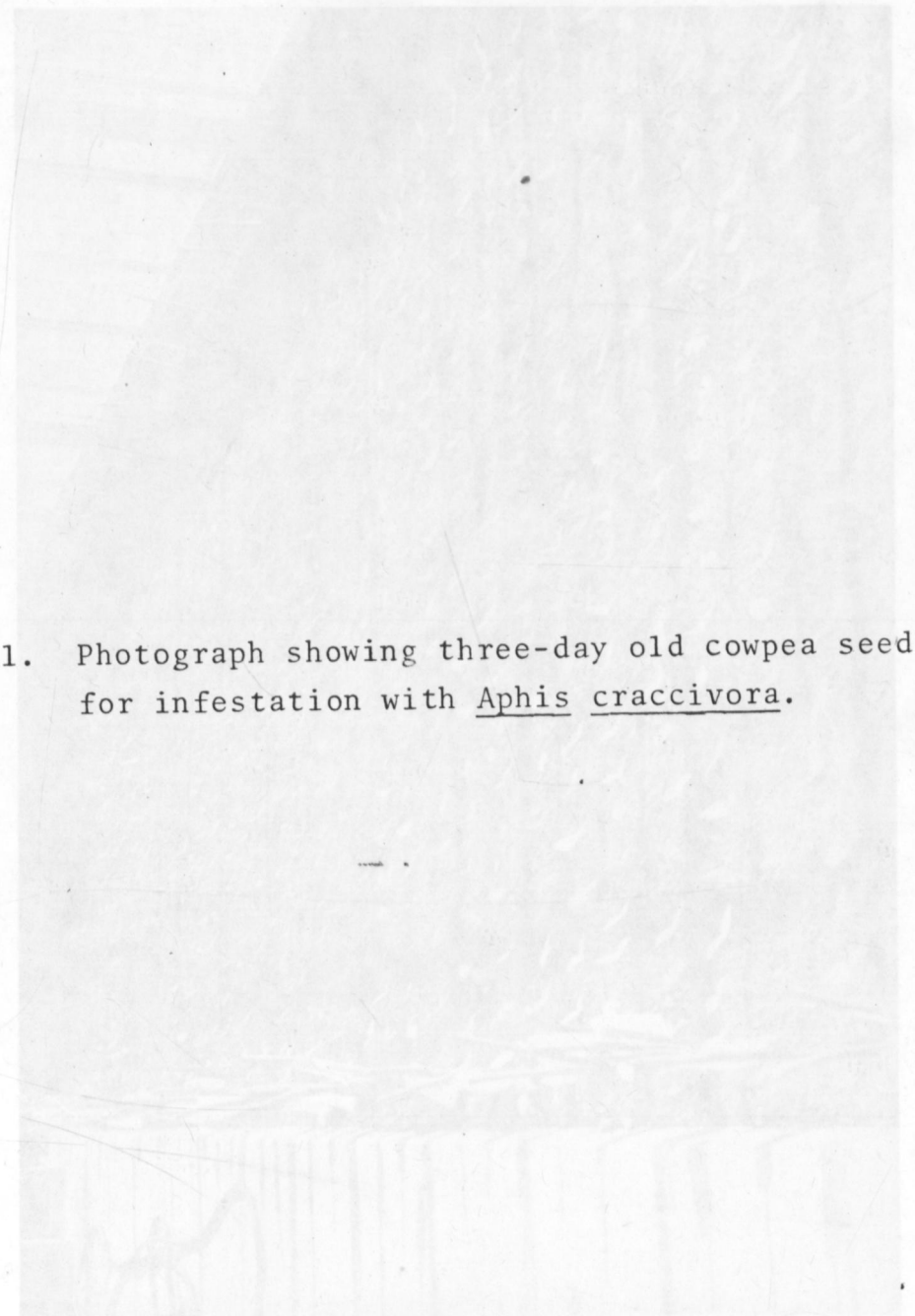


PLATE 1. Photograph showing three-day old cowpea seedlings for infestation with Aphis craccivora.

PLATE 1

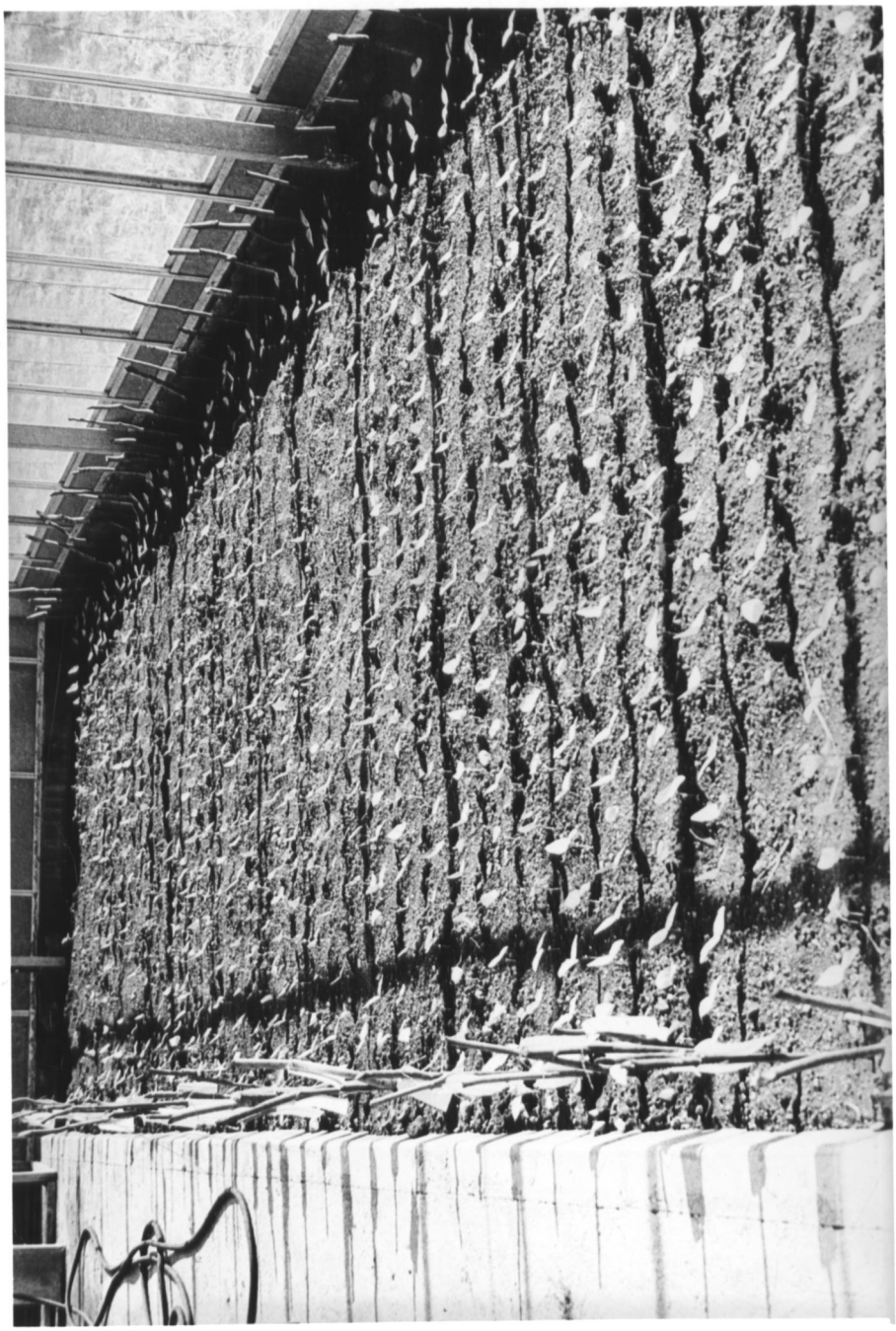


PLATE 2

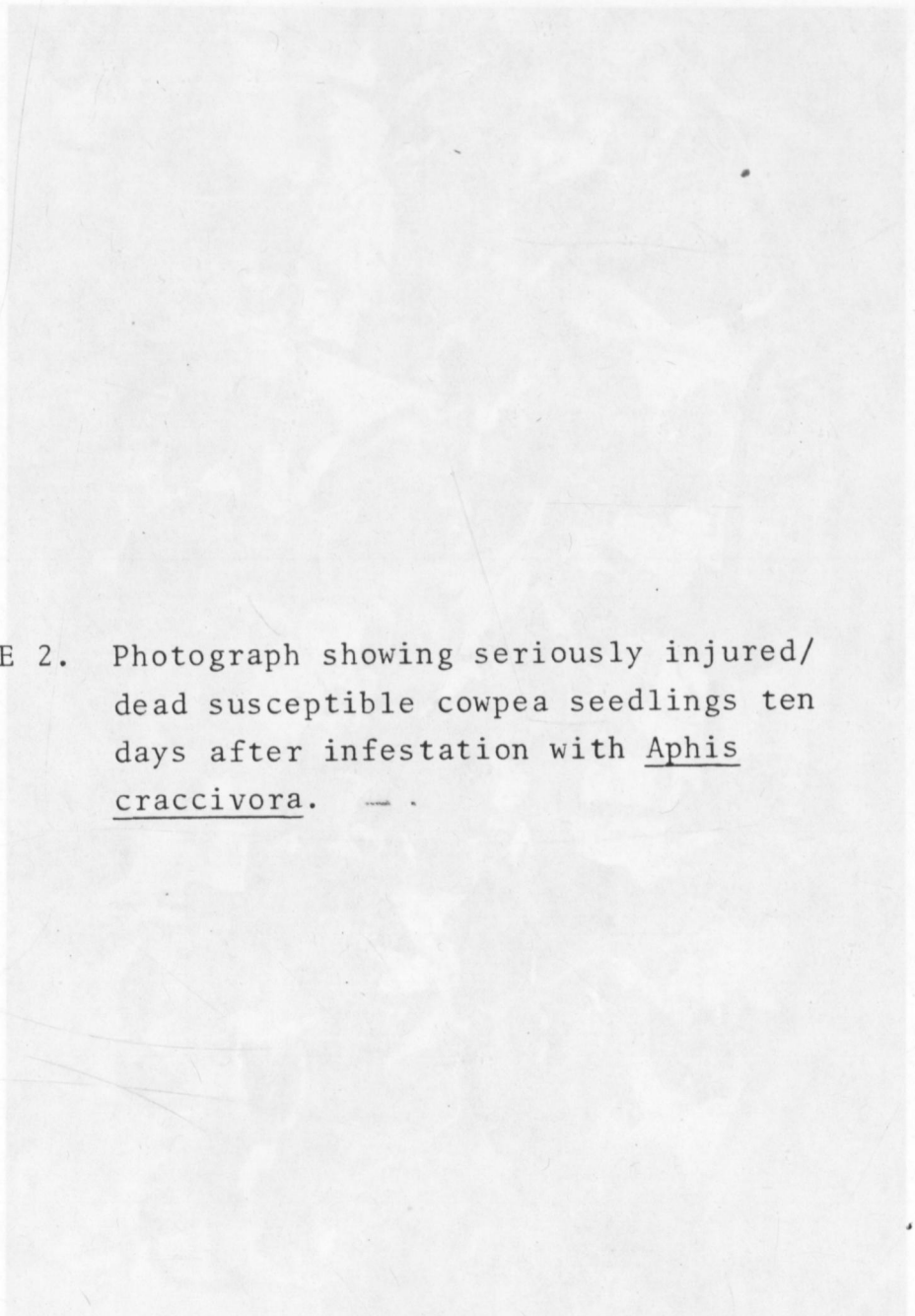


PLATE 2. Photograph showing seriously injured/ dead susceptible cowpea seedlings ten days after infestation with Aphis craccivora.

PLATE 2



between rows and 10 cm between plants. The F_2 in the set ICV 11 x TVU 310 contained 5 rows of 25 plants each while the set ICV 10 x TVU 310 contained only 4 rows of 25 plants each. The number of rows in each set depended on the availability of seed in a particular cross. No watering was done on the soil beds after planting to avoid seed displacement. Aphids were collected from cowpea fields and cultured on potted cowpea plants in the screenhouse. Three days old seedlings (Plate 1) were infested with 10 apterous adult aphids/plant using a camel hair brush. The seedling reaction was recorded 10 days after infestation when the seedlings in the susceptible rows were dead or severely injured (Plate 2). Counts of susceptible (dead) and resistant (surviving) seedlings in each progeny were taken.

Chi-square Test

Inheritance of resistance to the cowpea aphids was determined by the segregation numbers of F_2 and BC_1 progenies. The reaction of F_1 progenies indicated whether the resistance was determined by recessive or dominant gene(s). The segregation ratios in the F_2 and BC_1 were confirmed by the X^2 - test of goodness of fit.

The general formula for Chi-square is

$$X^2 = \Sigma \frac{(Ob - Ex)^2}{Ex}$$

Where,

Ob = observed counts of resistant or susceptible.

Ex = Expected counts of resistant or susceptible.

The X^2 values obtained were tested by comparing with values in a X^2 table at degrees of freedom one less than the number of classes. This indicated the probability (P) of obtaining deviations from expectancies, as large or larger than those observed, by chance alone.

CHAPTER 4

RESULTS

4.1. Genetics of Yield and its Components

4.1.1. Performance of parents and F_1 hybrids

The mean performance of the parents and their F_1 hybrids for grain yield per plant and component characters is presented in Table 1. Among the parents, the exotic variety TVU 310 had the highest, grain yield per plant (59.33 g), 100-seed weight (12.67 g), number of pods per plant (40), peduncles per plant (27), but was the latest to flower (45 days) and mature (70 days). The local variety ICV6 was the lowest yielder (25.19 g) while the other local variety ICV1 was the earliest to flower (40 days) and mature (61 days), and yielded about 32 g per plant. The mutant variety, ICV 11, had the longest pods (19.71 cm) with ICV 1 having the shortest pods (15.87 cm). Among the local varieties, ICV 10 had the highest grain yield per plant (53.03 g) and pod length (19.49 cm). The F_1 hybrids had higher grain yield per plant than their better parents except ICV 1 x ICV 10, ICV 6 x ICV 10 and ICV 10 x TVU 310. The number of pods per plant for the F_1 hybrids were also higher than their better parents for all except the cross ICV 10 x ICV 11. Similarly, number of

e 1. Means of parents and F_1s for grain yield and its components in cowpea

eny	Grain yield (g)/plant	100-seed weight (g)	Seeds/ pod	Pod length (cm)	Peduncle length (cm)	Pods/ plant	Peduncles/ plant	Pods/ peduncle	Days to first flowering	Days to maturity
	31.87	11.41	13.62	15.87	47.41	32.45	17.75	1.84	40.00	61.15
6	25.19	12.55	14.51	16.58	34.16	19.45	13.20	1.49	43.25	67.84
10	53.03	12.02	19.10	19.49	44.33	32.25	23.40	1.39	45.00	66.90
11	52.10	12.12	18.60	19.71	44.50	35.51	22.63	1.58	43.00	66.00
310	59.53	12.67	17.62	18.16	37.99	40.10	27.29	1.48	45.25	69.71
x ICV 6	46.78	11.97	14.02	16.15	47.82	41.54	23.31	1.77	40.25	62.96
x ICV 10	50.34	11.97	15.59	17.68	46.11	39.48	23.48	1.67	40.75	64.04
x ICV 11	61.73	12.01	16.24	16.44	49.22	49.05	27.07	1.81	41.00	64.45
x TVU 310	69.54	12.25	15.31	17.09	43.49	50.73	29.96	1.70	44.00	66.08
x ICV 10	47.54	12.88	15.21	17.35	41.36	36.67	23.59	1.55	42.25	65.40
x ICV 11	64.03	11.52	16.86	17.77	43.26	45.81	25.83	1.77	42.25	65.69
x TVU 310	71.42	12.37	16.18	17.58	42.98	55.85	35.29	1.58	44.25	67.30
10 x ICV 11	55.25	12.85	18.24	19.11	42.30	32.07	23.16	1.38	43.75	66.48
10 x TVU 310	57.94	12.28	18.16	18.60	42.15	40.88	26.51	1.54	44.50	68.11
11 x TVU 310	67.09	12.92	18.66	19.37	42.97	42.55	28.24	1.50	44.25	68.36
: F_1s + Parents	54.22	12.25	16.53	17.80	43.34	39.63	24.71	1.60	42.92	66.03
: F_1s Alone	59.16	12.30	16.45	17.71	44.16	43.46	26.64	1.63	42.73	65.89
(%)	27.58	4.97	3.68	5.45	7.28	25.87	21.94	9.82	3.14	2.38

Table 2. Analysis of variance table for grain yield and its components in cowpea

Source	d.f.	Mean squares									
		Grain yield (g)/ plant	100-seed weight (g)	Seeds/ pod	Pod length (cm)	Peduncle length (cm)	Pods/ plant	Peduncles/ plant	Pods/ peduncle	Days to first flowering	Days to maturity
Replications	3	89.21	0.49	2.49**	2.36*	13.93	16.07	1.55	0.05	5.13*	1.92
Treatments	14	672.79**	0.86*	12.98**	6.29**	57.41**	320.95**	103.62**	0.09**	12.20**	19.82**
Error	42	223.65	0.37	0.37	0.94	9.96	105.10	29.40	0.03	1.82	2.47
Total	59										

* Significant at $P \leq 0.05$; ** significant at $P \leq 0.01$.

peduncles per plant for the F_1's also exceeded the better parents except for the crosses I.CV 10 x I.CV 11 and I.CV 10 x TVU 310. However, the lengths of the F_1 hybrid pods were more or less intermediate between the two parents involved with non of the F_1's exceeding the better parent performance. The hybrid ICV 6 x TVU 310 had the highest grain yield per plant (71.42 g) followed by I.CV 1 x TVU 310 (69.54 g), both involving low yielding local varieties and the high yielding exotic variety. Similarly, the highest number of pods were recorded in the crosses I.CV 6 x TVU 310 (56 pods) and I.CV 1 x TVU 310 (51 pods). The number of days to first flower and maturity for the F_1 hybrids were generally intermediate between the two parents involved. The analyses of variance (Table 2) indicated significant differences between genotypes for all the characters (see appendix for raw data).

4.1.2. Estimates of Combining Abilities

4.1.2.1. Grain yield per plant

Analysis of variance for General combining ability (GCA) and specific combining ability (SCA) in respect of grain yield per plant and its components is given in Table 3. Mean squares for both GCA and SCA

e 3. Combining ability ANOVA for grain yield and its components in cowpea

rce	d.f.	Mean squares									
		Grain yield(g)/ plant	100-seed weight (g)	Seeds/ pod	Pod length (cm)	Peduncle length (cm)	Pods/ plant	Peduncles/ plant	Pods/ peduncle	Days to first flowering	Days to maturity
	4	268.02**	0.33*	10.74**	4.98**	33.05**	73.85*	35.29**	0.06**	8.94**	15.81**
	10	128.30*	0.17	0.25**	0.21	6.86*	82.79*	22.16**	0.01	0.69	6.11**
	42	55.91	0.09	0.09	0.24	2.49	26.28	7.35	0.01	0.46	0.62

* - Significant at P $\leq$ 0.05 and P $\leq$ 0.01, respectively.

were significant for grain yield per plant; the GCA variance being double that of SCA. The analysis indicated the importance of both additive and non-additive genetic variance in the inheritance of grain yield per plant.

The estimates of GCA effects and *per se* performance of the parents in respect to grain yield per plant and component characters are presented in Table 4. The GCA values for the local varieties, ICV 1, ICV 6 and ICV 10 were negative. The same varieties also had lower grain yield per plant than the better parent in the crosses ICV 1 x ICV 10, ICV 6 x ICV 10 and ICV 10 x TVU 310. The mutant variety, ICV 11 and the exotic variety TVU 310 had positive GCA values. TVU 310 was the best general combiner with positive and highly significant GCA value (8.53) while ICV 6 was the poorest general combiner with significant negative GCA value (-6.46). The other parents had non-significant (average) GCA effects. The correlations between the GCA effects and *per se* performance of parents were positive and significant for all the characters (Table 4) studied except number of pods per plant ($r = 0.73$). This indicated that the *per se* performance of the parents provided a fairly good indication of their combining ability for the characters studied. The mean

Table 4. GCA effects, mean values for yield traits and correlations (r_{gm}) between GCA effects and means in cowpea.

	Grain yield(g) plant		100-seed weight(g)		Seeds/ pod		Pod length (cm)		Peduncle length(cm)	
	GCA	Means	GCA	Means	GCA	Means	GCA	Means	GCA	Means
I.CV1	-4.75	31.89	-0.36**	11.41	-1.54**	13.62	-1.10**	15.87	3.06**	47.41
I.CV6	-6.46*	25.19	0.05	12.55	-1.13**	14.51	-0.68**	16.58	-2.33**	34.14
I.CV10	-1.18	53.03	0.07	12.02	0.87**	19.10	0.71**	19.49	0.08	44.33
I.CV11	3.85	52.10	0.00	12.12	1.15**	18.60	0.76**	19.71	0.96	44.50
TVU310	8.53**	59.53	0.24	12.67	0.63**	17.62	0.31	18.16	-1.78**	38.00
S.E.(g_i)	2.53		0.16		0.10		0.17		0.53	
S.E.(g_i-g_j)	4.00		0.16		0.16		0.26		0.84	
S.E.(means)		0.23		0.09		0.24		0.20		0.60
r_{gm}	0.90		0.91*		0.99**		0.99**		0.99**	

* significant at $P \leq 0.05$, ** significant at $P \leq 0.001$.

Table 4 (Contd...)

	Pods/ plant		Peduncles/ plant		Pods/ peduncle		Days to first flowering		Days to maturity	
	GCA	Means	GCA	Means	GCA	Means	GCA	Means	GCA	Means
ICV1	1.14	32.45	-1.28	17.75	0.14**	1.84	-1.64**	40.00	-2.34**	61.15
ICV6	-2.17	19.45	-1.98*	13.20	0.00	1.49	-0.29	43.25	0.12	67.84
ICV10	-3.45*	32.25	-0.68	23.40	-0.10**	1.39	0.54*	45.00	0.24	66.90
ICV11	0.39	35.51	0.18	22.63	0.00	1.58	-0.04	43.00	0.11	66.00
TVU310	4.64**	40.10	3.76**	27.29	-0.05	1.48	1.43**	45.25	1.87**	69.71
S.E.(g_i)	1.73		0.92		0.03		0.23		0.27	
S.E.(g_i-g_j)	2.74		1.45		0.04		0.36		0.42	
S.E.(means)		1.59		0.87		0.03		2.72		0.31
r_{gm}	0.73		0.85*		0.97**		0.96**		0.97**	

*, significant at $P \leq 0.05$; ** significant at $P \leq 0.01$.

Table 5. SCA Estimates for grain yield and its components in cowpea

Crosses	Grain yield(g) plant	100-seed weight(g)	Seeds/ pod	Pod length (cm)	Peduncle length (cm)	Pods/ plant	Peduncles/ plant	Pods/ peduncle	Days to first flowering	Days to maturity
CV1x ICV 6	3.76	0.03	0.16	0.13	3.75**	3.49	1.86	0.02	-0.74	-0.86
CV1 x ICV 10	2.04	0.00	-0.29	0.28	-0.37	2.17	0.72	0.02	-1.06*	0.11
CV1 x ICV 11	8.40	0.11	0.10	-1.02**	1.86	7.90*	3.45	0.06	-0.24	0.64
CV1 x TVU 310	11.53*	0.12	-0.31	0.08	-1.13	5.33	2.77	0.00	1.30**	0.52
CV6 x ICV 10	0.95	0.51*	-1.08**	-0.47	0.27	3.21	1.53	0.04	-0.92*	-0.99
CV6 x ICV 11	12.41*	-0.78**	0.31	-0.11	1.29	8.50*	2.91	0.16**	-0.35	-0.58
CV6 x TVU 310	15.12**	-0.16	0.15	0.15	3.75**	14.30**	8.80**	0.02	0.19	-0.72
CV10 x ICV11	-1.65	0.29	-0.33	-0.15	-2.08	-4.41	-1.06	-0.12*	0.33	0.10
CV10 x TVU 310	-3.64	-0.28	0.12	-0.21	0.51	0.07	-1.28	0.09	-0.38	-0.03
CV11 x TVU 310	0.49	0.43*	0.36	0.50	0.45	-2.10	-0.41	-0.06	-0.06	0.35
E.(S_{ij})	5.16	0.21	0.21	0.34	1.09	3.54	1.87	0.05	0.47	0.54
E.(S_{ij}-S_{ik})	9.79	0.40	0.39	0.64	2.07	6.71	3.55	0.10	0.89	1.03
E.(S_{ij}-S_{kl})	8.94	0.36	0.36	0.59	1.89	6.13	3.24	0.09	0.81	0.94

significant at $P \leq 0.05$; ** significant at $P \leq 0.01$.

performance of the parents and GCA estimates for grain yield per plant were correlated (r_{gm} = 0.90*).

The SCA effects (Table 5) for grain yield per plant were positive for all the crosses except ICV 10 x ICV 11 and ICV 10 x TVU 310. The exotic variety TVU 310 which was the best general combiner was involved in the two significant and positive SCA effects. It was interesting to note that the best cross combinations with higher SCA values involved the two poor general combiners, ICV 1 and ICV 6 and two good general combiners, TVU 310 and ICV 11. These crosses were ICV 6 x TVU 310 (15.12), ICV 6 x ICV 11 (12.41) and ICV 1 x TVU 310 (11.53).

The relative importance of GCA for grain yield per plant and component characters was expressed as $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ and is presented in Table 6. The value for grain yield per plant was 0.71 indicating that GCA was more important than SCA. The distribution of points around the regression line (Figure 1) indicated equal importance of additive and non-additive genetic components in the determination of grain yield per plant (Table 7). Heterosis was indicated for grain yield per plant in most of the crosses (Table 8). The crosses ICV 6 x TVU 310 (68.60%), ICV 6 x ICV 11 (65.67%) and ICV 1 x ICV 6 (63.67%) exhibited higher heterosis. It was noted that the cross between two low-

Table 6. Components of GCA($\bar{g}^2$) and SCA($\bar{s}^2$) and the relative importance of GCA and SCA.

	Grain yield(g)/ plant	100-seed weight(g)	Seeds/ pod	Pod length (cm)	Peduncle length (cm)	Pods/ plant	Peduncles/ plant	Pods/ peduncle	Days to first flowering	Days to maturity
2	38.29	0.05	1.53	0.71	4.72	10.55	5.04	0.01	1.28	2.26
2	31.09	0.06	0.09	0.09	1.97	20.93	5.74	0.00	0.23	0.17
$\bar{g}^2/(2\bar{g}^2+\bar{s}^2)$	0.71	0.63	0.97	0.94	0.83	0.50	0.66	0.87	0.92	0.96

ble 7. The expected cross means and r^2 estimates for yield components in cowpea

	Grain yield/ plant	100-seed weight	Seeds/ pod	Pod length	Peduncle length	Pods/ plant	Peduncles/ plant	Pods/ peduncle	Days to first flowering	Days t maturi
1 x ICV6	47.95	11.99	13.78	15.93	44.89	41.89	23.38	1.77	40.80	63.67
1 x ICV10	53.23	12.01	15.80	17.32	47.30	41.15	24.68	1.67	41.63	63.79
1 x ICV11	58.26	11.95	16.06	17.37	48.18	44.99	25.54	1.77	41.05	63.66
1 x TVU 310	62.94	12.18	15.54	16.92	45.44	49.24	29.12	1.72	42.52	65.42
6 x ICV10	51.52	12.42	16.21	17.74	41.91	37.30	23.98	1.53	42.98	66.25
6 x ICV11	56.55	12.35	16.47	17.79	42.79	41.14	24.84	1.63	42.40	66.12
6 x TVU310	61.23	12.59	15.95	17.34	40.05	45.39	28.42	1.58	43.87	67.88
10 x ICV11	61.83	12.37	18.49	19.18	45.20	40.40	26.14	1.53	43.42	66.24
10 x TVU310	66.51	12.61	17.97	18.73	42.46	44.65	29.72	1.57	44.70	68.00
11 x TVU310	71.54	12.54	18.23	18.78	43.34	48.49	30.58	1.58	44.12	67.87
r^2	0.49	0.26	0.92	0.84	0.53	0.40	0.41	0.75	0.84	0.89

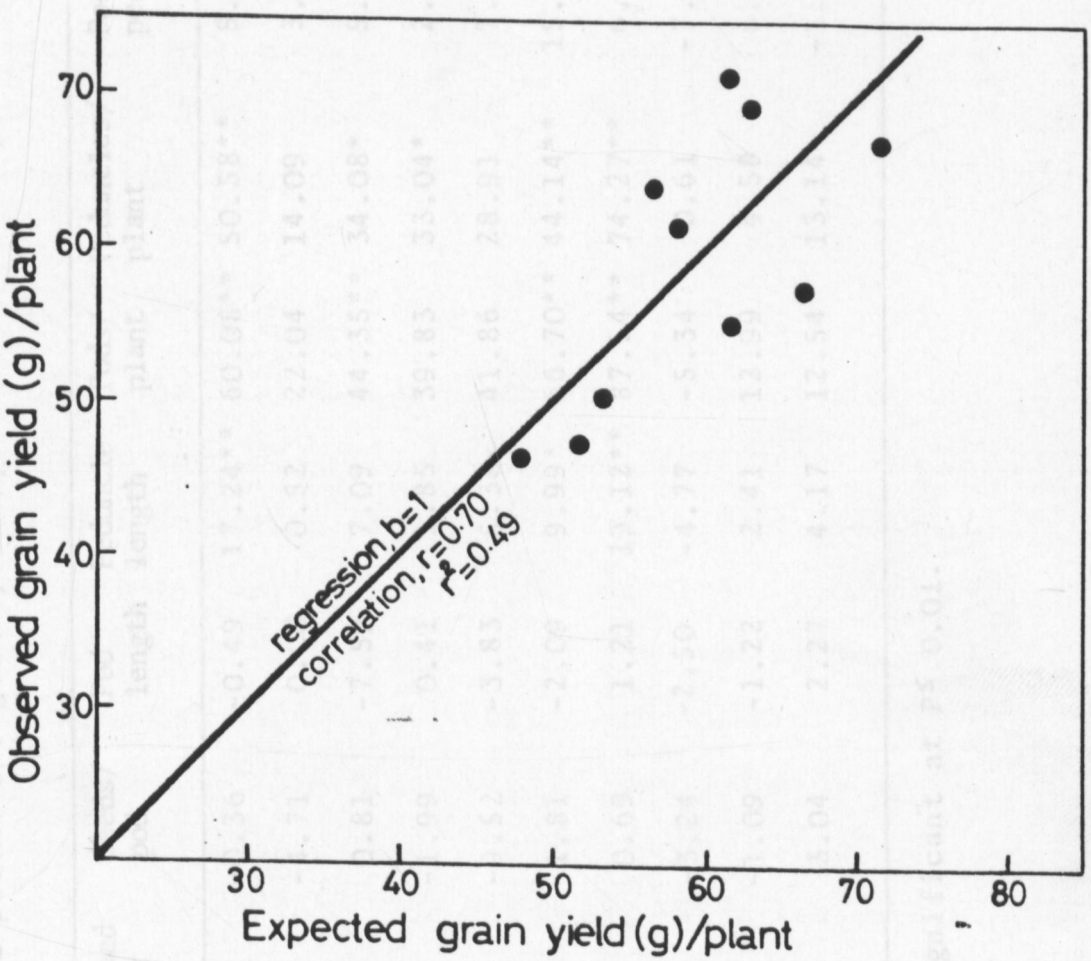


FIGURE 1. COMBINING ABILITIES FOR GRAIN YIELD/PLANT OBSERVED YIELDS OF PROGENIES PLOTTED AGAINST YIELDS PREDICTED FROM PARENTAL GCA

Table 8. Heterosis (%) over mid-parent for grain yield/plant and its components in cowpea.

	Grain yield/ plant	100-seed weight	Seeds/ pod	Pod length	Peduncle length	Pods/ plant	Peduncles/ plant	Pods/ peduncle	Days to first flowering	Days to maturity
ICV1 X ICV6	63.97**	-0.08	-0.36	-0.49	17.24**	60.08**	50.58**	5.99	-3.32	-2.39
ICV1 X ICV10	18.59	2.13	-4.71	0.00	0.52	22.04	14.09	3.09	-4.12	0.02
ICV1 X ICV11	47.01*	2.04	0.81	-7.59	7.09	44.35**	34.08*	5.85	-1.21	1.37
ICV1 X TVU310	52.17**	1.74	-1.99	0.41	1.85	39.83	33.04*	2.41	3.21	0.99
ICV6 X ICV10	21.56	4.80	-9.52	-3.83	5.38	41.86	28.91	7.64	-4.26	-2.92
ICV6 X ICV11	65.67**	-7.12	1.81	-2.09	9.99*	66.70**	44.14**	15.31	-2.04	-1.84
ICV6 X TVU310	68.60**	-1.90	0.69	1.21	19.12**	87.54**	74.27**	6.04	0.00	-2.15
ICV X ICV11	5.10	6.46	-3.24	-2.50	-4.77	-5.34	0.61	-7.38	-0.57	0.05
ICV10 X TVU310	2.95	-0.57	-1.09	-1.22	2.41	12.99	4.58	6.21	-1.40	-0.29
ICV11 X TVU310	20.19	4.19	3.04	2.27	4.17	12.54	13.14	-1.96	0.27	0.74

*Significant at $P \leq 0.05$, ** Significant at $P \leq 0.01$.

yielding local varieties ICV1 x ICV 6 exhibited high heterosis but the yield was comparatively low. The high-yielding parents, ICV 10, ICV 11 and TVU 310 gave high-yielding F_1 hybrids although the degree of heterosis displayed by them in crosses was not necessarily high.

4.1.2.2. 100-seed weight

The analysis of combining ability (Table 3) revealed that GCA mean square was significant while SCA mean square was non-significant. This indicated the relative importance of the additive component of variation in the inheritance of 100-seed weight. The GCA effects (Table 4) for all parents except ICV 1 were positive though non-significant. The local variety ICV 1 had a negative and significant GCA value (-0.36). Therefore, all the other varieties were average general combiners while ICV 1 was a poor combiner for seed size. There was a close agreement between the *per se* performance of the parents and their GCA values (r_{gm} = 0.91*).

A number of crosses showed average SCA effects. Only two crosses, ICV 6 x ICV 10 and ICV 11 x TVU 310 indicated significant and desirable (positive) SCA

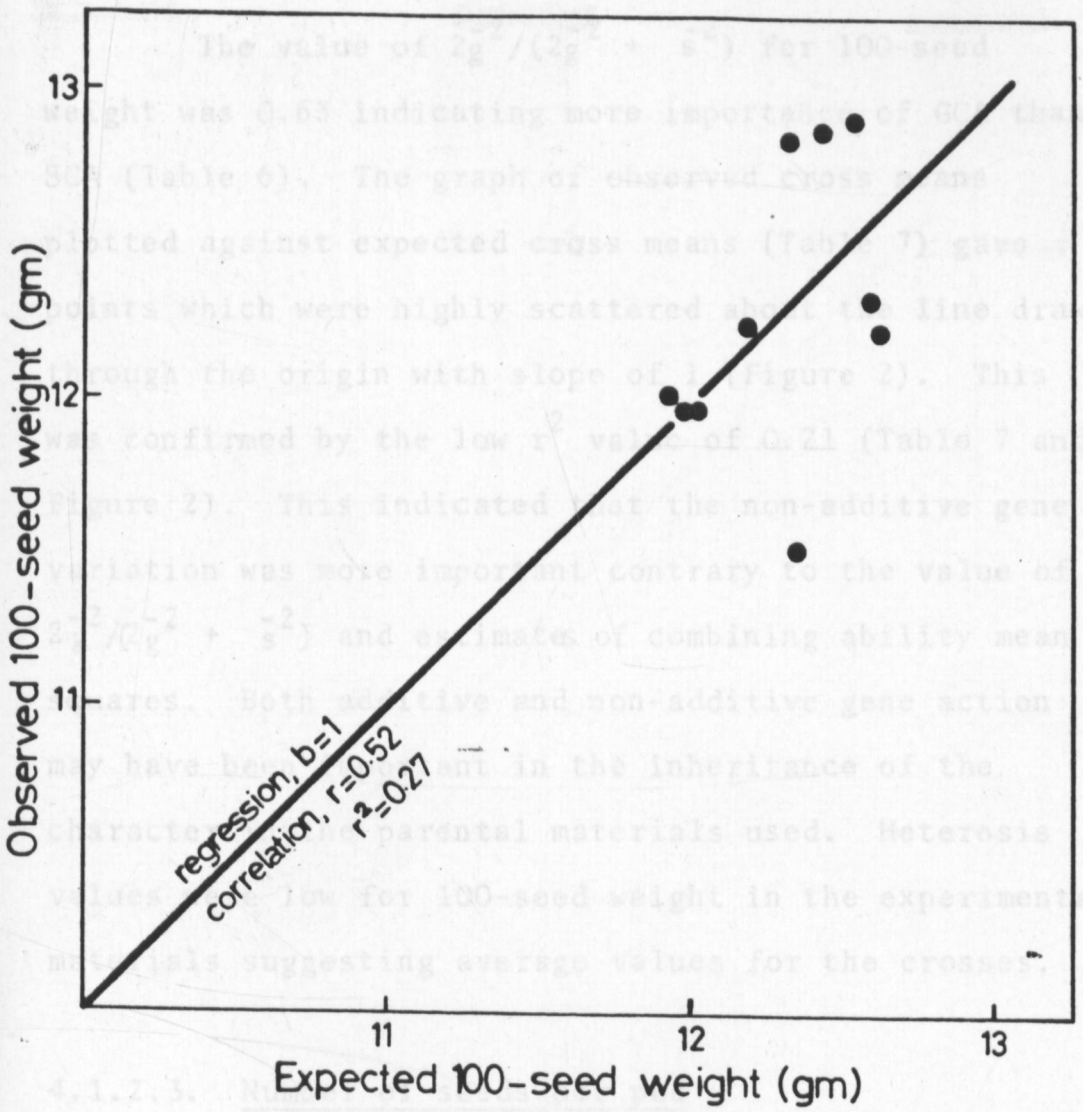


FIGURE 2. COMBINING ABILITIES FOR 100-SEED WEIGHT IN COWPEA. OBSERVED 100 -SEED WEIGHT OF PROGENIES PLOTTED AGAINST 100-SEED WEIGHTS PREDICTED FROM PARENTAL G

values. The cross ICV 6 x ICV 11 showed significant but undesirable (negative) SCA value.

The value of $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ for 100-seed weight was 0.63 indicating more importance of GCA than SCA (Table 6). The graph of observed cross means plotted against expected cross means (Table 7) gave points which were highly scattered about the line drawn through the origin with slope of 1 (Figure 2). This was confirmed by the low r^2 value of 0.21 (Table 7 and Figure 2). This indicated that the non-additive gene variation was more important contrary to the value of $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ and estimates of combining ability mean squares. Both additive and non-additive gene action may have been important in the inheritance of the character in the parental materials used. Heterosis values were low for 100-seed weight in the experimental materials suggesting average values for the crosses.

4.1.2.3. Number of seeds per pod

The diallel ANOVA (Table 3) for number of seeds per pod indicated both the GCA and SCA mean squares highly significant. Hence, both additive and non-additive gene variances were important in the variation of number of seeds per pod. The GCA effects for all

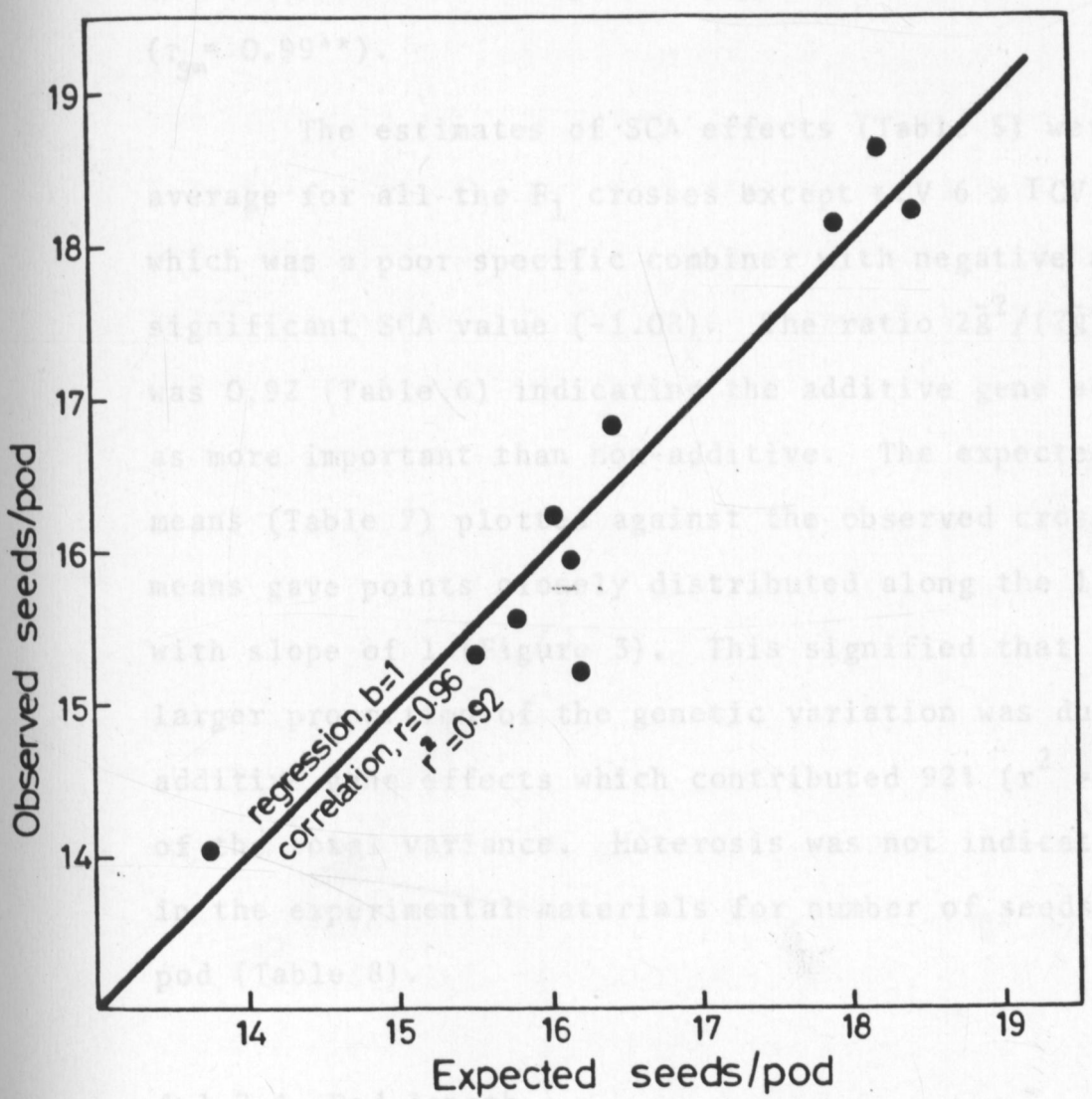


FIGURE 3. COMBINING ABILITIES FOR SEEDS/POD IN COWPEA. OBSERVED SEEDS/POD OF PROGENIES PLOTTED AGAINST SEEDS/POD PREDICTED FROM PARENTAL GCA

the parents were highly significant (Table 4), the best general combiners being ICV 11, ICV 10 and TVU 310 while ICV 6 and ICV 1 were the poor general combiners. The GCA effects and per se performance of the parents (Table 4) indicated highly significant correlations (r_{gm} = 0.99**).

The estimates of SCA effects (Table 5) were average for all the F_1 crosses except ICV 6 x ICV 10 which was a poor specific combiner with negative and significant SCA value (-1.08). The ratio $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ was 0.92 (Table 6) indicating the additive gene action as more important than non-additive. The expected means (Table 7) plotted against the observed cross means gave points closely distributed along the line with slope of 1 (Figure 3). This signified that a larger proportion of the genetic variation was due to additive gene effects which contributed 92% (r^2 = 0.92) of the total variance. Heterosis was not indicated in the experimental materials for number of seeds per pod (Table 8).

4.1.2.4. Pod length

The mean square due to GCA was highly significant but the SCA mean square was non-significant (Table 3). This indicated that the additive gene variance was the most

important in the manifestation of the genotypic variation among the parents and the progenies. The GCA effects (Table 4) were highly significant but undesirable in the local varieties, ICV 1(-1.10) and ICV 6 (-0.68) while highly significant and desirable in ICV 10 (0.71) and the mutant variety, ICV 11 (0.76). The exotic variety, TVU 310 was an average general combiner. The best general combiner was ICV 11 (0.76) and the poorest was ICV 1 (-1.10). There was a close agreement between the per se performance of the parents and their GCA (r_{gm} = 0.99**).

Only one cross, ICV 1 x ICV 11, indicated significant SCA value (Table 5). This cross was the poor specific combiner (-1.02) while the other crosses were average combiners. The relative importance of GCA (Table 6) indicated a high value for the ratio $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ of 0.94 indicating that GCA was more important than SCA and thus additive gene action. The observed means of the crosses plotted against expected cross means (Table 7) resulted in points which were closely distributed along the line of slope 1 passing through the origin (Figure 4). This was confirmed by a high r^2 value of 0.83 (Table 7 and Figure 4), indicating that additive genes contributed 83% of the total genotypic variation in the inheritance of pod

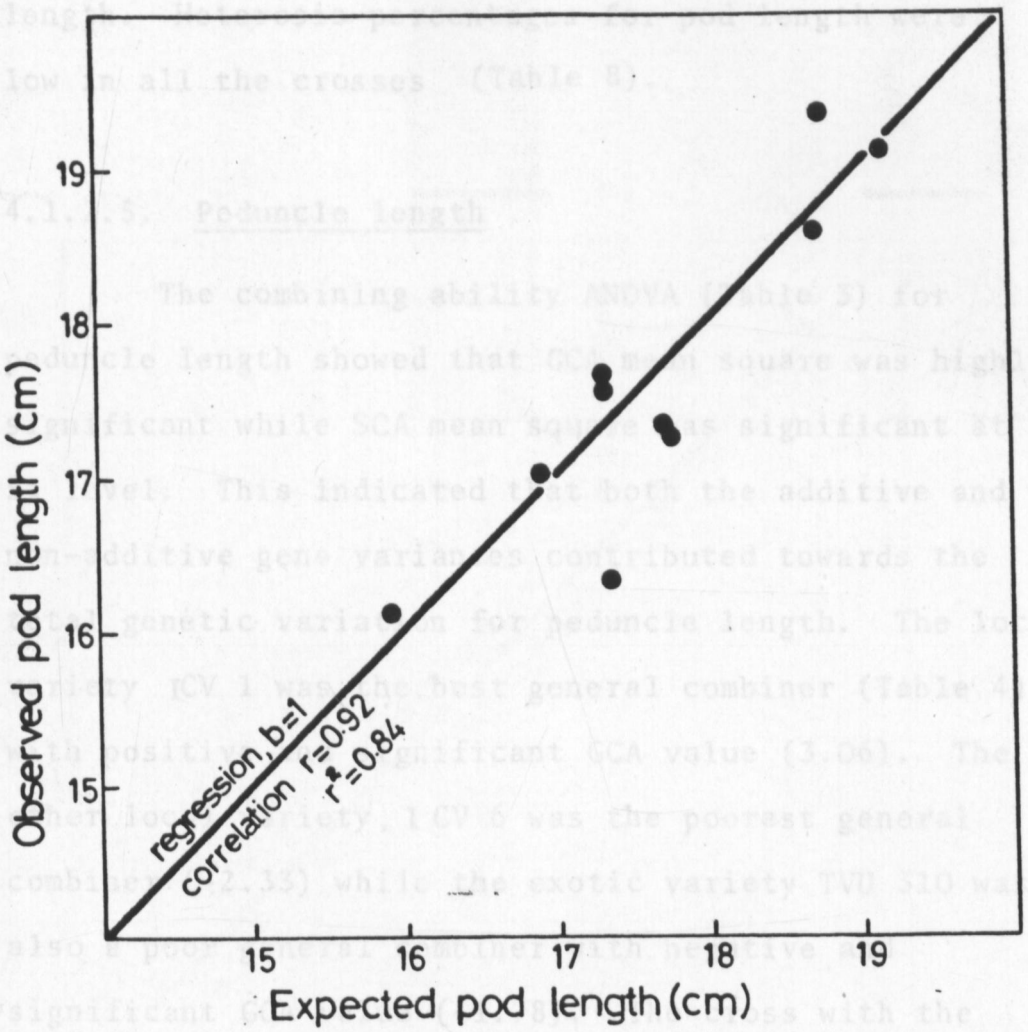


FIGURE 4. COMBINING ABILITIES FOR POD LENGTH IN COWPEA. OBSERVED POD LENGTHS (CM) OF PROGENIES PLOTTED AGAINST POD LENGTHS PREDICTED FROM PARENTAL GCA.

length. Heterosis percentages for pod length were low in all the crosses (Table 8).

4.1.2.5. Peduncle length

The combining ability ANOVA (Table 3) for peduncle length showed that GCA mean square was highly significant while SCA mean square was significant at 5% level. This indicated that both the additive and non-additive gene variances contributed towards the total genetic variation for peduncle length. The local variety ICV 1 was the best general combiner (Table 4) with positive and significant GCA value (3.06). The other local variety, I CV 6 was the poorest general combiner (-2.33) while the exotic variety TVU 310 was also a poor general combiner with negative and significant GCA value (-1.78). The cross with the longest peduncles, therefore, involved the best general combiner and an average general combiner (ICV 1 x ICV 11). The other cross with long peduncles involved the best general combiner and the poorest combiner (ICV 1 x ICV 6) (Table 1 and Table 4). The GCA effects were highly correlated with the per se performance of the parents (r_{gm} = 0.94**).

The SCA effects (Table 5) for peduncle length were positive and significant for the crosses ICV 1 x

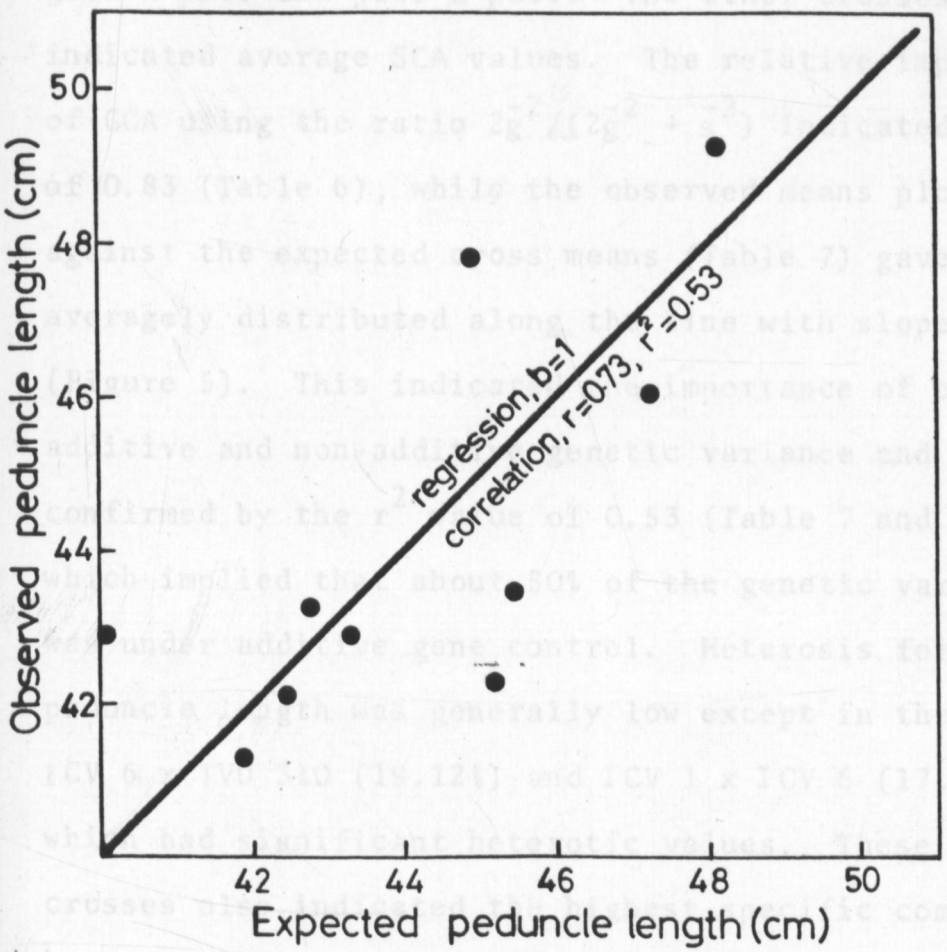


FIGURE 5. COMBINING ABILITIES FOR PREDUNCLE LENGTH IN COWPEA. OBSERVED PEDUNCLE LENGTHS (CM) OF PROGENIES PLOTTED AGAINST PEDUNCLE LENGTHS PREDICTED FROM PARENTAL GCA

ICV 6 (3.75) and ICV 6 x TVU 310 (3.75), both involving the poorest general combiner ICV 6. The two best specific combinations could be classified as good x poor and poor x poor. The other crosses indicated average SCA values. The relative importance of GCA using the ratio $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ indicated a value of 0.83 (Table 6), while the observed means plotted against the expected cross means (Table 7) gave points averagely distributed along the line with slope of 1 (Figure 5). This indicated the importance of both additive and non-additive genetic variance and was confirmed by the r^2 value of 0.53 (Table 7 and Figure 5) which implied that about 50% of the genetic variance was under additive gene control. Heterosis for peduncle length was generally low except in the crosses ICV 6 x TVU 310 (19.12%) and ICV 1 x ICV 6 (17.24%) (Table 8). which had significant heterotic values. These two crosses also indicated the highest specific combining abilities.

4.1.2.6. Number of pods per plant

The mean squares for both GCA and SCA were significant, with the SCA mean square being highly significant (Table 3). This indicated the importance of both additive and non-additive genetic variances in

the variation of the character. The estimates of GCA effects and per se performance of the parents for pods/plant (Table 4) were non-significantly correlated (r_{gm} = 0.73). The exotic variety, TVU 310 was the best general combiner (4.64) while the local variety ICV 10 was the poorest general combiner (-3.45). The other varieties were average general combiners.

The SCA effects for pods/plant (Table 5) were positive and significant in three crosses, ICV 6 x TVU 310 (14.30), ICV 6 x ICV 11 (8.50) and ICV 1 xICV 11 (7.90). The other crosses had non-significant SCA values which could be considered average. The high specific combiners, therefore, involved average x good and average x average general combiners. The relative importance of GCA from the ratio $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ was 0.5 (Table 6) indicating that pods/plant exhibited almost equal additive and non-additive variances. Similar indications were found from the plotting of observed cross means against expected cross means (Table 7). The points were moderately closely distributed about the line passing through the orign with slope of 1 (Fig. 6). The GCA effects were almost equal (r^2 = 0.40) to the SCA effects. This indicated that the non-additive gene action which accounted for about 50% of the variation was as important as the additive gene

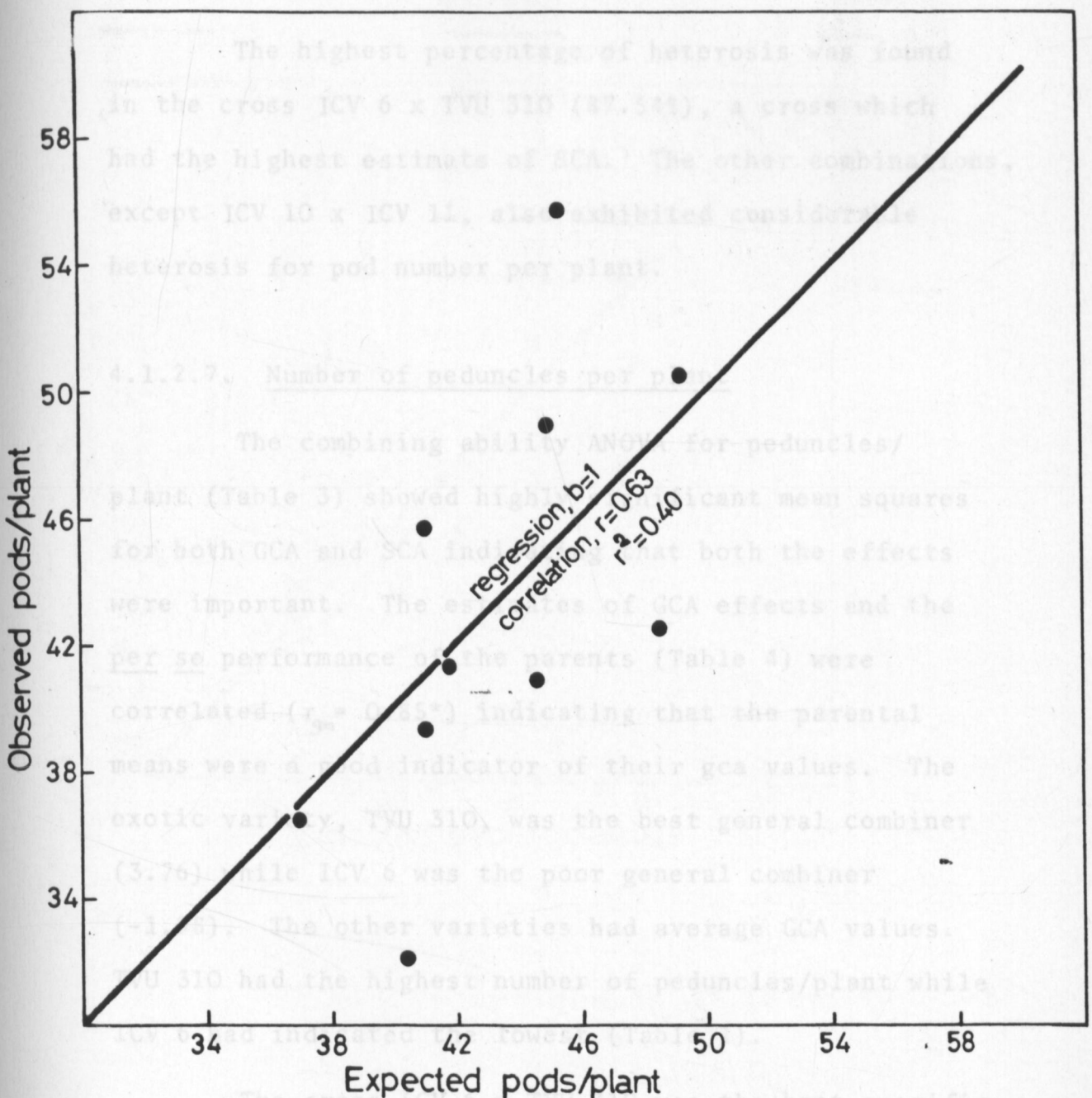


FIGURE 6. COMBINING ABILITIES FOR PODS/PLANT IN COWPEA. OBSERVED PODS/PLANT OF PROGENIES PLOTTED AGAINST PODS/PLANT PREDICTED FROM PARENTAL GCA

action in the inheritance of pods/plant.

The highest percentage of heterosis was found in the cross ICV 6 x TVU 310 (87.54%), a cross which had the highest estimate of SCA. The other combinations, except ICV 10 x ICV 11, also exhibited considerable heterosis for pod number per plant.

4.1.2.7. Number of peduncles per plant

The combining ability ANOVA for peduncles/plant (Table 3) showed highly significant mean squares for both GCA and SCA indicating that both the effects were important. The estimates of GCA effects and the per se performance of the parents (Table 4) were correlated (r_{gm} = 0.85*) indicating that the parental means were a good indicator of their gca values. The exotic variety, TVU 310, was the best general combiner (3.76) while ICV 6 was the poor general combiner (-1.98). The other varieties had average GCA values. TVU 310 had the highest number of peduncles/plant while ICV 6 had indicated the lowest (Table 1).

The cross ICV 6 x TVU 310 was the best specific combiner (Table 5) with significant and positive SCA effect. The other crosses had average SCA effects. The best specific combination was between poor x good

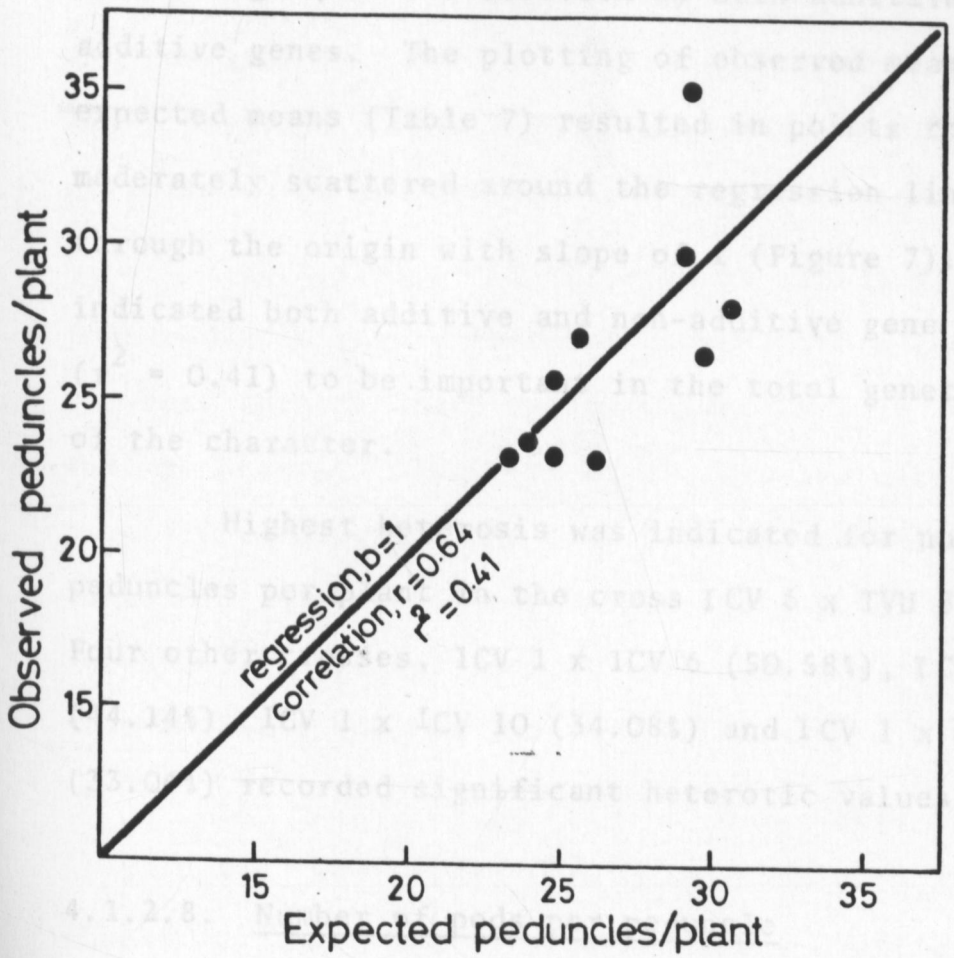


FIGURE 7. COMBINING ABILITIES FOR PEDUNCLES/PLANT IN COWPEA. OBSERVED PEDUNCLES/PLANT OF PROGENIES PLOTTED AGAINST PEDUNCLES/PLANT PREDICTED FROM PARENTAL GCA.

general combiners. The relative importance of GCA using the ratio $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ was 0.66 (Table 6) suggesting equal contribution by both additive and non-additive genes. The plotting of observed means against expected means (Table 7) resulted in points that were moderately scattered around the regression line passing through the origin with slope of 1 (Figure 7). This indicated both additive and non-additive gene actions (r^2 = 0.41) to be important in the total genetic variance of the character.

Highest heterosis was indicated for number of peduncles per plant in the cross ICV 6 x TVU 310 (74.27%). Four other crosses, ICV 1 x ICV 6 (50.58%), ICV 6 x ICV 11 (44.14%), ICV 1 x ICV 10 (34.08%) and ICV 1 x ICV 11 (33.04%) recorded significant heterotic values. (Table 8).

4.1.2.8. Number of pods per peduncle

The combining ability ANOVA (Table 3) for pods/peduncle indicated highly significant GCA mean square while the SCA mean square was non-significant. This indicated the importance of the additive variance component in the inheritance of number of pods/peduncle. The estimates of GCA effects (Table 4) were significant and positive (desirable) for ICV 1 parent but significant and negative (undesirable) in the ICV 10 parent. The

other parents showed average GCA values. The correlation between GCA effects and the per se performance of the parents (Table 4) was significant and positive (r_{gm} = 0.97**) implying that the parental means provided a fairly good indication of their performance in the crosses for this character.

The estimates of SCA effects (Table 5) for pods/peduncle showed that the cross ICV 6 x ICV 11 was the best specific combination while ICV 10 x ICV 11 was the poorest. The rest of the crosses were average specific combiners. The best specific combination therefore involved average x average general combiners. While poor x average general combiners resulted in a poor specific combination.

The value for $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ (Table 6) was high (0.87), indicating that GCA was more important than SCA. The graph of observed means plotted against expected cross means (Table 7) resulted in points closely distributed along the line of slope = 1 (Figure 8), indicating that GCA was more important. This was confirmed by the r^2 value of 0.75 suggesting that 75% of the total genetic variation was attributed to additive gene action.

Heterosis percentages for pods/peduncle in the experimental material indicated low values except in the

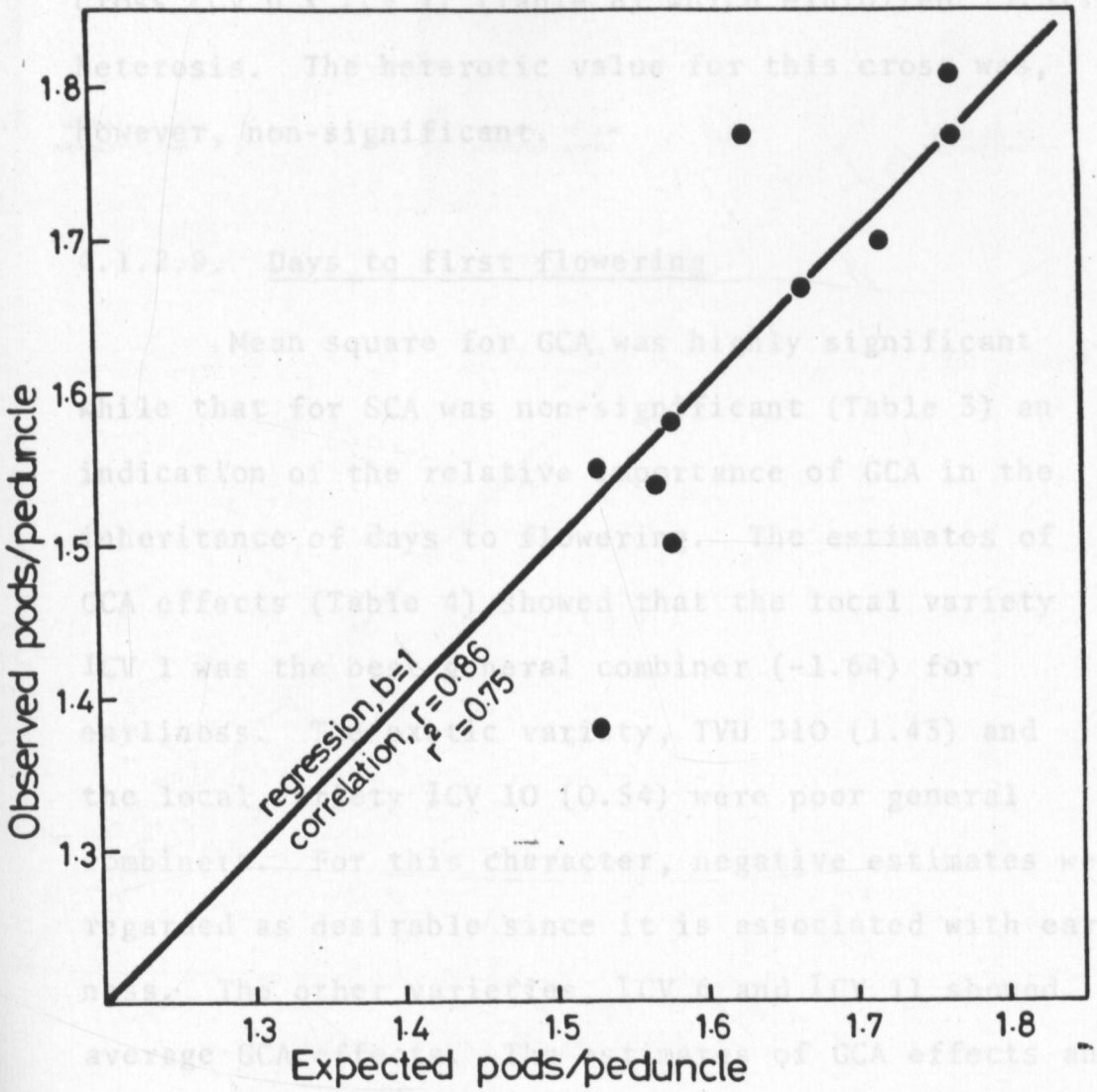


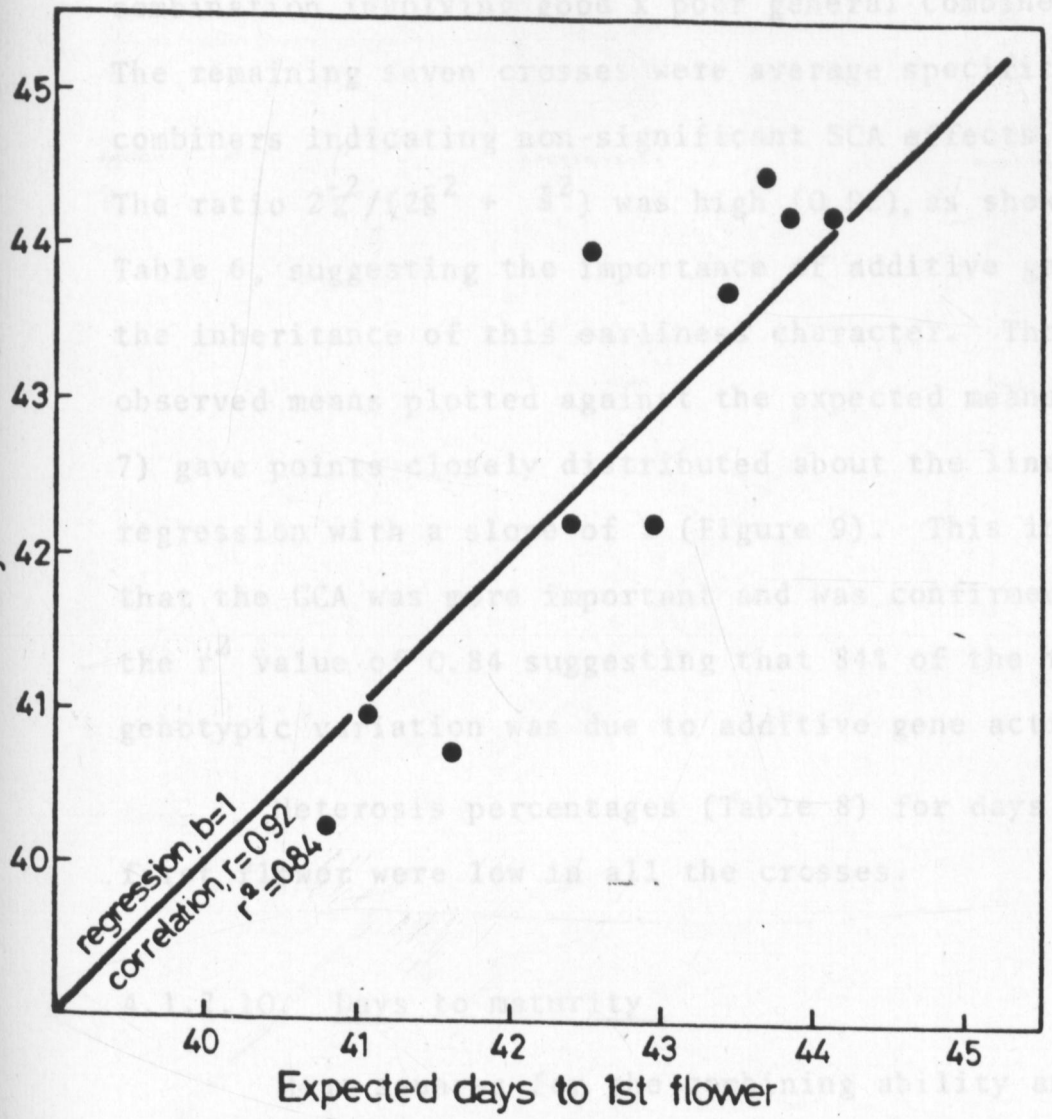
FIGURE 8. COMBINING ABILITIES FOR PODS/PEDUNCLE IN COWPEA OBSERVED PODS/PEDUNCLE OF PROGENIES PLOTTED AGAINST PODS/PEDUNCLE PREDICTED FROM PARENTAL GCA.

cross ICV 6 x ICV 11 (Table 8) which exhibited 15.31% heterosis. The heterotic value for this cross was, however, non-significant.

4.1.2.9. Days to first flowering

Mean square for GCA was highly significant while that for SCA was non-significant (Table 3) an indication of the relative importance of GCA in the inheritance of days to flowering. The estimates of GCA effects (Table 4) showed that the local variety ICV 1 was the best general combiner (-1.64) for earliness. The exotic variety, TVU 310 (1.43) and the local variety ICV 10 (0.54) were poor general combiners. For this character, negative estimates were regarded as desirable since it is associated with earliness. The other varieties, ICV 6 and ICV 11 showed average GCA effects. The estimates of GCA effects and per se performance of the parents (Table 4) were highly correlated (r_{gm} = 0.96**).

The SCA effects (Table 5) indicated two crosses ICV 1 x ICV 10 (-1.06) and ICV 6 x ICV 10 (-0.92) to be good specific combinations. These crosses involved good x poor and average x poor general combiners. The cross ICV 1 x TVU 310 (1.30) was the poor specific



RE 9. COMBINING ABILITIES FOR DAYS TO FIRST FLOWERING IN COWPEA OBSERVED DAYS TO FIRST FLOWERING OF PROGENIES PLOTTED AGAINST DAYS TO FIRST FLOWERING PREDICTED FROM GCA.

combination involving good x poor general combiners. The remaining seven crosses were average specific combiners indicating non-significant SCA effects. The ratio $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ was high (0.92), as shown in Table 6, suggesting the importance of additive genes in the inheritance of this earliness character. The observed means plotted against the expected means (Table 7) gave points closely distributed about the line of regression with a slope of 1 (Figure 9). This indicated that the GCA was more important and was confirmed by the r^2 value of 0.84 suggesting that 84% of the total genotypic variation was due to additive gene action.

Heterosis percentages (Table 8) for days to first flower were low in all the crosses.

4.1.2.10. Days to maturity

Mean squares for the combining ability analysis of the parents and their F_1 crosses (Table 3) showed that both GCA and SCA were highly significant. The mean squares for GCA were, however, higher than SCA mean squares. The GCA effects (Table 4) indicated the parent ICV 1 as the best general combiner (-2.34) while the exotic variety, TVU 310 was the poor general combiner (1.87). The negative effects were desirable for the earliness characters. The desirable ICV 1 had

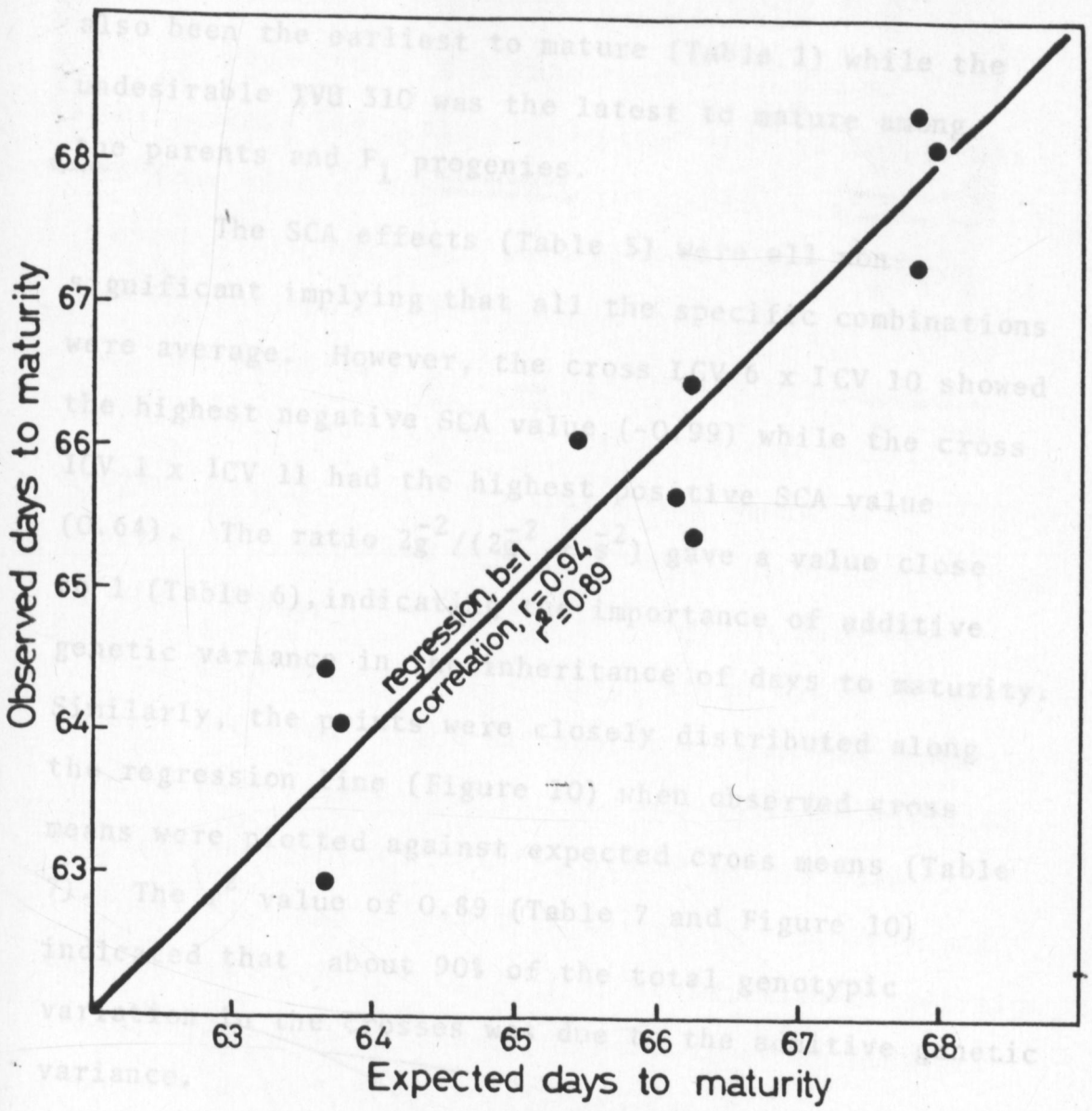


FIGURE 10. COMBINING ABILITIES FOR DAYS TO MATURITY IN COWPEA. OBSERVED DAYS TO MATURITY OF PROGENIES PLOTTED AGAINST DAYS MATURITY PREDICTED FROM GCA.

also been the earliest to mature (Table 1) while the undesirable TVU 310 was the latest to mature among the parents and F_1 progenies.

The SCA effects (Table 5) were all non-significant implying that all the specific combinations were average. However, the cross ICV 6 x ICV 10 showed the highest negative SCA value (-0.99) while the cross ICV 1 x ICV 11 had the highest positive SCA value (0.64). The ratio $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ gave a value close to 1 (Table 6), indicating the importance of additive genetic variance in the inheritance of days to maturity. Similarly, the points were closely distributed along the regression line (Figure 10) when observed cross means were plotted against expected cross means (Table 7). The r^2 value of 0.89 (Table 7 and Figure 10) indicated that about 90% of the total genotypic variation in the crosses was due to the additive genetic variance.

Heterosis percentages for the days to maturity were negligible (Table 8) for all the crosses of the experimental material

4.2. Correlations and Path-coefficient Analysis

Phenotypic and genotypic correlation coefficients for grain yield/plant and its components are presented in Table 9. Significant positive phenotypic correlations were observed between grain yield/plant and number of seeds per pod (r = 0.37**), pods per plant (r = 0.63**), peduncles per plant (r = 0.67**), pod length (r = 0.36**) and peduncle length (0.28*). 100-seed weight was found to be positively correlated with pod length (r = 0.29*), days to first flower (r = 0.33**) and days to maturity (r = 0.43**) while negative correlation was observed between 100-seed weight and number of pods per peduncle (r = -0.26*). Seeds per pod was positively correlated with pod length (r = 0.76**), peduncles per plant (r = 0.25*), days to first flowering (r = 0.57**) and days to maturity (r = 0.52**) while negative correlation was observed between seeds/pod and number of pods per peduncle (r = -0.43**). Pod length was found to have positive correlation with days to first flowering (r = 0.49**) and maturity (r = 0.47**) and negative correlation with number of pods per peduncle (r = -0.33**). Peduncle length was positively correlated with pods/plant (r = 0.41**), peduncles/plant (r = 0.29*), pods/peduncle (r = 0.38**) and negatively correlated with days to first

ble 9. Phenotypic (P) and genotypic (G) correlations among yield characters of cowpea

		100-seed weight	Seeds/ pod	Pod length	Peduncle length	Pods/ plant	Peduncles/ plant	Pods/ peduncle	Days to first flowering	Days to maturity
ain yield/ ant	P	0.11	0.37**	0.36**	0.28*	0.63**	0.67**	0.07	0.18	0.18
	G	0.07	0.65**	0.47**	0.18	0.58**	0.65**	-0.09	0.46**	0.41**
0-seed ght	P		0.21	0.29*	-0.24	-0.05	0.09	-0.26*	0.33**	0.43**
	G		0.45**	0.50**	-0.93**	-0.22	0.27*	-0.99**	0.82**	0.92**
eds/ d	P			0.76**	-0.05	0.04	0.25*	-0.43**	0.59**	0.52**
	G			1.00**	-0.16	0.05	0.38**	-0.68**	0.76**	0.70**
d length	P				-0.12	0.06	0.23	-0.33**	0.49**	0.47**
	G				-0.23	-0.18	0.24	-0.87**	0.78**	0.66**
duncle ngth	P					0.41**	0.29*	0.38**	-0.47**	-0.55**
	G					0.48**	0.18	0.70**	-0.70**	-0.84**
ds/ ant	P						0.92**	0.40**	-0.02	-0.03
	G						0.92**	0.34**	0.08	0.02
duncles/ ant	P							0.06	0.18	0.15
	G							-0.02	0.52**	0.43**
ds/ duncle	P								-0.45**	-0.38**
	G								-0.90**	-0.88**
ys to t flower	P									0.76**
	G									1.00**
ys to turity	P									
	G									

* Significant at $P \leq 0.05$; ** Significant at $P \leq 0.01$.

flowering (r = -0.47**) and maturity (r = -0.55**). Number of pods per plant was highly correlated with number of peduncles per plant (r = 0.92**) and pods per peduncle (r = 0.40**). Number of pods per peduncle was negatively correlated with days to first flower (r = -0.45**) and maturity (r = -0.38**). A close phenotypic correlation existed between days to first flowering and days to maturity (r = 1.00**).

Positive genotypic correlations were present between grain yield/plant and seeds/pod (r = 0.65**), pod length (r = 0.47**), pods/plant (r = 0.58**), peduncles/plant (r = 0.65**), days to first flowering (r = 0.46**) and days to maturity (r = 0.41**). Significantly positive genotypic correlations existed between 100-seed weight and seeds/pod (r = 0.45**), pod length (r = 0.50**), peduncles/plant (r = 0.27*), days to first flower (r = 0.82**) and days to maturity (r = 0.92**), while 100-seed weight and peduncle length (r = -0.93**) and pods/peduncle (r = -0.99**) were negatively correlated. Seeds per pod was associated perfectly with pod length (r = 1.00**) and positively correlated with peduncles/plant (r = 0.38**), days to first flower (r = 0.76**) and days to maturity (r=0.70**). While seeds/pod and pods/peduncle had negative

association (r = -0.68**). Positive association were present for pod length and days to first flower (r = 0.78**) and days to maturity (r = 0.66**), while negative correlation existed between pod length and pods/peduncle (r = -0.87**). Peduncle length was found to be positively correlated with pods/plant (r = 0.48**) and pods/peduncle (r = 0.70**) but negatively correlated with days to first flowering (r = -0.70**) and days to maturity (r = -0.84**). Pods/plant was highly correlated with peduncles/plant (r = 0.92**) and pods/peduncle (r = 0.34**). Number of peduncles per plant was positively correlated with days to first flowering (r = 0.52**) and days to maturity (r = 0.43**). Number of pods/peduncle was highly and negatively correlated to both days to first flower (r = -0.90**) and days to maturity (r = -0.88**). Very high positive correlation was present between days to first flowering and days to maturity (r = 1.00**).

The results of path coefficient analysis at genotypic level are shown in Table 10. The highest direct effect was exhibited by number of seeds/pod (1.20) followed by number of pods/plant (0.79) and number of days to maturity (0.65). The direct effect exihibited by number of pods/peduncle (0.03) was negligible. All the other characters exhibited negative direct effects on

Table 10. Direct (underlined) and indirect effects of yield components on grain yield per plant in cowpe

Characters	100-seed weight	Seeds/ pod	Pod length	Peduncle length	Pods/ plant	Peduncles/ plant	Pods/ peduncle	Days to first flower-ing	Days to maturity	Genotyp correla with yi plant
100-seed weight	-0.28	0.54	-0.19	0.14	-0.17	-0.09	-0.03	-0.45	0.59	0.06
Seeds/pod	-0.13	1.20	-0.38	0.03	0.04	-0.13	-0.02	-0.41	0.45	0.65
Pod length	-0.14	1.20	-0.38	0.04	-0.14	-0.08	-0.02	-0.43	0.43	0.48
Peduncle length	0.26	-0.19	0.09	-0.15	0.38	-0.06	0.02	0.38	-0.54	0.19
Pods/plant	0.06	0.06	0.07	-0.07	0.79	-0.30	0.01	-0.04	0.01	0.59
Peduncles/plant	-0.08	0.46	-0.09	-0.03	0.72	-0.33	0.00	-0.28	0.28	0.65
Pods/peduncle	0.28	-0.82	0.33	-0.11	0.27	0.01	0.03	0.49	-0.57	-0.09
Days to first flowering	-0.23	0.91	-0.30	0.11	0.06	-0.17	-0.02	-0.55	0.65	0.46
Days to maturity	-0.26	0.84	-0.25	0.13	0.02	-0.14	-0.02	-0.55	0.65	0.42

yield. The pod length (-0.38), number of peduncles/ plant (-0.08) and number of days to first flower (-0.43), which had significant positive genotypic correlations with yield manifested negative direct effects. 100-seed weight which had a non-significant correlation with yield/plant, r = 0.07, exhibited a substantial negative direct effect (-0.281) on yield. The indirect effect of 100-seed weight through number of seeds/pod was positive and of a high magnitude, (0.54). Similarly the indirect effect via days to maturity was almost of the same magnitude (0.59). A strong negative influence (-0.45) was registered indirectly by number of days to first flowering through 100-seed weight. The net effect in this system of opposing influences was that the negative effects counter-balanced the positive ones, resulting in the overall correlation between 100-seed weight and grain yield essentially zero. The direct effect of pod length on grain yield/plant was negative and substantial (-0.38), but the indirect effect through number of seeds/Pod (1.20) was appreciable to cancel out the negative resulting in a positive correlation (r = 0.47**) between effects, pod length and grain yield/plant. Number of pods/ plant exhibited a strong positive direct effect on grain yield/plant (0.79) while all the indirect effects via

the other variables were non-significant except for the indirect effect *via* peduncles/plant (-0.30) which was sizeable and negative. The number of peduncles/plant had a negative direct effect on yield (-0.33) but the positive correlation (r = 0.65**) was mainly through indirect effects *via* pods/plant (0.72) and seeds/pod (0.46). The days to first flowering showed a strong positive association with yield (r =0.46**) but the direct effect was quite sizeable and negative (-0.55). This pointed out that, with other variables held constant, decreasing days to first flowering would increase grain yield/plant. However, the subtle indirect effects *via* seeds/pod, (0.91) and days to maturity (0.65) play a more important part to result in a positive association, (r = 0.46**) with grain yield/plant. Days to maturity showed a positive direct effect (0.65),on grain yield/plant. The indirect effect *via* seeds/pod was positive (0.84). The other indirect effects *via* days to first flowering (-0.55), 100-seed weight (-0.26) and pod length (-0.25) were negative resulting in a positive correlation (r = 0.41**) between days to maturity and grain yield per plant.

4.3. Inheritance of Resistance to Cowpea Aphid, Aphis craccivora

The data on segregation with respect to resistance and susceptibility in the five different sets of crosses are presented in Table 11. The local variety ICV 1, was a common susceptible parent in crosses 1 and 2 while the exotic variety, TVU 310, and the mutant variety, ICV 11, were the resistant parents in cross 1 and cross 2 respectively. All plants of ICV 1 were susceptible while all plants of TVU 310 and ICV 11 were resistant. All the F_1 progenies in both the crosses were resistant to A. craccivora. This indicated complete dominance of resistance over susceptibility. The segregation ratios in the F_2 generations of both crosses resulted in a ratio of 3 resistant to 1 susceptible, hence indicating that the resistance in both TVU 310 and ICV 11 is controlled by a single dominant gene (monogenic). This was further confirmed by the 1 resistant:1 susceptible ratio in the backcross generation, ICV 1 x F_1 (ICV 1 x ICV 11) of cross 2. It was therefore concluded from the two sets that the reaction of resistance to Aphis craccivora Koch, as found in parents TVU 310 and ICV 11, is controlled by a single pair of resistance genes.

All the parents involved in the other three

crosses were resistant to A. craccivora infestation. The F_1 progenies in all the three crosses were resistant. The F_2 progenies in cross 3 (ICV 10 x ICV1 11) and cross 4 (ICV 11 x TVU 310) showed a segregation ratio of 15 resistant to 1 susceptible. This indicated that the resistance genes in the parents of cross 3 and cross 4 were non-allelic. This showed that resistance in the materials studied was monogenic and dominant. All the F_2 plants in cross 5 (ICV 10 x TVU 310) were resistant and did not segretate. This indicated that resistance genes in parent ICV 10 and TVU 310 are same while the resistance gene in parent ICV 11 was different.

Table 11. Segregation ratios in cowpea for resistance to the cowpea aphid, Aphis craccivora Koch.

Cross/progeny	Number of plants		X^2	P	Remarks
	Resistant	Susceptible			
1. ICV1	-	23			
TVU310	23	-			
F_1	24	-			
F_2	112	43	0.099	0.80-0.95	Good fit to 3:1 ratio
2. I CV1	-	20			
I CV11	22	-			
F_1	21	-			
F_2	140	49	0.087	0.70-0.80	Good fit to 3:1 ratio
Back-cross	10	11	0.048	0.80-0.90	Good fit to 1:1 ratio
3. I CV10	29	-			
I CV11	24	-			
F_1	9	-			
F_2	179	12	0.00035	0.98-0.99	Good fit to 15:1 ratio
4. I CV11	21	-			
TVU310	20	-			
F_1	21	-			
F_2	73	7	0.853	0.30-0.50	Good fit to 15:1 ratio
5. I CV10	24	-			
I CV310	22	-			
F_1	20	-			
F_2	75	-	No segregation		

CHAPTER 5

DISCUSSION

Genetics of Yield Characters

The diallel-cross analysis given by Hayman (1954 b) and Jinks (1954) is based on the following assumptions: (1) diploid segregation, (2) no reciprocal differences, (3) no non-allelic interaction (i.e. no epistasis), (4) absence of multiple alleles, (5) homozygous parents and (6) no linkage. The following assumptions were valid in the present investigation: (1) diploid segregation, cowpea being a diploid species (2) no reciprocal differences so far reported in cowpea (Kheradnam et al., 1975) and (3) homozygous parents, self fertilized, true breeding lines were used in the study. The assumption of genic interactions could not, however, be fulfilled while the other assumptions were not tested. Hayman (1954 b) showed that the assumption of no multiple allelism was not important until the F_2.

The parental varieties for the study were selected on the basis of their differences in resistance or susceptibility to the cowpea aphid, Aphis craccivora Koch and agronomic characters. There were significant differences among genotypes for all the agronomic characters under study (Table 2) making the combining

ability analysis valid. Griffing (1956 b) emphasised that only when significant differences are established among the F_1 hybrids and the parents, is there need to proceed with combining ability analysis. According to Griffing (1956 b), in an analysis based on a fixed model, one is concerned with comparisons of combining abilities of the actual parents used in the experiment and with identification of superior combinations. Therefore, the results of this investigation, in the strict statistical sense, apply to these specific varieties. Some extrapolations of the findings to other varieties for cowpea breeding programmes may not be considered appropriate.

On the basis of the average parental and F_1 hybrid- performance, the variance estimates for combining abilities and the GCA and SCA effects, grain yield per plant exhibited almost equal additive and non-additive genetic variances, suggesting importance of both additive and non-additive gene action in the inheritance of grain yield in cowpea. These findings support the earlier reports by Singh and Jain (1972) and Lal et al. (1975) in cowpeas, and Gritton (1975) and Singh et al. (1980) in peas. However, Imrie and Bray (1983) reported grain yield/plant to be under additive gene control in cowpea, while Kumar and Agrawal (1981) reported a predominance of non-additive genetic variance in peas.

In a situation like this, where both additive and non-additive genetic variances are important, the most suitable breeding procedure would be one which mops up the additive genetic variance, maintaining heterozygosity at the same time. Therefore it could be desirable to follow recurrent selection by intermating the most desirable segregants alternately with selection. In the case of a self-fertilized crop like cowpea, a breeding procedure proposed by Jensen (1970), "Diallel selective mating system", can be employed. A recessive gene for male sterility has been reported in cowpea (Sen and Bhowal, 1961). Outcrossing can be induced by introducing such male sterility genes into a population undergoing recurrent selection. This would lead to an elevation of the genetic plateau, by the accumulation of the fixable additive genes and simultaneous exploitation of the dominance variance. Finally, high yielding homozygous lines could be extracted from such improved populations. The per se performance of the parents were in close agreement with their GCA effects, therefore the selection of parents based on parental mean values should be reasonably effective.

Crosses involving TVU 310 and ICV 11 resulted in some of the best F_1 progenies. The two parents were also the best general combiners. So that, for improving

the grain yield, recurrent selection from crosses involving these two varieties could be suggested. Special mention would be for the hybrid combinations, ICV 6 TVU 310, ICV 1 x TVU 310 and ICV 6 x ICV 11. These crosses indicated the best specific combining abilities. The crosses also indicated the high heterosis percentages observed for grain yield per plant. Singh and Jain (1972) and Gritton (1975) also reported heterosis for grain yield/plant.

The diallel analysis for 100-seed weight indicated that the GCA variance contributed predominantly towards the variability of the character. The ratio $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ of 0.63 indicated the importance of both additive and non-additive gene actions for this character. Lal et al. (1975) reported higher GCA mean squares and, Imrie and Bray (1983) also found higher additive variance for seed weight in cowpea. Similar findings were reported by Krarup and Davis (1970) in peas. Singh and Jain (1972) reported the importance of both additive and non-additive gene action for seed weight in cowpea. These reports are in agreement with the present findings. The improvement of seed weight should be based upon exploitation of both components of genetic variance. Breeding methods such as recurrent selection may increase the chances of recovering the desired

recombinations.

The variation in seed weight among the parents and their F_1 progenies was little so that most of the combining abilities were non-significant. However, the crosses ICV 6 x ICV 10 and ICV 11 x TVU 310 showed desirable specific combining abilities and therefore could be utilized in the breeding for larger seeds. Non-significant heterosis was observed over mid-parent for 100-seed weight in the experimental materials. However, significant heterosis have been reported by other workers (Britingham, 1950; Singh and Jain, 1972; and Kheradnam et al., 1975). This indicates that the genetic diversity between parents for seed size in the present study was not appreciable.

The significance of both GCA and SCA variances for number of seeds per pod suggested that both additive and non-additive gene effects were responsible in the manifestation of variability among the crosses. However, the variability attributed to additive gene effects $/\bar{}2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2) = 0.97$ and $r^2 = 0.92/$ was much greater than the non-additive gene effects. This indicated a preponderance of additive gene effects and agrees with the reports of Lal et al. (1975) in cowpeas and Gritton (1975) and Kumar and Agrawal (1981)

in peas. Aryeetey and Laing (1973) reported low heritability estimates indicating non-additive gene action as important in cowpeas. Singh and Jain (1972), and Imrie and Bray (1983) reported non-additive gene action in cowpeas while similar results were obtained by Mak and Yap (1980) in long bean, Vigna sesquipedalis. It is encouraging to note that the genetic variation for seeds/pod in this cowpea population was due mainly to additive gene effects which are fixable and therefore easily exploitable. The exploitation of additive gene effects could be by selecting superior segregants in the early generations and (or) by single plant selection. Hence, transgressive segregants for seeds/pod may be obtained in segregating generations of selected crosses. The parents ICV 10, ICV 11 and TVU 310 could be utilized in crosses with single plant selections in the following generations. The crosses ICV 11 x TVU 310, ICV 10 x TVU 310 and ICV 10 x ICV 11 should be the best hybrid combinations for future selections for seeds/pod.

The diallel analysis for pod length indicated GCA effects to be more important than SCA effects towards the variability. The r^2 value of 0.83 and $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ ratio of 0.94 confirmed the preponderance of additive gene effects in the

inheritance of pod length. This finding agreed with the earlier reports by Aryeetey and Laing (1973), Lal et al. (1975) and, Kumar and Agrawal (1981). However, Singh and Jain (1972) reported both GCA and SCA as important for pod length variability. This suggests that selection for long pods could be made more effective by exploiting the fixable additive gene effects. Since it is under additive gene effects, useful predictions could be made from the parental GCA values. ICV 10 and ICV 11 could be used in crosses for selecting progenies with long pods. The crosses, ICV 11 x TVU 310 and ICV 10 x ICV 11 could be used in breeding for longer pods. Heterosis for pod length was not observed in the experimental materials though Singh and Jain (1972) observed heterosis in the material they used.

The present study revealed that most of the genetic variance for the peduncle length was associated with GCA which was highly significant, though the SCA variance was also significant. The $2\hat{g}^2/(2\hat{g}^2 + \hat{s}^2)$ ratio of 0.83 and r^2 value of 0.53 confirmed the relative importance of additive gene effects. An examination of SCA and GCA effects showed parent ICV 1 as the best general combiner and the cross ICV 1 x ICV 6 the best specific combination. ICV 6

was a poor general combiner. The combination between high x low general combiner showing significant SCA, is usually likely to produce desirable transgressive segregants, if the additive genetic system present in the good combiner and the complementary epistatic effects in the F_1 act in the same direction to maximize the desirable attribute. The cross ICV 1 x ICV 6 also indicated appreciable heterosis (17.24%), thus, a good number of transgressive segregants might be expected in the segregating generations of this cross for selection.

The diallel analysis for number of pods per plant indicated both GCA and SCA variances to be significant implying both additive and non-additive genetic variances to be important. The r^2 value of 0.40 and the $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ ratio of 0.50 also confirmed that both additive and non-additive gene effects were equally important. Similar results for pod number per plant were reported by Imrie and Bray (1983). In a situation, where additive and non-additive genetic variances are significant, the most suitable breeding procedure would be by intermating the most desirable segregants, followed by a more intensive selection in advanced generations, hence accumulating favourable additive genes and exploiting

the non-additive variance simultaneously. The best general combiner TVU 310 was also involved in the best specific combination, ICV 6 x TVU 310. An ideal combination is one in whch a high degree of SCA is present in addition to a large parental GCA. Therefore, the combination ICV 6 x TVU 310 could be utilized in the recurrent selection for number of pods/plant in cowpea. High level of heterosis was also observed for the character in the cross combination ICV 6 x TVU 310 (87.54%).

The significant mean squares for both SCA and GCA for number of peduncles per plant suggested that both additive and non-additive gene effects were responsible in the genetic variation among the experimental materials in this study. This was confirmed by the ratio $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ being 0.66 and the r^2 value of 0.41. This contradicted the previous reports by Lal et al. (1975) who found additive gene variance as being more important while Imrie and Bray (1983) reported importance of non-additive gene action. To improve the number of peduncles/plant in the material used in this study, biparental matings followed by selection in the advanced generations would be advisable. The best specific combination was in the cross ICV 6 x TVU 310 involving high x low general combiners. Heterosis was highest for the cross ICV 6 x

TVU 310, which could be utilized for breeding for high number of peduncles per plant by selecting desirable transgressive segregants following the cross.

The number of pods per peduncle indicated the predominance of additive gene effects as compared to the non-additive gene effects. This agreed with the report of Lal et al. (1975). The additive gene effects could be exploited by early generation single plant selection, since the effects are fixable and easily exploitable. The best cross combination was ICV 6 x ICV 11 which also indicated a 15.31% heterosis.

The earliness characters as measured from days to first flowering and days to maturity also indicated significant GCA. The SCA variance was non-significant. The r^2 values were 0.84 and 0.89 respectively, while the ratios $2\bar{g}^2/(2\bar{g}^2 + \bar{s}^2)$ were 0.92 and 0.96 respectively for the two characters. These indicated that both earliness characters were predominantly under additive gene control. Similar results were obtained by Lal et al. (1975), and Watts et al. (1970) and Snoad and Arther (1973) in peas. The additive gene effects are fixable and could be exploited by selecting superior segregants in the early generations. Heterosis in both the characters was minimal. The crosses ICV 1 x ICV 10 and ICV 6 x ICV 10 were the best

combinations for earliness, though, non of them were earlier than ICV 1, the earliest maturing parent.

Correlations and Path-coefficient Analysis

To make the results more meaningful, phenotypic, genotypic and environmental correlations among grain yield/plant and its components were worked out. Grain yield/plant had positive and significant phenotypic correlations with number of seeds/pod, pods/plant, peduncles/plant, pod length and peduncle length. The other components showed little relationship with yield. This suggested that any of the five characters with strong positive correlation with yield could be used in selecting for improved grain yield per plant. Two of the characters, number of seeds per pod and pod length, had indicated the fixable additive gene effects to control their inheritance. Therefore by improving these two components, through early generation selection, yield would be expected to improve. Doku (1970) reported significant positive correlation between seed yield/plant and number of pods per plant. Singh and Mehndiratta (1969) reported positive correlations between grain yield and peduncles/plant, number of pods per plant, seeds per pod and 100-grain weight. In the present study the 100-seed weight was not

correlated to yield. Similarly no correlation was observed for days to first flowering and days to maturity at the phenotypic level. Singh and Mehndiratta (1969) also reported no correlation for days to flowering and maturity with yield. Hence, it should be possible to select for high grain yield and earliness in cowpea. The close phenotypic correlation found between the days to first flowering and days to maturity indicated that first flowering can be used as a reliable measure of maturity in cowpea. Similar observation was made by Singh and Mehndiratta (1969) and Tikka et al. (1980). Association between pod length and seeds/pod was positive and high, indicating that longer pods tend to produce more seeds. A 100-seed weight in the longer pods was also more as shown by significant positive correlation between this character and pod length.

Phenotypic and genotypic correlation coefficients agreed very closely in most instances. This similarity was probably due to the replications which tended to reduce the error (environmental) variance to minor proportions. Had the environmental variance and covariance been reduced to zero, the phenotypic and genotypic correlation coefficients would of necessity be identical. Thus, the genotypic correlations between

grain yield per plant and seeds per pod, pod length, pods per plant and peduncles per plant were positive and significant. The genotypic correlations of Aryeetey (1973) were also strong and positive for grain yield/plant with pod length and seeds/pod. Components of yield are significantly influenced by the environmental flunctuations resulting in interactions which contribute to "genetic slippage" in selection for quantitative characters (Tikka et al. 1980). It could therefore be important to study the extent of correlations between yield and component characters under varying environmental conditions. However, it is often difficult and/or expensive to obtain enough F_1 seed, in self-pollinated crops like cowpea, to provide enough environment replicates. It is suggested that a study under different cowpea growing environmental conditions would be most appropriate.

According to Dewey and Lu (1959), when more variables are included in the correlation table, indirect associations among them become more complex. Path-coefficient analysis provides a means of finding the direct and indirect causes of association, and to determine the relative contributions of direct and indirect effects of the independent variables on the

dependent variable. The major components of yield seemed to be number of seeds per pod, and number of pods per plant. The former gave the highest direct effect on yield (1.20). Pod length which had shown significant positive genotypic correlation with yield gave negative direct effect. Similar results were observed by Singh and Mehndiratta (1970) and Tikka et al. (1980). The indirect effect of pod length through number of seeds per pod (1.20) was mainly responsible for its positive correlation with yield. A strong negative influence (-0.82) was registered indirectly by number of pods per peduncle upon grain yield per plant through number of seeds per pod due to the fact that the pods per peduncle were negatively correlated (r = -0.68**) with seeds per pod, which in turn had a large direct effect (1.20) upon seed yield. An examination of the correlation components reveals that number of seeds per pod and pods per plant were the two factors that exerted the greatest influence directly upon grain yield, whereas pod length had a negative direct influence. This analysis gives a somewhat different picture than does the simple correlation analysis. For example, the correlation between pod length and grain yield was positive and significant (r = 0.36**). The apparent

conflict between the two analyses arises largely due to the fact that the two methods measure different things. According to Dewey and Lu (1959), whereas correlation simply measures mutual association without regarded to causation, the path-coefficient analysis specifies the causes and measures their relative importance. The appreciable direct effects on seed yield by number of pods/plant and seeds/pod agreed with the report of Singh and Mehndiratta (1970). Chandel (1983), in peas, reported pods/plant to have appreciable direct and indirect effects on seed yield, but seeds/pod and 100-seed weight had small direct contribution to grain yield. The results therefore revealed that among, yield components considered under the study, emphasis in selection should be placed on number of seeds/pod and number of pods/plant. Pod length, though manifesting a negative direct effect on grain yield could still be used due to its indirect appreciable contribution via number of seeds/pod.

Inheritance of resistance to cowpea aphid (Aphis craccivora)

The two crosses, ICV 1 x TVU 310 and ICV 1 x ICV 11 involved the common susceptible parent ICV 1, and resistant parents, TVU 310 and ICV 11 respectively.

The F_1 in both crosses showed complete dominance of resistance over susceptibility. The F_2 ratio of 3 resistant:1 susceptible in both crosses suggested that the resistance to aphid is governed by a single pair of dominant genes. The segregation ratio of 1 resistant:1 susceptible in the backcross, F_1 (ICV 1 x ICV 11) to susceptible parent ICV 1, confirmed the monogenic inheritance.

To determine whether the resistance genes in three resistant parents, TVU 310, ICV 10 and ICV 11, were same or different, crosses were made among them. The F_2 seedling reaction in two crosses, namely, ICV 10 x ICV 11 and ICV 11 x TVU 310, resulted into a ratio of 15 resistant: 1 susceptible suggesting that the two resistance genes were different. All F_2 seedlings of the cross ICV 10 x TVU 310 were resistant indicating that the resistance genes in the parents ICV 10 and TVU 310 were same. It was therefore evident that the resistance gene in parent ICV 11 was different from that in ICV 10 or TVU 310. The resistance gene in ICV 10 and TVU 310 was designated as Ac_1 (i.e. Aphis craccivora dominant gene for resistance, number one) while the mutant parent, ICV 11 had the resistance gene Ac_2.

The resistance gene, Ac_2, found in ICV 11 appears to be a result of induced mutation in the

susceptible variety ICV 1 (gene ac_2) (Pathak, 1983), and was therefore non-allelic to the resistance gene, Ac_1, as found in varieties ICV 10 and TVU 310. Thus the genetic condition of resistant parents ICV 10 and TVU 310 may be symbolized as Ac_1 Ac_1 ac_2 ac_2 and that of the mutant parent, ICV 11, as ac_1 ac_1 Ac_2 Ac_2. The genotype of the susceptible parent, ICV 1, can be designated as ac_1 ac_1 ac_2 ac_2. The two dominant genes may be duplicate, confering the same level of resistance. Presence of a single or both dominant genes either in homozygous or heterozygous condition is essential for complete resistance to aphids, but both genes when homozygous recessive make the plant susceptible. The dominant genes may be with additive effects. Classification of the aphid intensity was not performed among the segregating F_2 population ratio of 15 resistant: 1 susceptible in this study. The resistance with a digenic inheritance was suggested to be desirable where the resistance genes are known to be additive in their effects (Russell, 1981).

In the previous studies the resistance to A. craccivora was reported to be governed by one dominant gene. In five crosses, Anon (1982) suggested one dominant gene for resistance. Similarly, Pathak (1984, 1985) identified a single dominant gene for

resistance in TVU 310 and two mutant varieties, ICV 11 and ICV 12. Kishaba et al. (1971) and Bohn et al. (1973) reported the resistance to melon aphid (Aphis gosypii) in muskmelon, was controlled by a single dominant gene which they designated Ag. Glover and Stanford (1966) reported one dominant gene as confering resistance to pea aphids (Acyrthosiphon pisum) in alfalfa. Manglitz and Gorz (1968) in studies of resistance to sweetclover aphid (Theriaphis riehmi) in sweetclover, reported a single dominant gene responsible and a complementary gene in some resistant lines. It appears from the literature that most of the resistance to aphids in various crops, apparently, is governed by a single pair of dominant genes for resistance. Insect pests are capable of evolving biotypes to overcome the resistance. Three biotypes of A. craccivora have been reported to be occurring, biotypes A and B in Nigeria, and biotype K in Upper Volta (IITA Research Highlights, 1981). Fine differences in resistance are, therefore, occurring in the different cultivars of cowpeas, as tests for identifying the biotypes implied.

Among the materials used in the present study, either of the resistance in the varieties ICV 10, TVU 310 or ICV 11 could be utilized in a breeding

programmė to incorporate resistance to the local popular varieties with acceptable agronomical characters. The most appropriate breeding technique for transferring the resistance would be the back-cross pedigree (Allard, 1960).

CONCLUSIONS

The data in the present study indicated both additive and non-additive gene effects to be responsible in the manifestation of variability in grain yield per plant, 100-seed weight, peduncle length, number of pods per plant and peduncles per plant, though the magnitude of additive gene variance was greater for 100-seed weight and peduncle length. Number of seeds per pod, pods per peduncle, days to first flower and days to maturity were predominantly under additive gene action.

Among the parental materials, TVU 310 appeared to be promising for use in breeding programme aimed at improving grain yield, since it had the highest general combining ability. The variety also had high general combining values for number of seeds per pod and pods per plant, which were associated positively with grain yield per plant. The crosses, ICV 6 x TVU 310, ICV 6 x ICV 11 and ICV 1 x TVU 310, which indicated high specific combining ability estimates for grain yield per plant, could be utilized in a selection programme for grain yield.

Important positive correlations were observed between grain yield per plant and number of seeds per

pod, pod length, pods per plant and peduncles per plant. Direct effects in the Path-coefficient analysis for number of seeds per pod and pods per plant were considerable. Indirect effect of number of pods per plant on grain yield per plant through seeds per pod was positive and considerable. The three characters, number of seeds per pod, pods per plant and pod length could be used reliably as selection criteria for grain yield in a cowpea improvement programme.

Based on seedling stage survival (resistance) or death (susceptibility) from aphid infestation, two resistance genes, Ac_1 and Ac_2, both dominant were found; the gene Ac_1 in the varieties ICV 10 and TVU 310, and the gene Ac_2 in the mutant variety, ICV 11. The two non-allelic genes may be located either in the same chromosome distant apart or in different chromosomes.

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A P P E N D I X

Appendix : Replications Data for Yield and its Components in Cowpea.

a. Grain yield per plant (g)

Progeny	Replication				
	I	II	III	IV	Totals
ICV1	31.83	35.91	31.11	28.64	127.49
ICV6	29.67	23.32	28.24	19.52	100.75
ICV10	39.36	64.52	55.51	52.73	212.12
ICV11	62.87	47.99	57.06	40.48	208.40
TVU310	59.78	68.24	58.98	51.10	238.10
ICV1 x ICV6	20.84	46.11	68.57	51.61	187.13
ICV1 x ICV10	31.79	76.59	49.89	43.08	201.35
ICV1 x ICVII	69.62	56.15	38.32	82.82	246.91
ICV1 x TVU310	52.29	72.19	60.04	93.64	278.16
ICV6 x ICV10	41.79	50.36	35.07	62.93	190.15
ICV6 x ICV11	72.57	59.93	85.37	38.23	256.10
ICV6 x TVU310	50.86	71.33	61.61	101.86	285.66
ICV10 x ICV11	56.88	53.08	44.16	66.86	220.98
ICV10 x TVU310	52.85	61.63	63.24	54.03	231.75
ICV11 x TVU310	90.26	58.27	72.74	47.09	268.36
Totals	763.26	845.62	809.91	834.62	3253.41

b. 100-Seed weight (g)

Progeny	Replication				
	I	II	III	IV	Totals
ICV1	11.25	11.99	11.21	11.18	45.63
ICV6	12.74	12.19	13.34	11.91	50.18
ICV10	12.06	12.21	11.88	11.91	48.06
ICV11	12.23	11.85	12.49	11.91	48.48
TVU310	13.01	12.88	12.49	12.31	50.69
1CV1 x ICV6	11.66	12.25	11.96	12.02	47.89
ICV1 x ICV10	11.72	12.77	11.90	11.48	47.87
ICV1 x ICV11	11.38	12.63	11.87	12.15	48.03
ICV1 x TVU310	11.39	12.23	12.05	13.33	49.00
ICV6 x ICV10	14.64	11.85	12.17	12.86	51.52
ICV6 x ICV11	10.06	11.98	11.93	12.11	46.08
ICV6 x TVU310	11.66	13.29	12.29	12.23	49.47
ICV10 x ICV11	12.94	13.26	12.44	12.40	51.40
ICV10 x TVU310	12.08	12.93	12.25	11.86	49.12
ICV11 x TVU310	13.07	13.03	13.11	12.46	51.67
Totals	181.89	187.70	183.38	182.12	735.09

c. Number of seeds per pod

Progeny	Replication				
	I	II	II	IV	Totals
ICV1	14.64	13.96	13.80	12.08	54.48
ICV6	15.04	15.08	14.64	13.28	58.04
ICV10	19.24	18.76	19.04	19.36	76.40
ICV11	19.32	18.88	18.20	18.00	74.40
TVU310	18.10	17.44	18.16	16.76	70.46
ICV1 x ICV6	13.45	14.33	14.60	13.70	56.08
ICV1 x ICV10	16.27	15.20	15.90	15.00	62.37
ICV1 x ICV11	16.64	16.20	17.32	14.80	64.96
ICV1x TVU310	15.70	15.75	15.07	14.73	61.25
ICV6 x ICV10	15.72	14.73	15.20	15.20	60.85
ICV6 x ICV11	17.35	16.87	17.30	15.90	67.42
ICV6 x TVU310	15.96	16.68	15.96	16.12	64.72
ICV10 x ICV11	19.15	17.47	17.93	18.40	72.95
ICV10 x TVU310	18.92	16.35	18.65	18.72	72.64
ICV11 x TVU310	19.20	18.70	18.50	18.24	74.64
Totals	254.70	246.40	250.27	240.29	991.66

d. Pod length (cm)

Progeny	Replication				
	I	II	III	IV	Totals
ICV1	15.48	16.70	16.05	15.24	63.47
ICV6	17.46	17.18	17.94	13.72	66.30
ICV10	19.21	20.14	19.34	19.26	77.95
ICV11	20.38	19.72	19.68	19.04	78.82
TVU310	18.56	17.73	18.58	17.77	72.64
ICV1 x ICV6	15.98	16.53	16.33	15.75	64.59
ICV1 x ICV10	17.81	17.83	18.45	16.58	70.67
ICV1 x ICV11	17.92	18.37	12.34	17.13	65.76
ICV1 x TVU310	16.77	17.85	17.42	16.33	68.37
ICV6 x ICV10	17.10	16.77	18.38	17.15	69.40
ICV6 x ICV11	17.53	18.13	17.90	17.50	71.06
ICV6 x TVU310	17.39	17.97	17.56	17.41	70.33
ICV10 x ICV11	20.14	18.73	18.51	19.04	76.42
ICV10 x TVU310	18.60	18.79	18.90	18.12	74.41
ICV11 x TVU310	20.01	19.33	19.69	18.46	77.49
Totals	270.34	271.77	267.07	258.50	1067.68

e. Peduncle length (cm)

Progeny	Replication				
	I	II	II	IV	Totals
ICV1	49.54	46.62	49.52	43.96	189.64
ICV6	31.36	33.48	33.34	38.41	136.59
ICV10	41.71	42.45	46.80	46.34	177.30
ICV11	48.43	41.16	42.78	45.62	177.99
TVU310	38.76	39.25	37.42	36.55	151.98
ICV1 x ICV6	45.09	45.31	50.71	50.17	191.28
ICV1 x ICV10	50.75	45.15	50.17	38.37	184.44
ICV1 x ICV11	50.10	45.49	50.83	50.44	196.86
ICV1 x TVU310	40.93	40.01	44.30	48.70	173.94
ICV6 x ICV10	41.63	37.76	41.27	44.76	165.42
ICV6 x ICV11	45.49	44.04	44.69	38.80	173.02
ICV6 x TVU310	39.28	43.94	44.04	44.67	171.93
ICV10 x ICV11	48.10	38.52	39.50	43.09	169.21
ICV10 x TVU310	43.52	42.03	43.06	39.98	168.59
ICV11 x TVU310	45.52	44.94	42.80	38.62	171.88
Totals	660.21	630.15	661.23	648.48	2600.07

f. Number of pods per plant

Progeny	Replication				
	I	II	III	IV	Totals
ICV1	34.60	32.40	30.20	32.60	129.80
ICV6	21.00	19.60	20.40	16.80	77.80
ICV10	25.40	37.60	35.80	30.20	129.00
ICV11	37.40	31.20	46.25	27.20	142.05
TVU310	43.00	45.80	36.60	35.00	160.40
ICV1 x ICV6	21.25	39.67	60.00	45.25	166.17
ICV1 x ICV10	28.67	55.00	37.75	36.50	157.92
ICV1 x ICV11	59.20	42.32	33.00	61.67	196.19
ICV1 x TVU310	45.75	53.50	47.00	56.67	202.92
ICV6 x ICV10	32.00	49.00	25.67	40.00	146.67
ICV6 x ICV11	63.25	43.00	51.00	26.00	183.25
ICV6 x TVU310	38.80	56.20	57.60	70.80	223.40
ICV10 x ICV11	34.75	29.00	25.33	39.20	128.28
ICV10 x TVU310	43.20	46.75	39.75	33.80	163.50
ICV11 x TVU310	61.25	36.25	41.50	31.20	170.20
Totals	589.52	617.29	587.85	582.89	2377.55

g. Number of peduncles per plant

Progeny	Replication				
	I	II	III	IV	Totals
ICV1	20.40	16.60	16.60	17.40	71.00
ICV6	16.20	12.80	11.80	12.00	52.80
ICV10	17.40	25.60	27.60	23.00	93.60
ICV11	20.80	21.00	24.50	24.20	90.50
TVU310	31.75	30.80	25.40	21.20	109.15
ICV1 x ICV6	12.50	22.67	33.33	24.75	93.25
ICV1 x ICV10	17.00	28.67	25.50	22.75	93.92
ICV1 x ICV11	32.20	22.33	19.40	34.33	108.26
ICV1 x TVU310	29.00	28.50	29.33	33.00	119.83
ICV6 x ICV10	21.20	29.67	17.00	26.50	94.37
ICV6 x ICV11	32.50	21.33	32.50	17.00	103.33
ICV6 x TVU310	26.20	35.40	39.80	39.75	141.15
ICV10 x ICV11	25.50	19.67	21.67	25.80	92.64
ICV10 x TVU310	29.20	27.00	25.25	24.60	106.05
ICV11 x TVU310	38.75	24.25	27.75	22.20	112.95
Totals	370.60	366.29	377.43	368.48	1482.80

mber of pods per peduncle

y	Replication				
	I	II	III	IV	Totals
	1.70	1.95	1.82	1.87	7.34
	1.30	1.53	1.73	1.40	5.96
	1.46	1.47	1.30	1.31	5.54
	1.80	1.49	1.89	1.12	6.30
	1.35	1.49	1.44	1.65	5.93
ICV6	1.70	1.75	1.80	1.83	7.08
ICV10	1.69	1.92	1.48	1.60	6.69
ICV11	1.84	1.90	1.70	1.80	7.24
TVU310	1.58	1.88	1.60	1.72	6.78
ICV10	1.51	1.65	1.51	1.51	6.18
ICV11	1.95	2.02	1.57	1.53	7.07
TVU310	1.48	1.59	1.45	1.78	6.30
x ICV11	1.36	1.47	1.17	1.52	5.52
x TVU310	1.48	1.73	1.57	1.37	6.15
x TVU310	1.58	1.50	1.50	1.41	5.99
	23.78	25.34	23.54	23.42	96.07

Number of days to first flowering

eny	Replication				
	I	II	III	IV	Totals
	40.00	39.00	41.00	40.00	160.00
	43.00	44.00	43.00	43.00	173.00
	45.00	45.00	45.00	45.00	180.00
	41.00	42.00	47.00	42.00	172.00
0	44.00	44.00	48.00	45.00	181.00
x ICV6	38.00	40.00	41.00	42.00	161.00
x ICV10	41.00	39.00	42.00	41.00	163.00
x ICV11	39.00	42.00	41.00	42.00	164.00
x TVU310	46.00	44.00	42.00	44.00	176.00
x ICV10	43.00	40.00	43.00	43.00	169.00
x ICV11	43.00	40.00	42.00	44.00	169.00
x TVU310	45.00	44.00	44.00	44.00	177.00
x ICV11	43.00	44.00	44.00	44.00	175.00
x TVU310	45.00	42.00	45.00	46.00	178.00
x TVU310	43.00	45.00	45.00	44.00	177.00
s	639.00	653.00	653.00	649.00	2575.00

j. Number of days to maturity

Progeny	Replication				
	I	II	III	IV	Totals
ICV1	59.40	60.80	62.20	62.20	244.60
ICV6	67.75	68.60	69.40	65.60	271.35
ICV10	66.20	67.20	66.80	67.40	267.60
ICV11	66.40	65.80	68.40	63.40	264.00
TVU310	70.25	68.60	71.20	68.80	278.85
ICV1 x ICV6	63.50	61.33	63.00	64.00	251.83
ICV1 X ICV10	64.00	62.67	65.00	64.50	256.17
ICV1 x ICV11	62.20	66.67	64.60	64.33	257.80
ICV1 x TVU310	66.25	65.40	65.67	67.00	264.32
ICV6 x ICV10	65.60	64.67	66.00	65.33	261.60
ICV6 x ICV11	66.00	64.33	65.67	66.75	262.75
ICV6 x TVU310	68.40	66.60	67.20	67.00	269.20
ICV10 x ICV11	66.00	66.33	67.00	66.60	265.93
ICV10 x TVU310	68.20	68.00	68.25	68.00	272.45
ICV11 xTVU 310	68.75	69.50	68.00	67.20	273.45
Totals	988.90	986.50	998.39	988.11	3961.90