INHERITANCE OF PROTEIN IN COWPEA (*VIGNA UNGUICULATA* (L.) WALP) AND ITS CORRELATION WITH YIELD AND YIELD COMPONENTS

BY

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DECLARATION

I hereby declare that this thesis was written by me and is a record of my own research work. It has not been presented before in any previous application for a higher degree. References made to published and unpblished literature have been duly acknowledged.

SULEIMAN DANGANA ABDUL — 9/5/90 Date

The above declaration is confirmed.

Professor I. Samarawira
Chairman,
Supervisory Committee — 11th May 1990 Date

DEDICATION

This work is dedicated

To the malnourished, the world over.

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ABSTRACT

Three cowpea (*vigna unguiculata* (L.) walp) lines were selected based on their per cent crude protein and used as parents in crosses in the following combinations: 2/180—4—12 (High) x 11/48-2 (Low); 2/180-4-12 (High) x L—25 (Low) *and* 11/48-2 (Low) x L—25 (Low). In the first cross the -following generations were obtained in addition to the parentals, reciprocal F_1's, reciprocal backcrosses and F_2. In the remaining two crosses only the reciprocal F_1's and F_2 populations were obtained in addition to the parentals,

The F_1 means per cent crude protein content were either closer to or lower than the low protein parent, thus indicating partial dominance to overdominance of low protein over high, No significant difference was observed between reciprocal F_1's, indicating the absence of maternal effects. The F_2 distributions for per cent protein were normal suggesting the involvement of multiple genes, thus supporting the estimates of three major genes with possible modifiers.

Broadsense heritabiiity estimates ranged from 40.7% in the cross low *x* low to 73.4% in the crosses high x low. Narrowsense heritabiiity estimates ranged from 26.8% to 40.3%. These estimates indicate considerable? genetic influence some of which were additive,

In all crosses, negative phenotypic and genotypic correlations predominated for yield, number of seeds/pod and number of days to flowering with per cent protein, Signific-ant negative phenotypic correlations were obtained between number of pods/plant and per cent protein, while 100—seed

weight showed mostly positive phenotypic and genotypic correlations with per cent protein. Positive correlations predominated between days to maturity and per cent protein. Some high yielding segregant had high protein percentage, suggesting that high yield and high protein percentage can be combined into a suitable genotype most especially with the weak negative correlation between these characters.

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CHAPTER ONE

1. INTRODUCTION

Cowpea (*Vigna unguiculata*) (L.) Walp) as a leguminous crop serves as one of the sources of cheap plant protein in the tropics. About 8 million hectares of land is devoted to cowpea cultivation with an estimated production of 2.27 million tonnes worldwide, two-third of which is from Africa, Nigeria being the leading poducer country (Rachie, 1981). Cowpea is eaten in the form of dry seeds, green pods, green seeds and tender green leaves. It is also utilised for fodder and quick-growing cover crop. The crop also has the ability to fix atmospheric nitrogen in the soil.

The major problem of cowpea production in the tropics is its characteristic low yield ranging from 240 to 300 kg/ha. This is attributed to heavy biotic pressure (insect pests and diseases), poor cultural practices on poor soils, excessively high temperature, drought or excess moisture. However, with good management yield as high as 1.5 tonnes/ha has been reported (I.A.R, 1989).

Cowpea seeds have considerably high per cent protein averaging 23 on dry weight basis and ranges between 19-35 per cent (Summerfield *et al*. 1974). This provides enough variability to allow for improvement of this character through breeding.

Cowpea protein is generally lacking in sulphur-amino acid (i.e. methionine and cystine). However its relatively high lysine content renders its use

complementary to cereals (which are generally low in lysine, but contain adequate amount of sulphur-amino acids) and, indeed in the case of tuber based diet, grain legumes may provide virtually the sole source of available protein (Bressani, 1973).

Inspite of the fact that animal protein is of high quality containing amino-acids in the correct proportions to more than satisfy human needs, in the tropics it is however costly and relatively scarce compared to cowpea crude protein that is cheap, transportable and highly digestable. Cowpea seeds also contribute significant amount of iron, nicotinamide, thiamine, and calcium to the local diet in tropical regions (Platt, 1962), and with suitable amino-acid supplements it is possible to raise its biological value to 95 per cent of that of egg albumin (Boulter *et al.*, 1973). Antinutritional factors in cowpea such as trypsin and chymotrypsin enzyme inhibitors are denatured by heat during cooking (Owusu-Domfeh, 1972).

Since protein analyses are time consuming and expensive, selection of plants with desirable protein content would be enhanced greatly if a significant relationship exist between protein content and some other easily identified characters.

The objectives of this study are to determine the inheritance of per cent protein in cowpea and its correlation (both genotypic and phenotypic) with yield and yield components in segregating populations.

CHAPTER TWO

2. LITERATURE REVIEW

2.1 Variability, Segregation and Mode of Gene Action of Per cent Crude Protein in Pulses

The success of any breeding programme depends on the presence of a significant range of variability in the trait(s) under consideration for improvement. In pulses several workers have identified variability in the seed protein content. Conducting variety trails over locations with chickpea (*Cicer arietinum*), dry beans (*Phaseolus vulgaris*), mungbean (*Vigna radiata*), lentils (*Lens esculenta*) and cowpea(*Vigna unguiculata*) Amirshahi and Tavakoli (1970) observed differences in per cent protein content between varieties in all the species mentioned, and differences within variety in different locations, showing the effect of the environment on protein content of the crops. Other workers also observed variability in seed protein content of dry bean (de Moraes and Angelucci, 1971; Leleji *et al.*, 1972; Kelly and Bliss, 1975; Mutschler and Bliss, 1981), chickpea, (Sandhu *et al.* 1974), pea, *Pisum sativum* (Quednau and Wolf, 1978), mungbean (Yohe and Poehlman, 1972 and Sandhu *et al.*, 1979), field bean, *Vicia faba* (Froblich *et al.*, 1974) and soyabean, *Glycine max* (Hymowitz *et al.*, 1972). Similarly, Bliss *et al.* (1973) working on some cultivars of cowpea observed significant genetic variability for per cent protein despite the small

number of cultivars assessed, and they came to the conclusion that sufficient variability exists to allow for considerable progress during selection in segregating populations. Although this might be vitiated by the significant genotype x environment interaction they equally observed.

In every genetic study the pattern of segregation in the F_2 population and the relationship among the parentals, F_1 and F_2 generation means give an insight into the genetic architecture of the character under consideration. In a cross between wild (high protein parent) and domesticated (low protein parent) soyabeans, Weber (1950) concluded that high protein is partially dominant to low protein. This observation was corroborated by Johnson *et al.* (1955a) while working on the same crop. Weber (1950) also reported transgressive segregation for high protein in F_2. In another cross between high and low protein parents of dry bean, Leleji *et al.* (1972) and Kelly and Bliss (1975) observed a slight partial dominance of low protein over high protein, contrary to the observation in soyabean. Mak and Yap (1980) concluded that protein content was controlled by dominance to overdominance genes in *Vigna sesquipedalis*, with high protein associated with recessive genes and high yielding parents carrying more of dominant genes. Singh *et al.* (1980) similarly reported overdominance in the control of protein content of chickpea.

Dahiya *et al.* (1976) and Leleji *et al.* (1972) observed maternal influence on protein

content in the F_1 hybrid of pigeon pea, (*Cajanus cajan*) and dry bean, respectively.

Although relatively few information is available regarding the minimum number of genes controlling per cent protein in pulses, the few estimates from different crops using various methods were at par Leleji *et al.* (1972) using the Castle-Wright (1921) equation reported between 2.0 to 3.5 genes in *Phaseolus vulgaris* crosses. In 1950, Weber equally using a modified Castel-Wright equation in soyabean calculated gene number ranging from 1 in the backcross to the low protein parent to 3 in the reciprocal backcross and 2.9 using the F_2 population.

2.2 Heritability Estimate for Percent Protein in Pulses

Many practical decisions in breeding programmes are based on the amount of heritable variation, since it serves as a measure of the degree to which a phenotype is genetically influenced. Heritability estimates and their predictive roles in selection in pulses have been reported by several workers. In soyabean, Thorne and Fehr (1970) reported broadsense heritability estimates of between 0.81-0.959 for per cent protein in the F_4 and F_5 populations of a 2-, and 3-way sets of crosses, respectively. Leleji *et al.* (1972) obtained broadsense heritability estimates of between 0.307 to 0.635 in dry bean crosses. The additive or average genetic variance expressed as a ratio (or percentage) of the total variance, estimates heritability in the narrowsense. Leleji *et al.* (1972) reported heritability estimates in the narrowsense of 0.201 based on

analysis using backcross generations and 0.05 to 0.12 based on Parent-Offspring regression analysis using F_2 and F_3 generations in the same crop. Mustchler and Bliss (1981) also working on *Phaseolus vulgaris* reported broadsense heritability estimates of 0.19 to 0.65 and narrowsense estimates (using standard units method) of between 0.59 to 0.86 by regressing the F_3 progenies on the F_2 parents (F_3/F_2). Still on the same crop Kelly and Bliss (1975) reported broadsense heritability estimates of between 0.16 to 0.72 and narrowsense estimates of 0.32 to 0.79 based on the regression (using standard unit method) of the F_4 and F_3 offsprings on their F_3 and F_2 parents, respectively.

In long bean, Mak and Yap (1980) reported a narrowsense heritability estimate of 0.18 in a diallel cross. Sandhu *et al.* (1968) and Sandhu *et al.* (1974)) reported broadsense heritability estimate for per cent protein of 0.75 and 0.70 respectively in chickpea. Green *et al.* (1977) while working on lupins (*Lupinus albus*) obtained a broadsense heritability estimate of 0.83 in the F_3 families. The available broadsense heritability estimate of 0.39 on cowpea was that reported by Bliss *et al.* (1973) while working with pure line cultivars.

On the whole broadsense and narrowsense heritability estimates averaged 0.536 and 0.48, respectively. Thus suggesting that gene action is predominantly additive. Most of the narrowsense heritability estimates quoted above were based on

parent-offspring regression analysis, which is likely to be an overestimation, since some dominance variance may be present with the additive variance in the numerator of the variance ratio (Frey and Horner, 1957). One other limitation is that the above averages were obtained from estimates using different crops. Mak and Yap (1980) observed that both additive and non-additive gene effects control protein in long bean. Similarly Sandhu *et al.* (1974) observed highly significant general combining ability (gca) and specific combining ability (SCA) effects in both F_1 and F_2 populations for per cent protein in chickpea. This observation supports the presence of both additive and non-additive genetic control of per cent protein. Singh *et al.* (1980) while working on the same crop concluded that the magnitude of specific combining ability variance was higher than general combining ability variance, which indicated preponderance of non-additive gene action in the control of protein content.

Significant genotype x environment interaction were reported in cowpea (Bliss *et al.*, 1973) and chickpea (Sandhu *et al.*, 1974) for per cent protein while evaluating different cultivars of the crops. Contrary to this observation, was that made by Green *et al.* (1977) while working on lipins. They grew some lines in two contrasting environments that significantly affected the mean values but showed no significant variety x environment interaction.

2.3 Correlation of Protein with Yield and Yield Components in Pulses

Grain protein analyses are time consuming and expensive. Therefore, if the relationship between this highly desirable character and some other easily identifiable yield components can be established, it will go a long way in enhancing breeding plans for its simultaneous improvement with yield. Correlated variation of two characters may be as a result of similar genetic cause (genotypic correlation) or similar response to environmental influence (phenotypic correlation).

Several reports are available on the relationship between the two important attributes of pulses, yield and per cent protein. In a review by Brim (1973) on series of studies on soyabean, phenotypic and genotypic correlations between yield and protein ranged from 0.22 to -0.42 and 0.35 to -0.58, respectively. However, negative correlations predominated for both the phenotypic and genotypic correlations. These studies reported by Brim (1973) dealt with F_3 or more advanced generations replicated over locations and years, and were therefore more reliable. Simpson, Jr. and Wilcox (1983) also observed large and variable genotypic correlation coefficients of 0.54 to -0.074 in different crosses of soyabean with negative values predominating. Leleji *et al.* (1972) observed both negative as well as positive correlations of yield with per cent protein in dry beans, (ranging from 0.044 to -0.446), but only negative values were statistically significant. Using F_4 generations, Kelly and

Bliss (1975) observed a significantly negative correlation of -0.30 between seed yield and percentage protein in dry bean. They concluded that although the correlation was significant it was small enough to allow for incorporation of high percentage protein in genotype with substantial yields. Pandey and Gritton (1975) working on pea observed both phenotypic and genotypic correlations of 0.02 to -0.34 and 0.22 to -0.49 in F_2 population. Similarly, in the F4 population they obtained 0.14 to -0.35 and 0.19 to -0.57 as the phenotypic and genotypic correlations, respectively. In the F_2 population only negative estimates were significant but a significant positive estimate was observed in the F_4 population of a cross between medium and low protein parents. Green *et al.* (1977) reported significant estimates of -0.36 and -0.53 as the phenotypic and genotypic correlations in lupins using F_2 populations. Griffiths and Lawes (1978) working on *Vicia faba* observed a non-significant correlation between seed yield and protein content, and Sandhu *et al.* (1979) observed no association between the two ccharacters in mungbean. Phenotypic and genotypic correlations of -0.14 and -0.38, respectively were reported in cowpea by Bliss *et al.* (1973) while evaluating some cultivars at different locations. In general inverse relationship between yield and protein percentage predominate, although mostly low in magnitude.

In soyabean crosses Simpson Jr. and Wilcox (1983) reported significant phenotypic correlation

coefficients ranging from 0.27 to -0.26 between protein percentage and 100-seed weight. Similarly Sandhu *et al.* (1974) observed both phenotypic and genotypic correlations of -0.57 to -0.67, respectively in chickpea varieties. Green *et al.* (1977) also observed significant phenotypic correlations of 0.17 and 0.20 respectively beetween protein and 100-seed weight. While Frolich *et al.* (1973) working on *Vicia faba* reported a non-significant positive correlation of 0.088. However, an estimate of 0.09 was given as phenotypic and genotypic correlation of protein with 50 seed weight in cowpea by Bliss *et al.* (1973).

There is, however, very little information relative to the association of protein with other yield components. In a Cross between high and low protein parents of soyabean, Simpson, jr. and Wilcox (1983) observed phenotypic correlations of -0.21 and 0.20 for protein percentage with seeds/pod and pods/plant, respectively. While Leleji *et al.* (1972) reported phenotypic correlations between protein andpods/plant ranging from 0.126 to -0.203 in F_2 and F_3 populations of dry bean. In cowpea, Bliss *et al.* (1973 reported significant phenotypic and genotypic correlation between per cent protein and seeds/pod of -0.86 and -1.05, respectively. They also reported phenotypic and genotypic correlation coefficients of 0.19 and -0.04 between protein and pods/plant. Johnson *et al.* (1955b) reported that high protein content is associated with late maturity in soyabean.

CHAPTER THREE

3. MATERIALS AND METHODS

3.1 Experimental Materials

In March, 1987 some cowpea lines from the Institute for Agricultural Research (IAR), Zaria were screened for their per cent crude protein content in the Institute's Food Technology Laboratory. Based on percentage protein in the dry seeds the following lines were identified for the purpose of this study. P_1, 2/180-4-12; P2, 11/48-2; and P_3, L-25. Hereafter, the code P_1, P_2 and P_3 will be used to refer to the respective parent lines. Table 1 gives some agronomic characteristics of these lines. All parents were considered homozygous.

Crosses were made using hand emasculation in the IAR screen house in the following combinations in 1987 and early 1988. P_1 x P_2 (High x Low protein), P_1 x P_3 (High x Low protein), and P_2 x P_3 (Low x Low protein). In the cross P_1 x P_2 the following generations were obtained, P_1, P_2, F_2, reciprocal backcrosses. In the second cross P_1 x P_3 only the generations P_1, P_3, F_2 reciprocal F_1's and reciprocal backcrosses were obtained. Similarly in the final cross P_2 x P_3 in addition to the parents only F_2 and reciprocal F_1's were obtained. In all the crosses only F_1's using the low protein parent as maternal parents were used in the generation of F_2's and backcrosses.

Table 1 *Yield, yield components and per cent protein of the parent lines grown at Samaru in 1988*

Character	Parent line		
	(P_1) 2/180-4-12	(P_2) 11/48-2	(P_3) L-25
Yield g/plant	69.93	51.76	57.81
100-seed weight (g)	18.52	16.64	14.71
No. seeds/pod	9.72	9.67	10.89
No. pods/plant	48.72	37.33	50.56
Days to flowering	63.33	60.89	56.50
Days to maturity	94.22	92.83	91.11
Per cent protein	25.13	20.05	19.68

3.2 Experimental Design

Materials from the first cross $P_1 \times P_2$ were grown in two locations, Kadawa and Samaru, while those from the crosses $P_1 \times P_3$ and $P_2 \times P_3$ were grown at Kadawa and Samaru, respectively. The Kadawa field is normally cultivated during the dry season using irrigation facilities. A randomised complete block design with three replications were used in both locations. Experimental materials were sown on 30th July, and 8th August, 1988 at Kadawa and Samaru respectively. Each replication had 1 row each of the nonsegregating populations, 2 rows each of the reciprocal backcross populations and 5 rows of F_2 population in the cross $P_1 \times P_2$. In the crosses $P_1 \times P_3$ and $P_2 \times P_3$ the nonsegregating populations also occupied 1 row each, while F_2 population occupied 3 and 4 rows each for the respective crosses. Rows of 7 metres length spaced 75 cm apart were used. On each row 15 seeds were sown. 150 cm separated the generations in each replication.

3.3 Cultural Practice

The fields were prepared by broadcasting 200 kg/ha of single superphosphate (P_2O_5) fertilizer after ploughing. This was followed by harrowing and ridging. 500 ml/20 litres galex was applied a day after sowing to control weeds, and this was supplemented by hand weeding as often as necessary during the growing period. Insect pests were controlled using a combination of cypermethrine (Cymbush 10E) and Dimethoate (Rogor 40 EC) each at the rate of

one litre/ha. Spraying was done at weekly intervals at the onset of flowering. A combination of 15 g/10 litres of water, Benlate plus 68.5 g/10 litre of water, Dithane M-45 were sprayed three times during the growing period to control fungal diseases. Both insecticides and fungicides were sprayed simultaneously when the need arose.

3.4 Data Collection

Data on the following characters were collected on individual plant basis:

1. Yield - grain yield in grams per plant.
2. 100-seed weight - weight of 100 randomly selected seeds.
3. Number of seeds/pod - total number of seeds per plant divided by the total number of pods/plant.
4. Number of pods/plant - total number of matured pods/plant at time of harvest.
5. Days to flowering - number of days from sowing to the day of first flower bud opening.
6. Days to maturity - number of days from sowing to the day when 90 percent of the pods turned brown
7. Per cent protein - nitrogen determination using microKjeldahl method was conducted at the I.A.R. Food TechnologyLaboratory after dried seeds were ground in Wiley laboratory mill and passed through 0.5 mm mesh screen. The nitrogen obtained was multiplied by a factor of 6.25 to obtain per cent protein.

For nonsegregating populations data were collected on six randomly selected plants per plot. In the backcross populations of the cross P_1 x

F_2, data were recorded on 48 plants at each of the two locations. As regard the F_2 segregating population of the cross $P_1 \times P_2$ data were taken on 96 plants at each of the two locations. Among the F_2's of the crosses $P_1 \times P_3$ and P2 x P3, 99 and 141 plants were used, respectively.

3.5 Statistical Analysis

Broadsense heritability was estimated using Weber and Moorthy (1952) formula.

The F_2 plants together with their parents, reciprocal F_1's and reciprocal backcrosses where available, were grown in three replications, and therefore, it was diserable to remove replication diffference in accordance with Weber and Moorthy (1952) formula (Appendix VII-IX). The resulting F_2 and backcross variances contained two parts, the genotypic fraction (including dominance and epistasis) due to genic action an that de to the environment. Adjustments for replication difference also were made for covariance between characters (Tables 11-13). Replication effects were also removed from the nonsegregating populations (i.e. parental and reciprocal F_1's) in a separate analysis of variance and covariance because of the relatively small number of plants in these compared to segregating populations (i.e. F_2's and back-crosses).

Error mean squares (variability from plant to plant within the nonsegregating populations) were used in estimating environmental variance. This was subtracted from the error mean square of the F_2

(i.e. total F_2 variance after removing replication effects) in obtaining the genotpic variance (Table 14). Similarly, environmental covariances were determined from the nonsegregating populations (Table 15). This method permits genotype x environment interaction to be included in the genotypic variance. To adjust for this inadequacy, one of the crosses P_1 x P_2 (High x Low protein) was grown at two locations so that genotype x environment interaction could be identified and removed (Table 8). In addition to this, location effect and interaction between locations and replication effects were removed. This was expected to improve the reliability of the estimates of the error mean squares for both segregating and nonsegregating populations. Similar covariance analyses were made (Table 12).

All analyses were conducted on individual plant basis.

$$H_x = \frac{\sigma^2XF_2 - \sigma^2XE}{\sigma^2XF_2} \times 100$$

where

H_x = Broadsense heritability for character X.

σ^2XF_2 = Total variance observed in character X.

σ^2XE = Environmental variance in the expression of the character X, which is obtained as the geometric mean of the nonsegregating populations (P_1, P_2 and F_1).

Heritability in the narrrowsense were estimated using Warner (1952) formula.

$$\text{Heritability} = \frac{2(VF_2) - (VB_1 + VB_2)}{VF_2}$$

Where

$$VF_2 = 1/2D + 1/4H + E$$

$$VB_1 + VB_2 = 1/2D + 1/2H + 2E$$

$$2(VF_2) - (VB_1 + VB_2) = 1/2D$$

so that

$$\text{Heritability} = \frac{1/2D}{VF_2}$$

and

1/2D = the additive genetic component of the variance of F_2.

VF_2 = total within variance of F_2

VB_1 and VB_2 = total within variance of the backcrosses of the F_1 to the respective parents.

In the above relationship

D = additive variance

H = dominance variance

E = environmental variance

Phenotypic and genotypic correlations between protein and other characters under consideration were obtained using Weber an Moorthy (1952) formulae

$$\text{Phenotypic } r_{xy} = \frac{\text{Covxy}F_2}{(\sigma^2XF_2 \cdot \sigma^2YF_2)^{1/2}}$$

$$\text{Genotypic } r_{xy} = \frac{\text{Covxy}G}{(\sigma^2XG \cdot \sigma^2YG)^{1/2}}$$

$$\text{and } \text{Covxy}F_2 = \text{Covxy}G + \text{Covxy}E$$

$$\sigma^2XF_2 = \sigma^2XG + \sigma^2XE$$

$$\sigma^2YF_2 = \sigma^2YG + \sigma^2YE$$

Where

σ^2XF_2 = Total variance observed in character X in the F_2 population.

σ^2YF_2 = Total variance observed in character Y in the F_2 population.

σ^2XG = Genotypic variance of the character X.

σ^2YG = Genotypic variance of the character Y.

σ^2XE and σ^2YE = Environmental variance in the expression of the characters X and Y respectively. They are obtained as the geometric means of nonsegregating populations (P_1, P_2 and F_1) of the respective characters.

$\text{Covxy}F_2$ = Total covariance observed between the characters X and Y in the F_2 population.

$\text{Covxy}G$ = Genotypic covariance observed between the characters X and Y in the F_2 population.

CovxyE = Environmental covariance in the expression of the character X and Y. This was obtained as the geometric mean of the covariances of the characters in non-segregating populations (P_1, P_2 and F_1).

Heritability estimates for per cent protein in the broadsense were computed for all the crosses, while narrowsense heritability estimates were available for only the cross $P_1 \times P_2$ where backcross populations were available. Both phenotypic and genotypic correlations were calculated where possible.

Phenotypic and genotypic coefficients of variation for per cent protein in the F_2 populations were calculated using formulae suggested by Burton (1952).

$$GCV = \frac{\sigma^2GF_2{}^{1/2}}{\bar{x}} \times 100$$

$$PVC = \frac{\sigma^2F_2{}^{1/2}}{\bar{x}} \times 100$$

Where

GCV = genotypic coefficient of variation.

PVC = phenotypic coefficient of variation.

σ^2F_2 = Total variance observed for the character in the F_2 population.

σ^2GF_2 = genotypic variance for the character in F_2 population.

$\bar{x}$ = F_2 mean for character.

Estimates of minimum number of genes controlling per cent protein were obtained using the following methods:

1. Wright (1921),

$$n = \frac{0.25\ (0.75 - h + h^2)D^2}{\sigma^2 F_2 - \sigma^2 F_1}$$

Where

$$h = \frac{\bar{F}_1 - \bar{F}_1}{\bar{P}_2 - \bar{P}_1}$$

$$D = \bar{P}_2 - \bar{P}_1$$

Where n = number of genes

$\bar{P}_1$ = mean of the smaller parent

$\bar{P}_2$ = mean of the larger parent

$\bar{F}_1$ = mean of the F_1 population

$\bar{F}_2$ = mean of the F_2 population

$\sigma^2\bar{F}_1$ = Variance of the F_1 population mean

$\sigma^2\bar{F}_2$ = Variance of the F_2 population mean.

The formula is expected to produce an unbiased estimate of gene number if the following assumption hold:-

(i) No linkage exists between pertinent genes.

(ii) One parent supplies only plus factors and the other only minus factors among those in which they differ.

(iii) All genes are equally important.

(iv) The degree of dominance of all plus factors is the same for all.

(v) No interaction exists between pertinent non allelic genes.

2. Castle and Wright (1921),

$$n = \frac{D^2}{8(\sigma^2 F_2 - \sigma^2 F_1)}$$

Modified formula (Weber, 1950) using the backcrosses,

$$n = \frac{D^2}{16(\sigma^2 BC - \sigma^2 F_1)}$$

Where,

n = number of genes

D = mean difference between the parents

$\sigma^2 F_1$ = variance of F_1 population mean

$\sigma^2 F_2$ = variance of F_2 population mean

$\sigma^2 BC$ = variance of either of the backcross populations.

With the following assumptions:

(i) No dominance.

(ii) Each gene has an equal effect.

(iii) Both parents are homozygous.

3. Mather and Jinks (1971),

$$K_i' = \frac{[1/2(\bar{a}_1 - \bar{a}_2)]^2}{D}$$

Where,

$D = S(d^2_a)$, the additive variance.

K_i = number of genes

$\bar{a}_1$ and $\bar{a}_2$ = means of the parents.

With the following assumptions:

(i) No interaction.

(ii) No linkage.

(iii) Equal increments for the different alleles, that is all d's are equal.

Frequency distributions were obtained for per cent protein for all crosses. Indications of mode of gene action governing protein inheritance were shown by comparing the mean performances of the generations.

CHAPTER FOUR

4. RESULTS

4.1 Generation Means

The mean performance of all the generations i.e. P_1, P_2, F_2, reciprocal F_1's and reciprocal backcrosses in the cross P_1 x P_2 (High x Low protein) are presented in Tables 2 to 4. Comparison of the F_1, parental and arithmetic mid-parent value in Kadawa location showed a high partial dominance of low protein parent over high protein paarent in this cowpea cross, with the F_2 mean falling between the F_1 mean and mid-parent value. The mean of backcross to the high protein parent was between mid-parent value and the high protein parent, while that of the reciprocal back-cross was between mid-parent value and that of low protein parent.

At Samaru location the F_1 mean was lower than the low protein parent mean, thus indicating overdominance. The F_2 mean fell between mid-parent value and the low protein parent. The mean of backcross to high protein parent was between mid-parent value and low protein parent, but closer to mid-parent, while the reciprocal backcross mean was lower than the low parent mean.

Combination of data from the two locations, Kadawa and Samaru showed the F_1 mean for per cent protein to be lower than the low protein parent. Thus indicating overdominance of low protein over high protein in this cowpea cross. The mean of

backcross to the high protein parent was between mid-parent value and high protein parent mean, while the reciprocal backcross mean was in between mid-parent value and low protein parent but closer to low parent. In the individual locations, and the two locations combined, no significant difference was observed between reciprocal F_1 means for per cent protein, although mean values using high protein parent as maternal parent were higher.

In the cross P_1 x P_3 (High x Low protein, Table 5) grown at Kadawa, a comparison of the generations means for per cent protein showed F_1 mean to be lower than the low protein parent, thus indicating overdominance of low protein over high protein. The F_2 mean was between mid-parent value and the high protein parent but closer to mid-parent value. Similarly no significant difference was observed between reciprocal F_1 means although mean values using high protein parent as maternal parent were higher.

Table 6 showed the means of per cent protein for the different generations of the cross P_2 x P_3 (Low x Low protein). The mean of the F_1 was between mid-parent value and the parent with lower protein percentage, thus showing partial dominance of low protein over high protein. No significant difference was observed for per cent protein between reciprocal F_1's although mean values using high protein parents as maternal parent were higher.

Table 2 Heritability, frequency distributions, means, standard deviations, phenotypic and genotypic coefficients of variability of per cent protein for the cross $P_1 \times P_2$ grown at Kadawa

	Number of Plants/Class of Percent Protein												Coefficient of Variability(%)	
Generation	13.5	15.5	17.5	19.5	21.5	23.5	25.5	27.5	29.5	N	$\bar{X}$	SD	Genotypic	Phenotypic
P_1						6	6	6		18	25.88	1.67		
P_2		2	1	9	6					18	19.96	1.94		
F_1 12			4	8	6					18	20.15	1.39		
F_1 21			2	10	5		1			18	20.68	2.05		
F_2		2	12	22	22	17	13	7	1	96	22.29	3.07	11.6	13.8
BC_1			2	7	15	10	9	5		48	23.25	2.68		
BC_2		3	7	14	14	7	1	1	1	48	21.25	2.81		
Mid-Parent											22.92			

Broadsense heritability = 71.0%
Narrowsense heritability = 40.3%

Table 3 *Heritability, frequency distributions, means, standard deviations, phenotypic and genotypic coefficients of variability of per cent protein for the cross $P_1 \times P_2$ grown at Samaru*

	Number of Plants/Class of Percent Protein											Coefficient of Variability(%)	
Generation	13.5	15.5	17.5	19.5	21.5	23.5	25.5	27.5	29.5	N	$\bar{X}$	SD	Genotypic	Phenotypic
P_1					1	8	6	3		18	25.13	1.87		
P_2			3	12	3					18	20.05	1.09		
F_1 12			8	8	2					18	19.39	1.61		
F_1 21		1	7	4	2	2	1	1		18	20.31	2.94		
F_2	1	2	21	24	19	21	5	2	1	96	21.18	2.79	11.2	13.2
BC_1		4	7	5	16	7	9	1		48	21.88	2.68		
BC_2		8	17	11	9	3				48	19.22	2.30		
Mid-Parent											22.59			

Broadsense heritability = 71.7%
Narrowsense heritability = 25.3%

Table 4 Heritability, frequency distributions, means, standard deviations, phenotypic and genotypic coefficients of variability of per cent protein for the cross $P_1 \times P_2$ combining Kadawa and Samaru locations

	Number of Plants/Class of Percent Protein											Coefficient of Variability(%)	
Generation	13.5	15.5	17.5	19.5	21.5	23.5	25.5	27.5	29.5	N	$\bar{Y}$	SD	Genotypic	Phenotypic
P_1					1	14	12	9		36	25.51	1.77		
P_2		2	4	21	9					36	20.00	1.58		
F_1 12			12	16	8					36	19.77	1.50		
F_1 21		1	9	14	7	2	2	1		36	20.49	2.53		
F_2	1	4	33	46	41	38	18	9	2	192	21.74	2.94	11.3	13.5
BC_1		4	9	12	31	17	17	6		96	22.57	2.78		
BC_2		11	24	25	23	10	1	1	1	96	20.23	2.57		
Mid-Parent											22.76			

Broadsense heritability = 67.0%
Narrowsense heritability = 26.8%

Table 5 *Heritability, frequency distributions, means, standard deviations, phenotypic and genotypic coefficients of variability of per cent protein for the cross $P_1 \times P_3$ grown at Kadawa*

	Number of Plants/Class of Percent Protein											Coefficient of Variability(%)	
Generation	15.5	17.5	19.5	21.5	23.5	25.5	27.5	29.5	N	$\bar{X}$	SD	Genotypic	Phenotypic
P_1					2	8	5	3	18	26.71	1.60		
P_3	1		8	8	1				18	20.74	1.53		
F_1 13		5	7	4	2				18	20.59	1.80		
F_1 31			3	10	5				18	22.16	1.28		
F_2	2	4	10	14	26	24	15	4	99	24.30	3.12	11.0	12.8
Mid-Parent										23.73			

Broadsense heritability = 73.4%

Table 6 Heritability, frequency distributions, means, standard deviations, phenotypic and genotypic coefficients of variability of per cent protein for the cross $P_2 \times P_3$ grown at Samaru

	Number of Plants/Class of Percent Protein									Coefficient of Variability(%)	
Generation	13.5	15.5	17.5	19.5	21.5	23.5	25.5	N	$\bar{X}$	SD	Genotypic	Phenotypic
P_2		3	5	5	5			18	19.11	1.98		
P_3			5	9	3	1		18	19.68	1.43		
F_1 23		2	8	5	1	2		18	19.28	1.81		
F_1 32		5	4	7	2			18	18.71	1.81		
F_2	1	20	49	33	26	11	1	141	19.32	2.24	7.40	11.60
Mid-Parent									19.40			

Broadsense heritability = 40.7%

4.2 Frequency Distribution

Distribuution of F_2 segregating population for the cross P_1 x P_2 (High x Low protein, Tables 2-4) grown at Kadawa was normal, with only one plant having protein percentage exceeding the high protein parent. The backcross to the high protein parent population also produced a normal distribution, while the reciprocal backcross showed a positive skewness towards the low protein parent, with one of the segregants exceeding the highest high protein parent. Similarly, the F_2 segregating population at Samaru produced a normal distribution with few plants having protein percentages lower than the lowest parent. The reciprocal backcross population also gave a normal distribution. Combination of the two locations gave a normal distribution of the F_2 and the backcross to the high protein parent segregants. Some F_2 segregants were either lower or higher than the lowest or highest protein parents. Thus suggesting bi-directional transgressiveness. Backcross to the low protein parent gave a positively skewed distribution

In the crosses P_1 x P_3 (High x Low protein) and P_2 x P_3 (Low x Low protein), Tables 5 and 6 the F_2 segregants showed a normal distribution with one plant each being lower and higher than the lowest and highest protein parent, respectively in the cross P_2 x P_3 (Low x Low protein).

4.3 Measure of Variability

Phenotypic and genotypic coefficients of variability using F_2 segregating populations were obtained for all crosses (Tables 2-6). In the cross P_1 x P_2 (High x Low protein) a phenotypic coefficient of variability as high as 13.8% and a genotypic value as high as 11.6% were recorded at Kadawa. In the cross P_1 x P_3 (High x Low protein), phenotypic and genotypic coefficients of variability as high as 12.8% and 11.0%, respectively were obtained. As regards the cross P_2 x P_3 (Low x Low protein) phenotypic and genotypic coefficients of variability of 11.6% and 7.4% respectively were recorded. The variability observed in the F_2 segrregating population of the crosses between high and low protein parents were generally higher than that of low x low protein parents.

4.4 Heritability Estimates

Broadsense heritability estimates, using the non-segregating populations variance as an estimate of environmental variance, were generally high. In the cross P_1 x P_2 (High x Low protein), broad-sense heritability estimates of 71.0% and 71.7% were obtained at Kadawa and Samaru, respectively, (Tables 2-4). Combination of the two locations with all identified environmental effects, including genotype x location interaction removed (Table 8), produced a broadsense heritability estimate as high as 67.0%. Similarly, narrowsense heritability estimates of

Table 7 Analysis of variance showing sources of variation, degrees of freedom and mean squares for F_2 populations of per cent protein yield and yield components grown at Kadawa and Samaru locations for the cross $P_1 \times P_2$

Source of Variation	Degree of Freedom	Mean Square (Variances)						
		Protein	Yield	100 Seed Weight	Number of Seeds/Pod	Number of Pods/Plant	Days to Flowering	Days to Maturity
Replication	2	2.451+	30985.093	39.254	31.572	9692.885	19.260	13.531
	2	24.890	2088.218	6.533	87.641	662.375	183.073	89.656
Error	93	9.425	1695.090	11.879	7.416	717.657	45.235	22.539
	93	7.799	1226.636	16.607	87.069	665.739	35.020	11.455
Total	95	9.278	2311.722	12.456	7.924	906.609	44.698	22.349
	95	8.159	1244.774	16.395	87.091	665.668	38.137	13.181

+ = Upper values are for Kadawa location while lower values are for Samaru location.

Table 8 Combine analysis of variance showing sources of variation, degree of freedom and mean squares for F_2 population of per cent protein, yield and yield components for the cross P_1 x P_2 grown at Kadawa and Samaru locations

Source of Variation	Degree of Freedom	Mean Square (Variances)						
		Protein	Yield	100 Seed Weight	Number of Seeds/Pod	Number of Pods/Plant	Days to Flowering	Days to Maturity
Replication	2	17.640	19110.356	17.307	111.778	6586.599	48.016	21.422
Location	1	59.096	5785.033	2.417	7.776	21.333	2303.255	9033.797**
Replication x Location	2	9.702	13962.955**	28.480	7.435	3768.661**	154.318*	81.766**
Genotypes x Location	31	10.586	1776.906	12.079	41.054	707.323	47.761	24.990
Error	155	8.217	1397.655	14.376	48.480	689.573	38.601	15.398
Total	191	8.982	1799.226	14.362	47.295	782.134	53.254	64.930

* = Significant at 5%
** = Significant at 1%

Table 9 Analysis of variance showing sources of variation, degrees of freedom and mean squares for F_2 populations of the cross $P_1 \times P_3$ and $P_2 \times P_3$ for per cent yield and yield components grown at Kadawa and Samaru respectively

Source of Variation	Degree of Freedom	Mean Square (Variances) Protein	Yield	100 Seed Weight	Number of Seeds/Pod	Number of Pods/Plant	Days to Flowering	Days to Maturity
Replication	2	29.774+	3743.606	65.284	7.243	5258.394	80.040	35.586
	2	21.641	987.514	2.544	20.639	1074.773	79.241	208.709
Error	96	9.720	2580.235	12.760	4.612	1521.030	12.943	11.972
	138	5.011	1107.638	5.300	4.066	875.715	32.339	14.666
Total	98	10.129	2604.079	13.832	4.666	1597.302	14.313	12.454
	140	5.249	1105.922	5.261	4.303	878.556	33.009	17.438

+ = Upper values are for the cross $P_1 \times P_3$ grown at Kadawa while lower values are for the cross $P_2 \times P_3$ grown at Samaru.

40.3% and 25.3% were obtained for Kadawa and Samaru, respectively (Tables 2-4), while the combination of the two locations gave 26.8%. These estimates were rather low. Estimates of both broadsense and narrowsense heritabilities combining data from the two locations were expected to be more reliable due to the removal of the genotype x location interaction in addition to the replication and location effects and the larger sample size.

Broadsense heritability estimate of 73.4% was obtained for the cross P_1 x P_3 (High x low protein), and 40.7% was obtained for the cross P_2 x P_3 (Low x low protein, Tables 5-6). Generally, crosses between high x low protein parents gave high broadsense heritability estimates, while the cross between low x low protein parents produced comparatively low estimate .

4.5 Phenotypic and Genotypic Correlations

Table 10 shows the phenotypic and genotypic correlations on per cent protein with yield and yield components in the cross P_1 x P_2 (High x Low protein) grown at Kadawa, Samaru and the combination of the two locations. Yield, 100-seed weight and number of pods/plant showed non-significant positive phenotypic correlation with per cent protein at Kadawa, although all values were low. Days to flowering and days to maturity showed a non significant negative phenotypic correlation with per cent protein at Kadawa. The only significant negative phenotypic correlation recorded at Kadawa was that between number of seeds/pod with per cent

Table 10 *Phenotypic and Genotypic correlations of protein with yield and yield components for the cross* $P_1 \times P_2$ *grown at Kadawa, Samaru and combination of the two locations.*

	Percent Protein		
Versus	Kadawa	Samaru	Combined
Yield	0.032+	-0.023	-0.046
	0.205	( )	( )
100-seed Weight	0.055	0.114	0.151*
	0.027	0.157	3.304**
No Seed/Pod	-0.228*	0.30	-0.017
	-0.528**	0.054	-0.061
No. Pods/Plant	0.059	0.059	-0.127
	0.244*	( )	( )
Days to flowering	-0.078	-0.076	0.059
	-0.227*	( )	0.071
Days to Maturity	-0.137	0.056	1.356**
	-0.693**	0.285**	( )

\+ Upper values represent phenotypic correlations, while lower values represents genotypic correlations.

* = Significant at 5%

** = Significant at 1%

( ) = Represent undetermined genotypic correlations due to negative genotypic variances for the characters.

Table 11 Covariance analysis showing sources of variation, degrees of freedom and cross product mean squares for F_2 populations of per cent protein with yield and yield components grown at Kadawa and Samaru locations for the cross $P_1 \times P_3$

Source of Variation	Degree of Freedom	Mean Square (Variances) Protein Vs Yield	Protein Vs 100 Seed Wt.	Protein Vs No. Seeds/Pod	Protein Vs No. Pods/Plant	Protein Vs Days to Flowering	Protein Vs Days to Maturity
Replication	2	63.330+	9.685	0.565	30.785	6.795	5.885
	2	5.505	-12.030	38.625	464.305	-61.495	-46.725
Error	93	3.991	0.579	-1.904	4.813	-1.606	-2.001
	93	-2.262	1.301	0.780	4.265	-1.262	0.525
Total	95	5.240	0.771	-1.852	5.360	-1.429	-1.835
	95	-2.099	1.020	1 577	13.950	-2.530	-0.470

+ = Upper values are for Kadawa location while lower values are for Samaru location.

Table 12 Combined covariance analysis showing sources of variation, degrees of freedom and cross product mean squares for F_2 populations of per cent protein with yield and yield components grown at Kadawa and Samaru locations for the cross $P_1 \times P_2$

Source of Variation	Degree of Freedom	Cross Product Mean Square (Variances)					
		Protein Vs Yield	Protein Vs 100-seed Wt.	Protein Vs No. Seeds/Pod	Protein Vs No. Pods/Plant	Protein Vs Days to Flowering	Protein Vs Days to Maturity
Replication	2	361.155	3.635	49.910	495.085	-239.155	-403.360*
Location	1	584.630	11.950	21.440	0.000	-368.910	-725.030**
Replication x Location	2	423.315**	8.450**	31.630**	495.095**	-29.110**	-16.345
Genotypes x Location	31	-16.285	-2.022µµ	-4.454**	43.008**	-0.111	-2.003
Error	155	-4.940	1.663	-0.330	-9.543	1.057	15.257
Total	191	4.623	0.953	-0 025	9.604	-3.901	-4.943

* = Significant at 5%
** = Significant at 1%

Table 13 Covariance analysis showing sources of variation, degrees of freedom and cross product mean squares for F_2 populations of the cross $P_1 \times P_3$ and $P_2 \times P_3$ for per cent protein with yield and yield components grown at Kadawa and Samaru, respectively

Source of Variation	Degree of Freedom	Cross Product Mean Squares: Protein Vs Yield	Protein Vs 100-seed Wt.	Protein Vs No. Seeds/Pod	Protein Vs No. Pods/Plant	Protein Vs Days to Flowering	Protein Vs Days to Maturity
Replication	2	-288.015+	14.730	-4.735	-390.46	45.78	29.479
	2	-54.025	3.165	-1.035	105.365	35.99	13.695
Error	96	-18.740	0.378	-0.022	-12.733	-1.902	-1.493
	138	3.766	0.682	-0.470	1.667	0.468	-0.057
Total	98	-24.235	0.671	-0.118	-20.441	-0.929	-0.861
	140	2.940	0.717	-0 478	0.138	0.976	0.139

+ = Upper values are for the cross $P_1 \times P_3$ grown at Kadawa while lower values are for the cross $P_2 \times P_3$ grown at Samaru.

protein. At Samaru, the phenotypic correlation between yield and per cent protein becomes negative, while that with number of seeds/pod becomes positively correlated phenotypically, contrary to observations at Kadawa, although both values were low and non significant. 100-seed weight and number of pods/plant maintained their positive phenotypic correlation with per cent protein at Samaru. Days to flowering was negatively correlated with per cent protein, while days to maturity gave a positive phenotypic correlation that was not significant with per cent protein at Samaru. Combination of the two locations produced a non significant negative phenotypic correlation for yield, number of seeds/-pod and number of pods/plant with per cent protein, respectively. 100-seed weight and days to maturity showed a significant positive phenotypic correlation with per cent protein, while days to flowering showed a nonsignificant positive phenotypic correl-ation with per cent protein. Generally values obtained using combination of data from the two locations were expected to be more reliable, because of the removal of genotype x location interaction in addition to replication and location effects (Table 12) and the larger sample size.

Positive genotypic correlations which were similar in sign with phenotypic values were observed for yield and number of pods/plant with per cent protein at Kadawa. Number of seeds/pod, days to flowering and days to maturity produced significant negative genotypic correlation with per cent protein

Table 14 Total variance (F_2 variance) genotypic variance and environmental variance for per cent protein for the crosses $P_1 \times P_2$, $P_1 \times P_3$, $P_2 \times P_3$ grown at different locations

Character and Variance		Cross and location(s) grown				
		$P_1 \times P_2$ Kadawa	$P_1 \times P_2$ Samaru	$P_1 \times P_2$ Kadawa and Samaru	$P_1 \times P_3$ Kadawa	$P_2 \times P_3$ Samaru
Protein	σ^2F_2	9.425	7.799	8.217	9.720	5.011
	σ^2E	2.731	2.205	2.715	2.582	2.970
	σ^2G	6.694	5.594	5.502	7.138	2.041
Yield	σ^2F_2	1695.090	1226.636	1397.655	2580.235	1107.638
	σ^2E	958.735	1790.876	1495.139	1899.918	1316.491
	σ^2G	736.355	-564.240	-97.484	680.317	-208.853
100-seed Weight	σ^2F_2	11.879	16.607	14.676	12.760	5.300
	σ^2E	10.411	7.349	8.707	6.857	1.966
	σ^2G	1.488	9.258	5.969	5.903	3.334
Number of Seeds/Pod	σ^2F_2	7.416	87.069	48.480	4.612	4.066
	σ^2E	6.410	3.202	5.317	5.224	2.602
	σ^2G	1.006	83.867	43.163	-0.612	1.464
Number of Pods/ Plant	σ^2F_2	717.657	665.739	689.573	1521.030	875.715
	σ^2E	341.090	1027.905	720.922	608.319	918.530
	σ^2G	376.567	-362.166	-31.349	912.711	-42.815
Days to Flowering	σ^2F_2	45.235	35.020	38.601	12.943	32.339
	σ^2E	19.876	38.173	30.969	32.779	35.904
	σ^2G	25.359	-3.153	7.632	-19.836	-3.565
Days to Maturity	σ^2F_2	22.539	11.455	15.398	11.972	14.666
	σ^2E	19.252	11.335	15.744	15.710	13.197
	σ^2G	3.287	0.120	-0.346	-3.738	1.469

Table 15 Total covariance (F_2 covariance), genotypic covariance and environmental variance between per cent protein with yield and yield components for the crosses $P_1 \times P_2$, $P_1 \times P_3$ and $P_2 \times P_3$ grown at different locations

		Protein				
Versus		$P_1 \times P_2$ Kadawa	$P_1 \times P_2$ Samaru	$P_1 \times P_2$ Kadawa and Samaru	$P_1 \times P_3$ Kadawa	$P_2 \times P_3$ Samaru
Yield	$Covxy F_2$	3.99	-2.26	-4.94	-18.74	3.77
	CovxyE	-10.38	19.74	4.96	-11.46	15.69
	CovxyG	14.37	-22.00	-9.90	-7.28	-11.69
100-Seed Weight	$Covxy F_2$	0.58	1.30	1.66	0.38	0.68
	CovxyE	0.67	0.17	-17.27	0.28	-0.39
	CovxyG	-0.09	1.13	18.93	0.10	1.07
Number of Seeds/ Pod	$Covxy F_2$	-1.90	0.78	-0.33	-0.02	-0.47
	CovxyE	-0.53	-0.38	0.60	0.34	-0.88
	CovxyG	-1.37	1.16	-0.93	-0.36	0.41
Number of Pods/ Plant	$Covxy F_2$	4.81	4.27	-9.54	-12.73	1.67
	CovxyE	-7.45	-4.61	3.90	-4.75	18.20
	CovxyG	12.26	8.88	-13.44	-7.98	-16.53
Days to flower-ing	$Covxy F_2$	-1.61	-1.26	1.06	-1.90	0.47
	CovxyE	1.35	-0.45	1.52	2.08	2.15
	CovxyG	-2.96	-0.81	-0.46	-3.98	-1.68
Days to Maturity	$Covxy F_2$	-2.00	0.53	15.26	-1.49	-0.06
	CovxyE	1.25	0.29	2.79	-1.71	-0.88
	CovxyG	-3.25	0.24	12.47	0.22	0.82

Table 16 Phenotypic and Genotypic correlations of protein with yield and yield components for the cross P_1 x P_3 and P_2 x P_3 grown at Kadawa and Samaru, respectively.

	Percent Protein	
Versus	P_1 x P_3	P_2 x P_3
Yield	-0.118+	0.051
	-0.105	( )
100-seed Weight (g)	0.034	0.132
	0.016	0.410**
No Seeds/Pod	-0.003	-0.104
	( )	0.235**
No. Pods/Plant	-1.105**	0.025
	0.099	( )
Days to flowering	-0.170	0.037
	( )	( )
Days to Maturity	-0.138	-0.007
	( )	0.478**

\+ Upper values represent phenotypic correlations, while lower values represents genotypic correlations.

** = Significant at 1%

( ) = Represents undetermined genotypic correlations due to negative genotypic variances for the characters.

at Kadawa, while a nonsignificant negative genotypic correlation was observed for 100-seed weight with per cent protein in the same location. All genotypic correlations observed at Samaru for 100-seed weight, number of seeds/pod and days to maturity with per cent protein were positive with only days to maturity having highly significant value. In the combined analysis of the two locations, number of seeds/pod and days to flowering showed a nonsignificant negative genotypic correlation with per cent protein. Values that were theoretically higher than 1 were obtained for 100-seed weight and days to maturity with per cent protein as genotypic and phenotypic correlations respectively. Genotypic correlations were not determined for yield, number of pods/plant, days to flowering and days to maturity with per cent protein in samaru location and combination of the two locations due to negative genotypic variances in those characters (Table 14).

In the cross $P_1 \times P_3$ (High x Low protein, Table 16), yield, number of seeds/pod, number of pods/plant, days to flowering and days to maturity showed negative phenotypic correlation with per cent

Table 17 Estimates of minimum number of genes controlling per cent protein in cowpea lines for the crosses $P_1 \times P_2$, $P_1 \times P_3$ and $P_2 \times P_3$ grown at various locations using various formulae

	Locations and generations used								
	Kaduna			Samaru			Kadawa and Samaru Combined		
Crosses	F_2	BC_1	BC_2	F_2	BC_1	BC_2	F_2	BC_1	BC_2
	0.814[1]	-	-	1.111	-	-	1.071	-	-
$P_1 \times P_2$	0.585[2]	0.419	0.368	0.620	0.282	0.594	0.692	0.372	0.481
	2.419[3]	-	-	3.263	-	-	3.446	-	-
$P_1 \times P_3$	1.069[1]	-	-	-	-	-	-	-	-
	0.984[2]	-	-	-	-	-	-	-	-
$P_2 \times P_3$	-	-	-	0.025[1]	-	-	-	-	-
	-	-	-	0.024[2]	-	-	-	-	-

NOTE: Rows with the superscripts 1, 2 and 3 are calculated using Wright, Castle and Wright and Weber and Mather and Jinks formulae respectively.

BC_1 = Backcross to high protein parent.

BC_2 = Backcross to low protein parent.

protein, with only number of pods/plant having a highly significant value. 100-seed weight showed a nonsignificant positive correlation with per cent protein. Nonsignificant genotypic correlations were observed for yield and number of pods/plant with per cent protein. 100-seed weight showed a low and nonsignificant positive genotypic correlation with per cent protein. Genotypic correlation for number of seeds/pod, days to flowering and days to maturity were not obtained due to negative genotypic variances of these characters (Table 14). Table 16 shows both phenotypic and genotypic correlation of the cross P_2 x P_3 (Low x Low protein). Yield, 100-seed weight, number of pods/plant and days to flowering showed nonsignificant positive phenotypic correlation with per cent protein. Nonsignificant negative phenotypic correlation for number of seeds/pod and days to maturity with per cent protein were observed. Genotypic correlation for 100-seed weight, number of seeds/pod and days to flowering with per cent protein were positive, and significant. Genotypic correlation for yield, number of pods/plant and days to flowering with per cent protein were not obtained due to the negative

genotypic variances of these characters (Table 14).

In all the crosses, negative phenotypic and genotypic correlations predominated for yield, number of seeds/pod and days to flowering with per cent protein. A highly significant negative phenotypic correlation was observed between number of pods/plant and per cent protein, while 100-seed weight showed preponderance of positive phenotypic and genotypic correlations with per cent protein. Both positive and negative correlations were observed between per cent protein and days to maturity with positive values predominating.

4.6 Gene Numbers

Estimates of minimum number of genes controlling per cent protein using different formulae in these crosses are presented in Table 17. Estimates for the cross P_1 x P_2 (High x Low protein) grown at Kadawa, Samaru and the combination of the two locations, using Wright's formula approximated 1 major gene. Castle and Wright's formulae using both the F_2 and reciprocal backcrosses for the cross P_1 x P_2 gave estimates of less than 1. Mather and Jinks formula using the same cross gave an estimate of about 3 major genes. The cross P_1 x P_3 (High x Low protein) gave similar estimates using Wright and Castle and Wright's formulae. For the cross P_2 x P_3 (Low x Low protein), all estimates using the above two formulae were less than 1.

CHAPTER FIVE

5. DISCUSSION

5.1 Generation Means

Partial dominance to overdominance of low protein over high protein were observed in the crosses P_1 x P_2 and P_1 x P_3 (High x Low protein). Similar observations were obtained by Leleji *et al.* (1972), Kelly and Bliss (1975), Mak and Yap (1980) and Singh *et al.* (1980) in various pulses. Overdominance effects appear to be of more importance in the genetic control of per cent protein in these crosses. In the cross P_2 x P_3 (Low x Low protein) partial dominance of low protein over high protein was observed. This is in harmony with observations by Leleji *et al.* (1972) and Kelly and Bliss (1975). Overdominance of low protein over high protein in this study contrasted with the dominance of high protein over low protein in soyabean (Weber, 1950; Johnson *et al.* 1955a). In all the crosses maternal influence was not detected in the control of per cent protein, but crosses using high protein parent as maternal parent were generally higher in per cent protein. Weber (1950) also reported no differences between reciprocal F_1 hybrids in terms of per cent protein in soyabean. This is contrary to the observation in pigeon pea crosses by Dahiya *et al.* (1976) and in dry bean Leleji *et al.* (1972).

5.2 Frequency Distribution

Unimodality observed in the distribution of percentage protein in the generation F_2 for all the crosses indicate the involvement of polygenes in the control of this character. Burton (1951) stated that smoothness, apparent normality or unimodality of F_2 distribution can be used as evidence of multiple factor inheritance provided that major portion of the F_2 variance is genetic. Normal distribution of the segregating F_2 populations were also reported in soyabean by Weber (1950) and in dry bean by Leleji *et al.* (1972), for per cent protein. The positive skewness of the distribution of backcross to low protein parent indicates that low protein was controlled by factors with considerable dominance, while the reciprocal backcross gave a normal distribution with none exceeding parental observations. The presence of transgressive segregation, in some instances bi-directional, in the crosses indicates the presence of complementary gene action. Transgressive segregation for high protein was observed by Weber (1950) in the F_2 and F3 populations of soyabean.

5.3 Heritability Estimates

Broadsense heritability estimates in crosses involving high and low protein parents were generally high, indicating considerable genetic control for per cent protein in these crosses. Broadsense heritability estimates of similar magnitude were obtained in the crosss P_1 x P_2 (High x Low protein) grown at Kadawa and Samaru locations. This

observation is supported by the absence of significant genotype x location interaction for per cent protein in the cross (Table 8). Estimate of broadsense heritability of 67.0% from the combined analysis is more reliable, since genotype x location interaction has been removed. Narrowsense heritability estimates were generally low. Although low in magnitude, it suggests the presence of additive genes that are of significance in breeding programmes. Similarly, narrowsense heritability estimate of 26.8% from the combined analysis of Kadawa and Samaru locations is more reliable, since genotype x location interaction has been removed. Considering the magnitude of difference between broadsense and narrowsense heritability estimates, non-additive gene action appears to be of more importance in the control of per cent protein in the cross P_1 x P_2. Singh *et al.* (1980) working on chickpea corroborate this observation.

Broadsense heritability estimate from the cross P_2 x P_3 (Low x Low protein) was lower (40.7%) than those from crosses involving high x low protein parents. This is attributable to low genetic variability in low x low protein cross compared with those of high x low protein crosses. Although estimates of both broadsense and narrowsense heritability by other workers varied, those of Lelaji *et al.* (1972), Kelly and Bliss (1975), Mutschler and Bliss (1981) in dry bean, Sandhu *et al.* (1974) in chickpea, and Green *et al.* (1977) in lupins were of similar magnitude with those obtained in this study.

5.4 Phenotypic and Genotypic Correlations

Phenotypic and genotypic correlation of seed yield and per cent protein showed both positive and negative correlations, with negative values predominating. All the negative values were small and nonsignificant. This relationship could be explained by the source - sink relationship. Postulating a physiological relationship, where both protein synthesis and yield depend on the availability of carbohydrate, competition would ensue. Protein synthesis utilises more energy compared to yield, therefore most carbohydrates produced during photosynthesis would go into protein synthesis in high protein genotypes making little available for yield. The reverse would be expected in high yielding genotypes. Although negative correlation predominates between yield and per cent protein, some high yielding segregants had high protein percentage. Therefore, considering the weak relationship between yield and per cent protein, possibilities exist for incorporating high per cent protein into high yielding genotypes. Significant negative correlation between yield and protein were reported by Leleji *et al.* (1972) and Kelly and Bliss (1975) in dry bean. Despite this observation they concluded that both high yield and high per cent protein could be combined in a suitable genotype. Number of seeds/pod and number of pods/plant being yield components showed negative correlation with per cent protein as expected. Leleji *et al.* (1972) made similar observation in dry bean. 100-seed weight showed a positive correlation with per cent protein.

Thus suggesting that large seed size with high protein can be obtained in selection from crosses involving lines in this study. Direct selection for heavy seeds will bring about increase in per cent protein and yield, as Singh *et al.* (1982) and Zaria (1988) observed positive correlation between yield/plant and seed size. The negative correlation observed in these crosses for days to flowering with per cent protein was of great advantage. This, shows that genotypes with high protein percentage, that would flower early can be realised. However, days to maturity showed significant positive correlation with per cent protein that exceeds the theoretical limit of 1. This observation is subject to experimental errors and is therefore, not absolutely reliable. Johnson *et al.* (1955b) reported a positive correlation between per cent protein with days to maturity in soyabean similar to observation in this study. Some phenotypic and genotypic correlations exceeded 1 or were less than -1, which is theoretically impossible. Small sample size and experimental errors and the inadequacy of estimating environmental variance of segregating population from nonsegrregating population might have resulted in these observations.

5.5 Gene Numbers

Estimates of minimum number of major genes controlling per cent protein in crosses between high x low protein ranges from values less than 1 to 1 using Wright's (1921) and Wright and Castle, (1921) formulae, while Mather and Jinks (1971) formula gave

values that approximate 3 major genes. The material used in this study do not appear to meet the assumptions that go with those formulae, and there were no possibilities for testing some of the assumptions. Estimate of a minimum of 3 major genes using Mather and Jinks formula looks more acceptable Considering the normal distribution of the F_2 populations, transgressive segregation, presence of overdominance and high broadsense heritability estimates and low narrowsense heritability estimates, the estimate of a minimum of 3 major genes using Mather and Jinks formula looks more convincing but possibilities of modifiers could not be ruled out.

CHAPTER SIX

6. SUMMARY AND CONCLUSION

The high broadsense heritability estimate of about 70% suggests high genetic control for per cent protein in these crosses. Considering the over-dominance of low protein over high protein, distribution pattern of segregating population and the positive skewness observed in the distribution of population of backcross to low protein parent, the estimate of a minimum of 3 major genes using Mather and Jinks formula with possible modifiers appears plausible.

Correlation between yield and per cent protein were negative but nonsignificant, therefore possibilities exist in identifying genotypes that combine high yield with high protein percentage among segregating populations. The positive correlation observed between 100-seed weight and per cent protein could be put to advantage in selection for high yield as it would lead to a simultaneous increase in per cent protein. Bliss *et al.* (1974) observed that three generations of selection for percentage protein *per se* resulted in populations significantly higher in percentage protein, but with greatly reduced yield. To circumvent such undesirable effects the authors suggested that selection should first be practised for high yielding families based on mean performance since yield improvement is of utmost importance and easily determined.

The overdominance of low protein over high protein seems to introduce some complications into

the genetic control of per cent protein. Fortunately some additive components of genetic variability have been identified, though of small magnitude. Therefore, the use of backcrossing technique of breeding with low protein parent as recurrent parent, among high yielding genotypes, emphasising selection for large seed size and yield at every stage could bring success in the effort to combine high yield with high protein percentage in these cowpea lines

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APPENDIX I

Variances of the respective characters and generations for the cross $P_1 \times P_2$ grown at Kadawa after removing replication effects

	Variance						
Generation	Protein	Yield	100-seed Weight	No. Seeds/ Pod	No. Pods/ Plant	Days to Flowering	Days to Maturity
P_1	7.794	730.422	16.620	10.944	294.700	19.622	16.211
P_2	3.773	1376.543	6.344	4.418	464.811	26.678	38.500
F_1 12	1.933	876.459	10.706	5.447	289.700	15.000	11.433
F_1 21	4.188	1215.405	9.400	7.223	445.833	24.156	24.111
F_2	9.425	1695.090	11.879	7.416	717.657	45.235	22.539
BC_1	7.166						
BC_2	7.890						

APPENDIX II

Variances of the respective characters and generations for the cross $P_1 \times P_2$ grown at Samaru after removing replication effects

Generation	Variance						
	Protein	Yield	100-seed Weight	No. Seeds/ Pod	No. Pods/ Plant	Days to Flowering	Days to Maturity
P_1	3.489	1990.692	14.781	4.508	1110.011	27.311	29.933
P_2	1.187	1317.224	2.509	2.627	703.044	45.711	8.278
F_1 12	2.587	2190.447	10.741	2.772	1391.711	44.556	5.878
F_1 21	8.631	2967.943	14.313	5.097	890.600	42.789	28.767
F_2	7.799	1226.636	16.607	87.069	665.739	35.020	11.455
BC_1	8.317						
BC_2	5.307						

APPENDIX III

Variances of the respective characters and generations for the cross $P_1 \times P_2$ grown at Kadawa and Samaru after removing replication, location, replication x location and genotype x location effects

	Variance						
Generation	Protein	Yield	100-seed Weight	No. Seeds/ pod	No. Pods/ plant	Days to flowering	Days to maturity
P_1	3.086	1509.215	17.045	9.034	749.431	23.271	22.214
P_2	2.493	1539.921	4.154	3.520	577.597	39.068	22.258
F_1 12	2.600	1462.818	9.323	4.728	865.583	32.671	7.893
F_1 21	5.764	1920.465	11.939	5.673	638.268	36.770	25.241
F_2	8.217	1397.655	14.676	48.480	624.765	38.601	15.398
BC_1	7.696						
BC_2	6.536						

APPENDIX IV

Variances for the respective characters and generations for the cross $F_1 \times P_3$ grown at Kadawa after removing replication effects.

	Variance						
Generation	Protein	Yield	100-seed Weight	No. Seeds/ pod	No. Pods/ plant	Days to flowering	Days to maturity
P_1	2.559	2355.993	14.522	5.394	551.922	47.291	19.344
P_3	2.351	996.492	2.082	3.417	462.845	24.633	20.544
F_1 13	3.242	2921.168	10.662	7.736	881.211	30.223	9.756
F_1 31	1.639	2506.750	8.327	7.653	537.600	7.833	9.167
F_2	9.720	2580.235	12.760	4.612	1521.030	12.943	11.972

APPENDIX V

Variances for the respective characters and generations for the cross P_2 x P_3 grown at Samaru after removing replication effects.

Generation	Variance						
	Protein	Yield	100-seed Weight	No. Seeds/ pod	No. Pods/ plant	Days to flowering	Days to maturity
P_2	3.924	1115.821	3.224	2.077	1006.033	37.078	27.944
P_3	2.046	777.760	1.077	4.100	727.756	30.678	10.822
F_1 23	3.263	2629.137	2.188	2.069	1059.533	40.689	7.600
F_1 32	3.262	1476.059	3.753	2.333	1885.545	32.689	7.578
F_2	5.011	1107.638	5.300	4.066	875.715	32.339	14.666

APPENDIX VI

Covariances of the respective characters and generations for the cross $P_1 \times P_2$ grown at Kadawa after removing replication effects.

Generation	Cross product mean square					
	Protein Vs *Yield*	Protein Vs *100-seed* weight	Protein Vs *No. Seeds/* pod	Protein Vs *No. Pods/* plant	Protein Vs *Days to* flowering	Protein Vs *Days to* maturity
P_1	-15.982	-0.632	1.842	-7.401	-2.936	-2.060
P_2	9.099	-0.515	-0.243	9.237	0.920	-0.534
F_1 12	7.699	0.904	0.338	6.036	-0.908	1.775
F_1 21	-23.904	0.288	-1.288	-12.490	-0.455	-1.267
F_2	3.991	0.579	-1.904	4.813	-1.606	-2.001

APPENDIX VII

Covariances of the respective characters and generations for the cross $P_1 \times P_2$ grown at Samaru after removing replication effects

Generation	Cross product mean square					
	Protein Vs Yield	Protein Vs 100-seed weight	Protein Vs No. Seeds/ pod	Protein Vs No. Pods/ plant	Protein Vs Days to flowering	Protein Vs Days to maturity
P_1	22.394	-0.575	-0.509	19.295	0.050	0.230
P_2	-15.805	0.022	-0.088	0.021	1.141	0.216
F_1 12	-21.743	-0.405	-1.214	0.495	-1.589	0.502
F_1 21	53.934	2.980	0.614	40.499	-5.612	0.774
F_2	-2.262	1.301	0.780	4.265	-1.262	0.525

APPENDIX VIII

Covariances of the respective characters and generations for the cross $P_1 \times P_2$ grown at Kadawa and Samaru after removing replication, location, replication x location and genotype x location effects

Generation	Cross product mean square					
	Protein Vs Yield	Protein Vs 100-seed weight	Protein Vs No. Seeds/ pod	Protein Vs No. Pods/ plant	Protein Vs Days to flowering	Protein Vs Days to maturity
P_1	7.471	62.529	0.731	11.223	-4.133	-3.631
P_2	3.282	-1.769	-0.374	0.428	0.850	-1.432
F_1 12	4.975	46.555	-0.796	12.373	**-0.989**	-3.907
F_1 21	26.364	43.823	0.086	16.692	-4.289	-2.968
F_2	-4.940	1.663	-0.330	-9.543	1.057	15.257

APPENDIX IX

Covariances for the respective characters and generations for the cross P_1 x P_2 grown at Kadawa after removing replication effects

Generation	Cross product mean squares					
	Protein Vs Yield	*Protein* Vs 100-seed weight	*Protein* Vs No. Seeds/ pod	*Protein* Vs No. Pods/ plant	*Protein* Vs Days to flowering	*Protein* Vs Days to maturity
P_1	-42.15	3.051	-0.919	-20.757	1.050	-2.371
P_2	-2.737	-0.007	0.505	-3.797	-2.844	-0.859
F_1 13	-13.03	-0.992	-0.087	-1.360	-2.997	-2.451
F_1 31	17.707	1.79	-0.36	7.38	0.046	0.443
F_2	-18.740	0.378	-0.022	-12.733	-1.902	-1.493

APPENDIX I

Covariance for the respective characters and generations for the cross $P_2 \times P_3$ grown at Samaru after removing replication effects.

Generation	Cross product mean square					
	Protein Vs Yield	Protein Vs 100-seed weight	Protein Vs No. Seeds/ pod	Protein Vs No. Pods/ plant	Protein Vs Days to flowering	Protein Vs Days to maturity
P_2	11.006	-1.298	1.449	17.41	-4.139	-2.412
P_3	15.722	-0.635	1.715	12.109	**0.376**	-0.165
F_1 23	22.299	-0.071	-0.270	28.574	-6.392	-1.736
F_1 32	-25.428	0.551	-0.936	-8.111	-4.218	0.494
F_2	3.766	0.682	-0.470	1.667	0.468	-0.057