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GENETICAL LINKAGE IN THE COWPEA

(*VIGNA UNGUICULATA* (L.) WALP

A THESIS SUBMITTED BY

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I the undersigned, ASANTE, E.I.K., the author of this thesis do hereby declare that no part or parts of this thesis has been submitted for a degree elsewhere.

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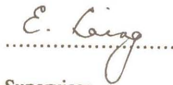

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ABSTRACT

The investigation of the local (Ghanaian) varieties of cowpeas confirms that the varieties are generally selfers but can be cross-fertilized. Inheritance and linkage analysis were based on F_2 data. The following vegetative characters were found to be monogenic: chlorophyll factor, plant pigmentation, and flower colour. However, it is likely that about five factors condition seed-coat pattern. The presence of R, the gene for red seed-coat pattern, suppresses the small eye seed-coat pattern. The following traits were observed to be metrical characters: pod length, seed weight, number of seeds per pod, leaf length and percentage seed set. There was possible linkage of 2 loci in seed coat pattern. Major gene and polygene linkage was found between chlorophyll factor and median leaf length, seed size and seed coat pattern, and flowering-time and chlorophyll factor.

Six linkage systems involving different genes were observed. Pairs of genes and their linkage values are as follows:

(i) Black seed-coat and Brown small eye seed-coat pattern

36.07%

Bl ———————— Y_{br}

(ii) Brown seed-coat pattern and streakless seed-coat pattern

25.72%

Br ———————— S_L

(iii) Pale green patch at leaflet base and Purple flower

30.32%

Pgp ———————— P_f

(Treated as disturbed linkage)

24.32%

Pgp ———————— P_f

(In the face of partial manifestation)

(iv) Red bud-tip and Red calyx

10.97%

B^R ———————— R_{cy}

(v) Purple branch-base and Red leaflet-base ; (vi) Red pod tip and Red calyx

13.02%

———————— L_{rb} ;

20.08%

p^t ———————— R

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CHAPTER 1

INTRODUCTION

Vigna unguiculata (L.) Walp commonly called cowpea belongs to the plant family Papilionaceae. It is the main cultivated species of the genus *Vigna* and is grown throughout the tropics and subtropics as an annual crop. Varieties have different growth habits namely, semierect, erect or climbing, and pods are of different shapes - curved, crescent or linear. The stems bear dark green or light green trifoliate compound leaves with two lateral leaflets which are almost identical in shape, and a median leaflet different in shape from the laterals. At the base of the petiole are two green, opposite stipules. The flowers are zygomorphic and hermaphrodite. There are five sepals which are more or less fused and encircle the base of the flower after maturity. The five petals of the corolla are of three types - a posterior petal normally called the standard petal, two smaller lateral ones usually called the wings and two others, fused along their lower margins to form the keel. This is a boat-shaped structure which encloses the reproductive parts (gynoecium and androecium) of the flower (Figure 1A). Ten diadelphous stamens constitute the androecium. The gynoecium consists of a straight ovary, a hairy style and a disc-shaped stigma (Figure 1B). The cowpea is an important leguminous crop providing food for millions of people and feed for a vast number of livestock (Sellschop, 1962 in Agble, 1969). The chemical composition of the seeds is similar to that of most edible legumes, consisting of about 24 per cent protein, 62 per cent soluble carbohydrates and small amounts of other nutrients (Elras, 1964 in Singh and Rachie, 1985).

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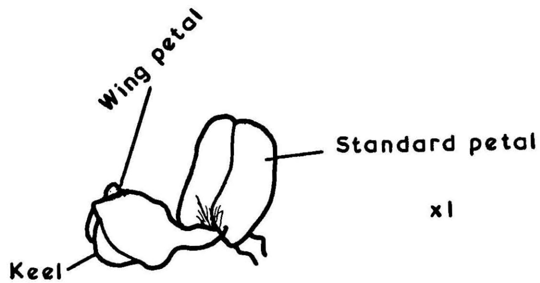
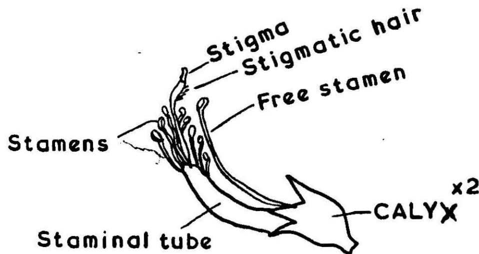


AN OPENED FLOWER OF THE COWPEA SHOWING THE THREE MAIN TYPES OF PETALS

FIG. 1 A



A COWPEA FLOWER (WITH ALL PETALS REMOVED) SHOWING THE REPRODUCTIVE PARTS

FIG. 1 B

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The cowpea is almost ideal for plant breeding and genetics research. It is a diploid with a relatively short life cycle which makes it possible to raise 2-3 generations in a year. The large flowers and untwisted keels make the cowpea one of the easiest legumes to emasculate and pollinate (Singh and Rachie, 1985). Although the cowpea has been reported to undergo limited outcrossing (Harland, 1919a; Mackie and Smith, 1935; Purseglove, 1968; Rachie and Silvestre, 1977; Williams and Chambliss, 1980 in Singh and Rachie, 1985), it exhibits self-pollination under most environmental conditions. Although much work has been done on the cowpea, research on genetical linkage has been minimal, and much of the information on linkage need further study and verification. The aim of this study, therefore, is to carry out further linkage analysis in the crop.

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CHAPTER 2

LITERATURE REVIEW

2.1 Segregation of major genes.

Segregation analysis of suitable genes has contributed much to genetical method of investigation; for instance, the analysis of the organization of linkage groups depends to a large extent on the detection of dependent segregation of two or more genes.

A given distinction between two types is controlled by a single factor. This hypothesis can be tested, primarily, by two different methods:

(i) showing that in a diploid, only three genotypes exist for this factor: two of them are pure breeding and only one shows segregation at gametogenesis;

(ii) evidence from numerical relations of the classes in a segregating progeny. For a single factor there is only one type, (the heterozygote), capable of producing two different gametes in equal numbers, by hypothesis. On backcrossing such a heterozygote to a pure recessive, a 1:1 segregation should be obtained. An intercross of two heterozygotes gives an F_2 ratio of 3:1 in the presence of dominance.

For complementary factors, it can be demonstrated that an F_2 ratio of 9:7 and a backcross ratio of 1:3 can be obtained. The following ratios are also possible 9:3:4, 12:3:1, 13:3 and 9:6:1.

For duplicate factors an F_2 ratio of 15:1 can be obtained.

2.2 Quantitative Variability (POLYGENIC SEGREGATIONS)

More specific evidence for the multiple factor hypothesis was supplied by Nilsson-Ehle's complete Mendelian analysis of quantitatively varying colour characters of oats and wheat. The multiple-factor hypothesis for quantitative variability was given substance especially by the extensive experiments of East and Hayes (1911), Emerson and East (1913), Hayes (1913) and East (1916, in Wright, 1968).

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In his paper, East(1916,in Wright, 1968) listed eight principles that should hold under the multiple factor hypothesis, if all populations after the original cross are obtained by self-fertilization.

(i) Crosses between individuals belonging to races which, from long continued self-fertilization or other close inbreeding, approach a homozygous condition, should give F_1 populations comparable to the parental races in uniformity.

(ii) In all cases where the parent individuals may reasonably be presumed to approach complete homozygosis, F_2 frequency distributions arising from extreme variants of the F_1 population should be practically identical, since in this case all F_1 variation should be due to external conditions.

(iii) The variability of the F_2 population from such crosses should be much greater than that of the F_1 population.

(iv) When a sufficient number of F_2 individuals are available, the grandparental types should be recovered.

(v) In certain cases, individuals should be produced in F_2 that show a more extreme deviation than is found in the frequency distribution of either grandparent.

(vi) Individuals from various points in the frequency curve of an F_2 population should give F_3 populations differing markedly in their modes and means.

(vii) Individuals from the same or from different points in the frequency curve of an F_2 population should give F_3 populations of diverse variabilities extending from that of the original parent to that of the F_2 generation.

(viii) In generations succeeding the F_2, the variability of any family may be less but never greater than the variability of the populations from which it came.

When the distribution of the alleles is not polarised, F_2 individuals may arise that fall beyond the phenotypic range of the parental generation. This is known as transgressive segregation.

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2.2.1. **Number of Loci**

Castle (1922 in Wright, 1968) raised the question of the number of independently segregating pairs of alleles from his investigation on the rabbit-cross. The formula applied for the estimate of number of loci is subject to limitations because of the many assumptions involved.

In his estimate he assumed that the loci are segregating independently of each other and that their effects are additive; P_1 and P_2 representing lower and higher parents respectively. Taking the grade of the lower parent as the base, with genotype $\Sigma \alpha_i \alpha_i$, it is convenient to represent the differential contribution of a heterozygote Aa by α_1, and the increment contributed by a second dose of A by α_2 .

Genotypes	Contribution	F_2 frequency
AA	$\alpha_1 + \alpha_2$	$\frac{1}{4}$
Aa	α_1	$\frac{2}{4}$
aa	0	$\frac{1}{4}$

$$P_2 - P_1 = \Sigma\alpha_1 + \Sigma\alpha_2$$

$$F_1 = \Sigma\alpha_1$$

$$F_2 = 3/4\Sigma\alpha_1 + 1/4\Sigma\alpha_2$$

$$\sigma^2_{F2} - \sigma^2_E = \frac{1}{16}[3\Sigma\alpha_1^2 + 2\Sigma\alpha_1\alpha_2 + 3\Sigma\alpha_2^2]$$

To obtain an estimate of the number of independent loci, it is necessary to make assumptions with respect to the signs and relative magnitudes of the contributions α_1 and α_2 of the loci. We assume that

(i) the parents are at opposite extremes (α_1 and α_2 positive at all loci);

(ii) there is semidominance ($\alpha_2 = \alpha_1$) at all loci; and

(iii) all loci make equal contributions (all are equal in value).

From these assumptions we derive the formula for number of loci (n) as follows:

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$$\bar{P}_2 - \bar{P}_1 = 2n\alpha_1$$

$$\bar{F}_2 = \bar{F}_1 = n\alpha_1$$

$$\sigma^2_{F2} - \sigma^2_E = 1/2\ n\alpha^2_1.$$

Thus

$$n = \frac{(\bar{P}_2 - \bar{P}_1)^2}{8(\sigma^2_{F2} - \sigma^2_E)}$$

but Wright (1968) restated it as

$$n = \frac{R^2}{8(V(F_2) - V(F_1))}$$

where

n: the number of loci, or pairs of polygene

R: the range between the mean values of the extreme phenotypes no matter in which generation they occur

$V(F_2) = \sigma^2(F_2)$: the phenotypic variance of the F_2 generation

$V(F_1) = \sigma^2(F_1)$: the phenotypic variance of the F_1 generation (Wright, 1968).

2.3 F_2 Linkage Analysis

The primary and immediate aim of linkage experiments is the estimation of recombination fraction—a summary which is interpreted in terms of map distance, giving a clue to the level of interference along the chromosome. In the absence of disturbing factors, the recombination fraction and its precision can be estimated from a backcross or an F_2.

The recombination value is affected by various factors two of which are:

(a) agents that change the recombination value itself, possibly by affecting the meiotic process of the mechanics of the chromosome (Bridges and Morgan 1923, Wallace 1954, 1957 in Laing 1957).

(b) agents that may be regarded as operating after meiosis to change the proportions of the meiotic products.

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These unusual factors can be dealt with in the following three main ways:

(a) standardization, of the environment, of the genetic material, or of both.

(b) the use of a balanced linkage experiment, or orthogonal design, in which, for each pair of linked factors, the coupling and repulsion phases are equally represented.

(c) choice of an appropriate mathematical model which, incorporating the disturbance, allows a valid estimate of the recombination fraction to be made. More than one of these means may be employed in any investigation (Laing, 1957).

2.3.1. Detection of Linkage by χ^2 Analysis of Orthogonal Functions

With good gene segregations and no linkage the relative frequencies of the four classes of the double intercross

AaBb = AaBb are as follows:

Phenotypic class	AB	Ab	aB	ab	Total
Observed number	a	b	c	d	n
Expected proportion	m_1	m_2	m_3	m_4	1

where

$$m_1 = \frac{9}{16}, \quad m_2 = m_3 = \frac{3}{16} \quad \text{and} \quad m_4 = \frac{1}{16}$$

For a χ^2 analysis, three degrees of freedom are available, which include three components:

(i) one for the deviation of the A/a segregation from the 3:1 ratio

(ii) one for the deviation of the B/b segregation from 3:1 ratio and

(iii) the remaining one for detecting association of A/a and B/b in segregation.

Segregation of A/a was tested as follows:

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Pooled Class	Class	Expected proportion
AB + Ab	A	m_A
aB + ab	a	m_a

χ^2 testing segregation of A and a depends on the comparison

$$(m_a a_A - m_A a_a) = \frac{a_A}{4} - \frac{3a_a}{4} \qquad (1)$$

where, in terms of the observed frequencies,

$a_A = a + b$

$a_a = c + d$

Various linear functions of the observed frequencies may be taken, the general form being

$$x = k_1a_1 + k_2a_2 + k_3a_3 + k_4a_4 \qquad (2a)$$

Where V_x is the random sampling variance of the linear function x, it can be shown that $\frac{x^2}{V_x}$ is distributed as a χ^2 for one degree of freedom. If the coefficients of a, b, c and d are chosen correctly the resulting χ^2 will detect deviations from some specific expectation of the class frequencies. For F_2 family segregating for two factors and from (1) our linear function of the observed frequencies can be stated as

$$x_1 = a + b - 3c - 3d \qquad (2b)$$

Comparing (2a) and (2b),

$$k_{11} = k_{12} = 1 \text{ and } k_{13} = k_{14} = -3$$

If the expected value of x, that is,

$k_1m_1 + k_2m_2 + k_3m_3 + k_4m_4$, is 0 the value of V_x is obtained from the formula $1/n\ V_x = S(mk^2)$ where n is number of individuals in the family.

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If the expected value of x is not 0 this formula for V_x does not hold.

Therefore coefficients are chosen to make the expectation of x zero.

In this case

$k_1m_1 = \frac{9}{16}$, $k_2m_2 = \frac{3}{16}$, $k_3m_3 = -\frac{9}{16}$, $k_4m_4 = -\frac{3}{16}$ and so S(km) = 0.

Then

$$\frac{1}{n}V_x = S(mk^2) = \frac{1}{16}(9+27+3+9) = 3$$

$$\therefore V_x = 3n \text{ and } \chi^2 = \frac{x^2}{3n}$$

Therefore χ^2 testing the deviation of the A/a segregation from the 3:1 ratio is given by

$$\chi^2_{1(A:b)} = \frac{(a+b-3c-3d)^2}{3n} \qquad (3a)$$

Similarly, for the B/b segregation, the χ^2 testing the deviation from the 3:1 ratio is given by

$$\chi^2_{1(B:b)} = \frac{(a-3b+c-3d)^2}{3n} \qquad (3b)$$

For the test of linkage, the two genes are each expected to segregate in the 3:1 ratio. Thus

= (A - 3a) (B - 3b) = AB - 3Ab - 3aB + 9ab

Thus the linear function becomes

$$x_3 = a - 3b - 3c + 9d \qquad (2c)$$

It follows from this that

$k_3m_1 = \frac{9}{16}$, $k_3m_2 = -\frac{9}{16}$, $k_3m_3 = -\frac{9}{16}$. $k_3m_4 = \frac{9}{16}$

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Then $\frac{1}{n}V_x = \quad S(mk_3^2) = \quad \frac{1}{16}(9+27+27+81) = 9$

$$\therefore V_x = 9n \text{ and } \chi^2 = \frac{x^2}{9n}$$

Therefore $\chi 2$ testing association of the two primary factors A:a and B:b in segregation is given by

$$\chi^2_{1(L)} = \frac{(a-3b-3c+9d)^2}{9n} \qquad (3c)$$

A summary for the three formulae that test for deviation of the two primary factors from the ratio 3:1 segregation and the test for linkage is therefore as follows:

$$\chi^2_{1(A:a)} = \frac{(a+b-3c-3d)^2}{3n}$$

$$\chi^2_{1(B:b)} = \frac{(a-3b+c-3d)^2}{3n}$$

$$\chi^2_{1\,(Linkage)} = \frac{(a-3b+3c+9d)^2}{9n}$$

2.3.1.1 **Disturbed Linkage Detection**

Considering a case where one of the loci is segregating by a 9:7 ratio, and for a χ^2 analysis of orthogonal functions, the following summary is arrived at for linkage detection:

$$\chi^2_{1(Linkage)} = \frac{(7a-21b-9c+27d)^2}{189n}$$

or the following hypothetical 2x2 contingency table can be used for linkage detection as follows:

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	dark	light	
male	a	b	a + b
female	c	d	c + d
	a + c	b + d	N

where a,b,c and d are observed numbers.

$$\chi^2 = \frac{(ad-bc)^2 N}{(a+b)(a+c)(b+d)(c+d)} \qquad (5)$$

2.3.2 **Estimation of Linkage**

The significance of evidence for linkage is a useful preliminary before making a statistical estimate, such as the intensity of linkage (Fisher, 1946).

Two criteria must be satisfied in the case of linkage estimation, consistency and precision. This implies that the estimate should have the smallest variance, or standard error, that the data can give. The method of maximum likelihood (Fisher 1922, 1925) with its application as a system of scoring data (Fisher 1935, 1946) has been shown always to lead, in the theory of large samples, to an efficient statistic, i.e. an estimate having the smallest standard error.

General

For a sample of n observations, all independently distributed with the same frequency function, the logarithm of likelihood is L, where L is a function of just one unknown parameter y. Then the usual maximum likelihood (ML) equation for y is

$$S(y) \equiv \frac{dL}{dy} = 0 \qquad (6)$$

with solution $\hat{y}$.

Expected amount of information in the sample is defined as

$$I(y) = -\frac{d^2L}{dy^2} \qquad (7)$$

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In testing the significance of the departure of $\hat{y}$ from some hypothetical value y_o, we can estimate the amount of information for $y = y_o$ (i.e. $I(y_o)$, can be found) and apply the statistic

$$\frac{\hat{y} - y_o}{[I(y_o)]^{-1/2}} = (\hat{y} - y_o)\,[I(y_o)]^{1/2}, \quad (8a)$$

Alternatively, the χ^2 with one degree of freedom given by

$$\chi_1^2 = (\hat{y} - y_o)^2\, I(y_o) \qquad (8b)$$

can be used.

2.3.2.1 **Application to Double Intercross**

Suppose that the recombination fraction for males is p_1 and for females p_2 consider the mating:

AB/ab = AB/ab.

Average gametic output of each is as indicated by the first line of the data below, where P is replaced by p_1 or p_2 according to sex.

Phenotype	AB	Ab	aB	ab	Total
Expected numbers	$\frac{1}{4}n(2+P)$	$\frac{1}{4}n(1-P)$	$\frac{1}{4}n(1-P)$	$\frac{1}{4}nP$	n
Observed	a	b	c	d	n

where $P = (1 - p_1)(1 - p_2)$

$$e^L = \left(\frac{2 + P}{4}\right)^a \left(\frac{1 - P}{4}\right)^{b+c} \left(\frac{P}{4}\right)^d$$

2.3.3 **Product Formula**

This formula accounts for disturbed linkage or segregation in one factor.

Considering the following table (Bailey, 1961):

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Phenotype	AB	Ab	aB	ab	Total
Expected number	$\frac{n\mu(2+P}{3\mu+1}$	$\frac{n\mu(1-P)}{3\mu+1}$	$\frac{n(1-P)}{3\mu+1}$	$\frac{nP}{3\mu+1}$	n
Observed number	a	b	c	d	n

where μ is the differential viability.

The product formula (Fisher and Balmakund, 1928; Immer, 1930) consists in equating the ratio ad/bc to the expression given by replacing each observed number by its expectation, i.e.

$$\frac{P(2+P)}{(1-P)^2} = \frac{ad}{bc}$$

The estimate of μ is given by the ML method-

$L = \text{const} + a \log(2+P) + (b+c)\log(1-P) + d \log P.$

Differentiating then gives the score

$$S_P \equiv \frac{dL}{dP} = \frac{a}{2+P} - \frac{b+c}{1-P} + \frac{d}{P} = 0$$

The ML estimate of P is thus provided by the equation $S_P = 0$, ie.

$$nP^2 - (a-2b-2c-d)P - 2d = 0$$

Amount of information about P is

$$I_P = -E\frac{d^2L}{dp2} = \frac{n(1+2P)}{2P(1-P)(2+P)}$$

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$$e^{L} \propto \frac{\mu^{a+b}(2+P)_{a}(1-P)^{b+c}P}{(3\mu + 1)^{n}}$$

Thus

$$S\mu = \frac{\partial L}{\partial \mu} = \frac{a+b}{\mu} - \frac{3n}{3\mu + 1}$$

$$\mu = \frac{a + b}{3(c + d)}$$

the information function for μ is

$$I\mu\mu = \frac{3n}{\mu(3\mu + 1)^{2}}$$

Amount of information on P is

$$Vp = \frac{2 P (1 - P) (2 + P)}{n(1 + 2 P)}$$

2.3.4 Partial Manifestation: Disturbed Linkage

Double intercross with A $\longrightarrow$ a

We assume a proportion λ, of A phenotypes are misclassified as a; we can write the observed and expected numbers as shown below

(Bailey, 1961):

	Observed	Expected
AB	a	$\frac{1}{4}n(2+P)(1-\lambda)$
Ab	b	$\frac{1}{4}n(1-P)(1-\lambda)$
aB	c	$\frac{1}{4}n[1-P) + \lambda(2+P)]$
ab	d	$\frac{1}{4}n[P+\lambda(1-P)]$
Total	n	n

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The likelihood is

$$e^{L} \propto (2 + P)^{a} (1-P)^{b} (1- \lambda)^{a+b} [(1-P) + \lambda(2+P)]^{c}[P + \lambda(1+P)]^{d}$$

This yields the scores

$$S_P = \frac{a}{2+P} - \frac{b}{1-P} - \frac{C(1- \lambda)}{(1-P)+ \lambda(2+P)} + \frac{d(1- \lambda)}{P + \lambda(- P)}$$

ML solutions are found to be

$$S_\lambda = - \frac{a+b}{1-\lambda} + \frac{c(2+P)}{1-P+\lambda(2+P)} + \frac{d(1-P)}{P+\lambda(1-P)}$$

$$\hat{P} = \frac{ab + 3ad - 2bc}{4ab + 3ad + bc}$$

$$1 - \hat{\lambda} = \frac{a}{a+c} + \frac{b}{3(b+d)}$$

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The large -sample variance of P is

$$\mathrm{Var}(P) = \frac{4(2+P)^2(1-P)^2}{27n(1-\lambda)}\left[4\lambda + \frac{1+2P}{(2+P)(1-P)}\right]$$

$$\mathrm{Var}(\hat{\lambda}) = \frac{4(1-\lambda)}{27n}\left[2(1-P)(1+2P) + (4P^2-2P+7)\right]$$

In practice

$$\mathrm{Var}(\hat{\lambda}) = \frac{ac}{(a+c)^3} + \frac{bd}{9(b+d)^3}$$

The test for linkage, admitting partial manifestation, comes out to be

$$\chi^2_1 = \frac{16(ad-bc)2}{3n(a+b)(c+d)}$$

2.4 Linkage and Selection

When genes are linked selection tends to build up 'balanced' combinations in which the genes are predominantly in the repulsion phase, thus minimising the effect of chromosome as a whole. To keep the genes in combinations appreciably different from a random arrangement either the selection has to be strong or the linkage must be very strong (Lewontin, 1964; Mather, 1941).

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CHAPTER 3

MATERIALS AND METHODS

3.1 Parental, F_1 and F_2 plants.

The investigation was carried out on experimental plot behind the carpenter's Workshop of the Department of Botany, University of Ghana, Legon.

Six parental cowpea (Vigna unguiculata (L) Walp) varieties collected from the Department of Crop Science, University of Ghana, Legon were used. These parental cowpea varieties were:

Dark Mottled (DM)
Ibadan Market (IM)
IVX 2724-OIF (IVX)
Local Sesquipedalis (LS)
1977
4557

The characters which were selected for this study relate to:

1. The difference in the form of leaflets base chlorophyll. Leaflets base is either light green patch or normal.
2. The difference in the colour of the flower. Flower colour is either purple or white.
3. The difference in the seed-coat pattern. The seed coat patterns are dark mottled, black, holstein, small eye (brown), watson and red with streaks.
4. The difference in the pigmentation of branch base. The branch base is either red pigmented or non-pigmented i.e possesses the normal green colour of the stem.

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5. The difference in the colour of the tip of the flower buds. They are either red or light green.

6. The difference in the pigmentation of the base of the peduncles. The peduncle bases are either pigmented or non-pigmented i.e. possess the normal green colour of the stem.

7. The difference in the pigmentation of the base of the petiolets. They are either pigmented or non-pigmented i.e. possess the normal green colour of the stem.

8. The difference in the colour of the sepals. They are either red or light green.

9. The difference in the colour of the tip of the unripe pods. They are either red or light green.

10. The difference in the pigmentation of the whole plant. The whole plant is either non-pigmented or is pigmented in one or many parts.

11. The difference in flowering times: Number of days from seed germination to flower opening is constant for each variety. In order to be able to discriminate, the early flowering time of 30 to 31 days was always crossed with the late flowering time of 38 to 40 days.

12. The difference in the length of the median leaf. Leaf length varies in some forms but constant for each variety. To be able to discriminate, the long leaf of 10.7 ± 0.25 to 12.11 ± 0.31 cm was crossed with the short one of $6.86+0.27$ to 8.27 ± 0.19 cm.

13. The difference in the number of seeds per pod. The high number of seeds per pod of 15 to 20 was crossed with the lower number of seeds per pod of 10 to 14.

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14. The difference in percentage seed set. The high percentage seed set of 90.5 ± 6.9 to 97.5 ± 5.10 was crossed with the low percentage seed set of 64.16+3.55.

15. The difference in the length of the pods. The longer pod of 17.01 ± 1.65 to 19.7 ± 1.05 cm was crossed with the shorter pod of 13.04 ± 1.54 to 16.35 ± 1.08 cm.

16. The difference in 100-seed weight. The larger seed of 0.148 ± 0.003 to 0.197 ± 0.0005g was crossed with the smaller seed of 0.117 ± 0.002 to 0.120 ± 0.003g.

With respect to these factors, the six parental varieties are described as follows:

DM: normal leaflet base; purple flower colour; dark mottled seed coat; pigment at bases of branch, peduncle, petiolet; whole plant pigmentation; red sepal; red pod tip; red flower bud tip; late flowering time; small median leaf length; high number of seeds per pod; high percentage seed set; short pod and small seed.

IM: light green patch at leaflet base; purple flower; black seed coat; pigment at bases of branch, peduncle, petiolet; whole plant pigmentation; red sepal; red pod tip; red flower bud tip; early flowering time; large median leaf length; high number of seeds per pod; low percentage seed set; long pod and large seeds.

IVX: normal leaflet base; purple flower; holstein seed coat pattern; pigment at bases of branch, peduncle, petiolet; whole plant pigmentation; red sepal; red pod tip; large median leaf length; high number of seeds per pod; high percentage seed set; long pod and large seeds.

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IVX: normal leaflet base; purple flower; holstein seed coat pattern; pigment at bases of branch, peduncle, petiolet; whole plant pigmentation; red sepal; red pod tip; red flower bud tip; early flowering time; large median leaf length; high number of seeds per pod; high percentage seed set; long pod and large seeds.

LS: normal leaflet base; purple flower; red seed coat with streaks; pigment at bases of branch, peduncle, petiolet ; whole plant pigmentation; green sepal; light green unripe pod tip; light green flower bud tip; late flowering time; large median leaf length; high number of seeds per pod; high percentage seed set; long pod and large seeds.

1977: normal leaflet base; white flower; brown small eye seed coat pattern; pigment at bases of branch, peduncle, petiolets; whole plant pigmentation; green sepal; light green unripe pod tip; early flowering time; small median leaf length; small number of seeds per pod; high percentage seed set; short pod length and small seeds.

4557: normal leaflet base; white flower; Watson seed coat pattern; no pigment at bases of branch, peduncle, petiolet; whole plant non-pigmentation; green sepal; light green unripe pod tip; late flowering time; small median leaf length small number of seeds per pod; high percentage seed set; short pod length and small seeds.

Thirty seeds each from the parental varieties were sown in the field on Thursday, 7/8/90.

Two varieties with contrasting characters were crossed as follows to generate F_1 seeds:

DM X IM

DM X IVX

1977 X LS

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1977 X IM

4557 X LS

Individuals in the segregating progeny were marked by labels. Each plant at maturity was studied carefully and classified according to the characters under study. Similarly, at the time of harvest a single typical pod was picked from every plant and then classified according to the characters under study.

The main characters studied during the investigation were grouped under major gene and polygene.

Major gene

a. Chlorophyll factor (pale green patch at leaflet base).

b. Anthocyanin factors:

(i) sepal pigmentation (plate 2)
(ii) flower bud tip pigmentation (plates 2 and 3A)
(iii) unripe pod tip pigmentation (plates 3A and 3B)
(iv) peduncle base pigmentation
(v) base of branch pigmentation
(vi) petiolet base pigmentation (Plates 4A and 4B)

c. Flower colour

Polygene

(i) pod length
(ii) seed weight
(iii) number of seeds per pod
(iv) leaf length
(v) percentage seed set
(vi) seed-coat pattern

Table 1 shows a list of gene indices including those for these characters studied.

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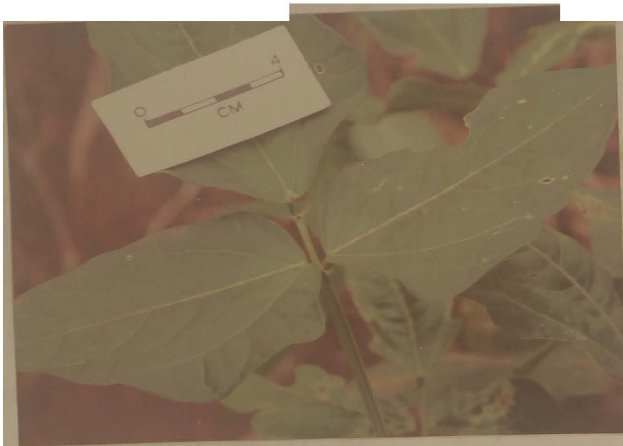

PLATE 1. IM Leaves showing Chlorophyll factor (pale green patch at leaf base) (8/6/91).

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PLATE 2. DM plant showing

(i) Sepal pigmentation (red calyx).

(ii) Flower bud tip pigmentation (red bud tip).

Note diseased leaves in the foreground (8/6/91)

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PLATE 3A. 1977 plant showing

Unripe pod-tip pigmentation (light green tip). Note

(i) the light green calyx and light green tip of the flower bud in the background.

(ii) the diseased leaves and

(iii) the insect resting on the pod. (8/6/91)

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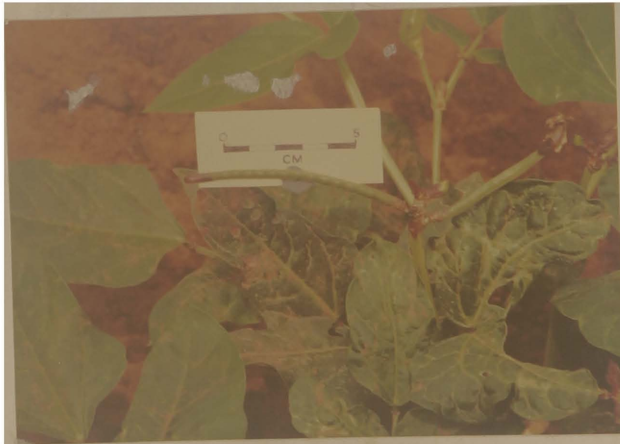

PLATE 3B. DM plant showing unripe pod tip pigmentation (red pod tip).

Note the diseased leaves. (8/6/91)

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PLATE 4A. WB plant showing petiolet base pigmentation.

(red pigment at the base of the petiolet)(8/6/91)

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PLATE 4B. 4557 plant showing petiolet base pigmentation (green base of the petiolet). (8/6/91)

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TABLE 1

Cowpea gene index. (Extract from Singh and Rachie, 1985)

(* Author's own suggestion)

efered Symbol	Symbol	Character	Reference
	(*B*, *Bb*), *P*^{b}	Black seed coat; also conditions anthocyanin production in the pod tip, calyx and peduncle; heterozygote produces mottled seeds.	Harland, 1919a,b, 1920; Franckowiak and Barker, 1974; symbol by Fery, 1980
	(*Y*)	Brown pod; dominant to straw colour	Saunders, 1960b; symbol by Fery, 1980
		Brown seed-coat dominant to red seed-coat	*
		Red bud tip	*
		Buff seed-coat	Brittingham, 1950
	(*R*)	Colour factor (general)	Spillman, 1912; Harland 1919a Spillman and Sando, 1930
2	(*Be*)	New Era seed-coat pattern	Franckowiak and Barker, 1974, symbol by Fery, 1980.
f	(B^{f})	Blue seed-coat (fine speckling pattern)	Franckowiak and Barker, 1974; symbol by Fery, 1980.
	(B^{l})	Light spots on Black seed-coat	Franckowiak and Barker, 1974; symbol by Fery, 1980.
s	(B^{s})	Black spots on seed-coat	Franckowiak and Barker, 1974; symbol by Fery, 1980.

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!^{t}	(B^t)	Taylor seed-coat pattern	Franckowiak and Barker, 1974; symbol by Fery, 1980.
ɘ	(*C*)	Cerise (reddish) pod	Saunders, 1960a; symbol by Fery, 1980.
	w	Dark flower colour	Harland, 1919a.
		New Era seed-coat pattern; also conditions anthocyanin production in the pod tip, calyx and peduncle	Harland, 1920.
f-1	*Ef1*	Early flowering - 1	Ojomo, 1971; symbol by Fery, 1980.
f-2	*Ef2*	Early flowering - 2	Ojomo, 1972; symbol by Fery, 1980.
		Tinged flower	Harland, 1920.
ı	(*G*)	Green pod; dominant to *gny* and recessive to *Gnd*; conditions similar colour response in leaf calyx and dorsal surface of standard	Sen and Bhowal, 1961; symbol by Fery, 1980.
ı^d	(G^D)	Dark green pod; dominant to Gn and *gnY*; conditions similar colour in leaf, calyx and dorsal surface of standard	Sen and Bhowal, 1961; symbol by Fery, 1980.
ı^Y	(*g*)	Yellow green pod; recessive to *Gn* and *Gnd*; conditions similar colour in leaf, calyx and dorsal surface of standard	Sen and Bhowal, 1961; symbol by Fery, 1980.
r		Green bud; dominant white bud	Singh and Jindla, 1971.
-1	(*H*)	Holstein seed-coat pattern	Spillman, 1911, Sen and Bhowal, 1961.

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h-2	(*H2*)	Holstein seed-coat	Harland, 1919a; symbol by Fery, 1980.
L		Pale flower	Harland, 1919a.
Lgf-1	(*Lg-a*)	Light-green foliage-1; complementary to *Lgf-2*	Kolhe, 1970; symbol by Fery, 1980.
Lgf-2	(*Lg-b*)	Light-green foliage-2; complementary to *Lgf-1*	Kolhe, 1970; symbol by Fery, 1980
Llf		Long leaf	Kolhe, 1970.
Lrb		Red leaflets-base	*
Ls		Leaf size; small leaf recessive to large leaf	Krishnaswamy et al., 1945.
Mv		Mottled seed-coat pattern	Franckowiak and Barker, 1974.
N		Anthocyanin pigment factor	Spillman, 1912; Spillman and Sando, 1930.
Na	(*E*)	Narrow eye seed-coat pattern.	Spillman and Sando, 1930; symbol by 1980.
O		Hilum ring seed-coat pattern.	Saunders, 1960a.
P		Purple pod; dominant to green; also causes anthocyanin production in the calyx and peduncle	Harland, 1920.
P^b,	B1	Red pod-tip	Mortensen and Brittingham, 1952.
P_b		Purple petiole base	Sen and Bhowal, 1961.
Pbr		Purple branch-base	Sen and Bhowal, 1961.
Pf		Purple flower	Kolhe, 1970.

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'gp		Pale-green patch at leaf base	*
'g	*(g)*	Pale-green plant	Saunders, 1960a; symbol by Fery, 1980.
'r		Whole plant non-pigmented	*
:		Red seed-coat	Spillman, 1912.
:cy		Red calyx	*
'l		Streakless seed-coat	*
'pk	*(S)*	Speckled seed-coat	Saunders, 1959; symbol by Fery, 1980.
:tp	*(E)*	Stippling seed-coat pattern; characteristic of New Era.	Saunders, 1959; symbol by Fery, 1980.
:tx		Sesquipedalis-like texture of pod (soft)	Premsekar and Raman, 1972; symbol by Fery, 1980.
'		Seed-coat mottling; charateristic of Brabham.	Saunders,1959.
'i-1	*(T,V)*	Vining-1	Brittingham, 1950; Norton, 1961; Kolhe,1970; Singh and Jinda, 1971; symbol by Fery, 1980.
'i-2	*(V,V2,T2)*	Vining-2	Norton, 1961;Kolhe, 1970; Singh and Jindla, 1971; symbol by Fery, 1980.

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i-3	*(T3)*	Vining-3	Singh and Jindla, 1971; symbol by Fery, 1980.
	I,W,D	Watson seed-coat pattern; eye with indefinite margin	Spillman, 1911; Harland 1919a; Spillman and Sando, 1930;Sen and Bhowal, 1961.
'h	*(W)*	Whippoorwill-type seed-coat pattern	Spillman and Sando, 1930; symbol by Fery, 1980.
		Anthocyanin coloration in the vegetative parts.	Harland, 1991b, 1920.
		Very small eye seed-coat pattern.	Harland, 1922.
'br		Brown mottled small eye seed-coat pattern.	*
'stp		Yellow strip on petals.	Kolhe, 1970.

Phenotypic correlation coefficients between the yield components: number of seeds per pod and log of percentage seed set per pod; and pod length and number of seeds per pod were estimated.

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3.2 Quantitative Characters

3.2.1 Pod Length

Two dried pods chosen at random from each plant were used for scoring pod length. A thread was used to follow the course of a pod from the stylar end to the point of attachment of the pod to the stalk. The thread was then stretched out on a meter rule and the pod length was read off in centimetres.

3.2.2 Seed Weight

The score for seed weight was based on 100-seed weight. The seeds were dried in bright sun after harvest for seven days to ensure that seeds were of about the same dryness. The seeds were then weighed carefully by the use of the Ohaus Galaxy 1200 balance.

3.2.3 Number of Seeds per pod

Pods which were used to score pod length were opened by hand. For every pod opened, the seeds were counted and scored for number of seeds per pod.

3.2.4 Leaf Length

The score for leaf length was based on five median leaves each from a plant chosen at random. A piece of copper wire was placed from the leaf apex to the leaf base. The corresponding length was marked on the copper wire with a pen. The piece of copper wire was laid against a metre rule and the measurement was read off and recorded in centimetres.

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3.2.5 Percentage Seed Set

The pods which were used to investigate number of seeds per pod were also used for the study of this character. For every pod opened, the total number of ovules and the total number of seeds were counted and recorded. The total number of seeds was expressed as a percentage over the total number of ovules and then scored for percentage seed set.

3.2.6 Plant Pigment, Flower and Seed-coat Colours

The Exotica Horticulture Colour Guide (E.H.G.G.) (Graf, 1963) was used to determine plant pigmentation, flower and seed-coat colours. Colour of the inner surface of the standard petal was taken as the colour of the flower. Plant pigment (plant portion was stripped with a razor blade), flower, and seed-coat colours were matched against selected colours from the colour chart and colours that blended with those for identification were scored as plant pigment, flower, and seed-coat colours.

3.2.7 Flowering-time

This character was measured from the date the first flowers opened to the date the last flowers opened.

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CHAPTER IV

RESULTS

4.1 Primary Segregation (Major gene)

In the investigation eight characters were found to segretate in simple Mendelian fashion.

a. **Chlorophyll Factor**: F_2 segregation for this factor is presented in Table 2. The 3:1 ratio was consistent in three out of the four families studied for this character. The heterogeneity χ^2_2 testing agreement between three families was not significant (χ^2_2= 0.4942, P = 0.50 - 0.30). This suggests control by one locus, the double dose of the recessive allele *pgp* producing normal patch.

	Genotype	Phenotype
homozygous recessive	*pgp pgp*	normal
heterozygote	*Pgp pgp*	pale green patch at leaflet base
homozygous dominant	*Pgp pgp*	

b. **Flower colour**

Three families were studied for this character.

F_2 segregation for flower colour showed a 3:1 ratio and this was consistent in all the three families as presented in Table 3. The heterogeneity χ^2 = 1.9706 for two degrees of freedom has a probability of 0.5-0.30. The three families thus agree with one another in showing a 3:1 ratio for the flower factors purple flower and white flower. This suggests control by one locus, the double dose of the recessive allele *pf* producing white flower.

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TABLE 2

F_2 segregation for the factors pale green patch and normal at leaflet base

Family	Number of plants: Pale green patch	Normal	χ^2
1	108	37	0.0207
2	67	29	1.3880
3	33	14	0.2707
			1.6794
	208	80	1.1852

	χ^2	D.f	P
Deviation	1.1852	1	0.30 - 0.20
Heterogeneity	0.4942	2	0.50 - 0.30
Total	1.6794	3	

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	Genotype	Phenotype
homozygous recessive	*pf pf*	white
heterozygote	P^f *pf*	Purple
homozygous dominant	P^f P^f	Purple

c. **Flower bud tip colour**

Two families were studied for this character and from Table 4, the families are homogeneous in showing a 3:1 segregation ratio; heterogeneity χ^2 = 0.0895, P=0.80-0.70. This suggests control by one locus of the factors: pigmented bud tip and light green bud tip, the double dose of the recessive allele b^R produces a light green bud tip.

	Genotype	Phenotype
homozygous recessive	b^R b^R	light green bud cip
heterozygote	B^R b^R	Pigmented bud tip
homozygous dominant	B^R B^R	Pigmented bud tip

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TABLE 3

F_2 Segregation for the factors purple flower and white flower

Family	Number of plants: Purple	Number of plants: White	χ^2
1	54	14	0.7059
2	29	12	0.3984
3	16	8	0.8889
			1.9932
	99	34	0.0226

	χ^2	D.f.	P
Deviation	0.0226	1	0.98-0.95
Heterogeneity	1.9706	2	0.50-0.30
Total	1.9932	3	

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TABLE 4

F_2 segregation for the factors pigmented bud tip and light green bud tip.

	Number of plants		
Family	Pigmented bud tip	light green bud tip	χ^2
1	31	8	0.41880
2	43	13	0.0952
			0.5140
	74	21	0.4245

	χ^2	D.f	P
Deviation	0.4245	1	0.70-0.50
Heterogeneity	0.0895	1	0.80-0.70
Total	0.5140	2	

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d. **Flower sepal colour**

Two families were studied to investigate F_2 segregation for this character. Table 5 shows that the families agree with one another in showing a 3:1 ratio (heterogeneity χ^2 = 1.3189 P = 0.30-0.20). This suggests control by one locus of the factors red calyx and green calyx. The double dose of the recessive allele *rcy* produces light green calyx.

	Genotype	Phenotype
homozygous recessive	*rcy rcy*	light green calyx
heterozygote	*Rcy rcy*	red calyx
homozygous dominant	*Rcy Rcy*	red calyx

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TABLE 5

F_2 segregation for the factors red calyx and light green calyx.

Family	Red calyx	Light green calyx	χ^2
	Number of plants		
1	59	18	0.1082
2	39	18	1.5239
			1.6321
	97	36	0.3132

	χ^2	D.f	P
Deviation	0.3132	1	0.70-0.50
Heterogeneity	1.3189	1	0.30-0.20
Total	1.6321	2	

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e. **Flower peduncle base pigment**

One family was available for the study of this character. The two factors considered were pigmented peduncle base and green peduncle base. Fifty-two plants were studied and forty of them had pigmented peduncle base whilst twelve had no pigmented peduncle base. χ^2 value for one degree of feeedom is 0.3132, P = 0.70-0.50 shows a 3:1 ratio agreement. This suggests control by one locus of the factors, and the double dose of the recessive allele p^b produces a green peduncle base.

	Genotype	Phenotype
homozygous recessive	$p^b\ p^b$	non-pigmented peduncle base
heterozygote	$P^b\ p^b$	pigmented peduncle base
homozygous dominant	$P^b\ P^b$	

f. **Whole plant pigmentation**

Fifty-three plants were studied for this character. Forty-one of them were pigmented whilst twelve were non-pigmented. A χ^2 value for one degree of feeedom is 0.1572, P = 0.70-0.50.

This agrees with a 3:1 ratio and thus suggests control by one locus of the two factors pigmented whole plant and green whole plant, the double dose of the recessive allele p_w produces a whole green plant.

	Genotype	Phenotype
homozygous recessive	$p_w\ p_w$	whole green plant
heterozygote	$P_w\ p_w$	whole pigmented plant
homozygous dominant	$P_w P_w$	

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g. **Petiolet base pigmentation**:

Fifty-nine plants were studied for this character. Thirty-nine of these plants had pigmented petiolet base whilst twenty of them had green petiolet base. A χ^2 value of 2.4928 for one degree of freedom with P = 0.20 - 0.10, shows an agreement for 3:1 ratio. This suggests control by one locus of the factors: pigmented petiolet base and green petiolet base, the double dose of the recessive allele p^l produces green petiolet base.

	Genotype	Phenotype
homozygous recessive	$p^l p^l$	green petiolet base
heterozygote	$P^l p^l$	pigmented petiolet base.
homozygote dominant	$P^l P^l$	

h. **Unripe pod-tip pigmentation**

Fifty-one plants were studied. Thirty-nine out of these plants showed pigmented unripe pod-tip, whilst light green unripe pod tip was observed in twelve plants. A χ^2 value of 0.0735 for one degree of feedom with P = 0.80-0.70 shows an agreement for a 3:1 ratio. This suggests control by one locus of the factors: pigmented unripe pod tip and green unripe pod tip. The double dose recessive allele p^t produces light green unripe pod tip.

	Genotype	Phenotype
homozygous recessive	$p^t p^t$	light green unripe pod tip
heterozygote	$P^t p^t$	pigmented unripe pod tip
homozygous dominant	$P^t P^t$	

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4.2. Disturbed Segregation

In the investigation disturbed segregation seems to have occurred in the following factors.

a. **Chlorophyll factor**. In one of the four families studied for this factor there was a deviation from the 3:1 mendelian ratio, $\chi^2 = 0.4803$ for 1 d.f., P = 0.50-0.30). This reflects a 2-factor interaction.

Genotype	Ratio	Phenotype
$Pgp_1 - Pgp_2 -$	9	pale green patch
$Pgp_1 - p\,p_2p\,p_2$	7	normal
$pgp_1pgp_1Pgp_2-$		
$pgp_1pgp_1pgp_2pgp_2$		

b. **Branch base pigmentation**. This factor deviates from the 3:1 F_2 ratio but agrees with 9:7 segregation fashion ($\chi^2 = 1.2940$ for one degree of freedom P = 0.30-0.20). This therefore reflects a 2-factor interaction.

Genotype	Ratio	Phenotype
$Pbr_1 - Pbr_2 -$	9	purple branch base
$Pbr_1 - pbr_2\,pbr_2$	7	Non-purple branch base.
$pbr_1\,pbr_1\,Pbr_2 -$		
$pbr_1\,pbr_1\,pbr_2\,pbr_2$		

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4.3 Quantitative Inheritance

Mean values for the following quantitatively inherited features are presented in Tables 6, 7, 8, 9 and 10.

(i) pod length

(ii) percentage seed set

(iii) seed weight

(iv) number of seeds per pod and

(v) leaf length.

Pairs of polygenes and broad-sense heritability percentages are presented in Tables 11 and 12 respectively. The mode of dominance of these five characters are shown in figures 2-6. Table 13 shows the phenotypic correlation coefficients between yield components in parental and F_1 populations.

(a) Pod Length

The means of the parental, F_1 and F_2 populations for the cross: DMxIVX are presented in Table 6. The means of the F_1 and F_2 populations in comparisons with the midparent value suggest partial dominance for long pod as shown in figure 2. The number of pairs of polygenes for pod length was 3.82 (Table 11) and the broad-sense heritability estimate was 88.0% (Table 12). Pod length was highly and positively associated with number of seeds per pod as presented in Table 13. It is therefore likely that breeding for long pods would lead to high yield.

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TABLE 6

Means for Parental, F_1 and F_2 populations, with their standard errors and midparent value for pod length (cm) for the cross: DM x IVX.

Population/midparent	Mean/midparent value (cm)
P_1 (IVX)	16.15 ± 0.15
P_2 (DM)	13.04 ± 0.22
Midparent	14.60
F_1	15.56 ± 0.26
F_2	15.55 ± 0.62

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ILLUSTRATION OF MODE OF DOMINANCE IN THE COWPEA FOR POD LENGTH (CM). FOR THE CROSS : DM x IVX .

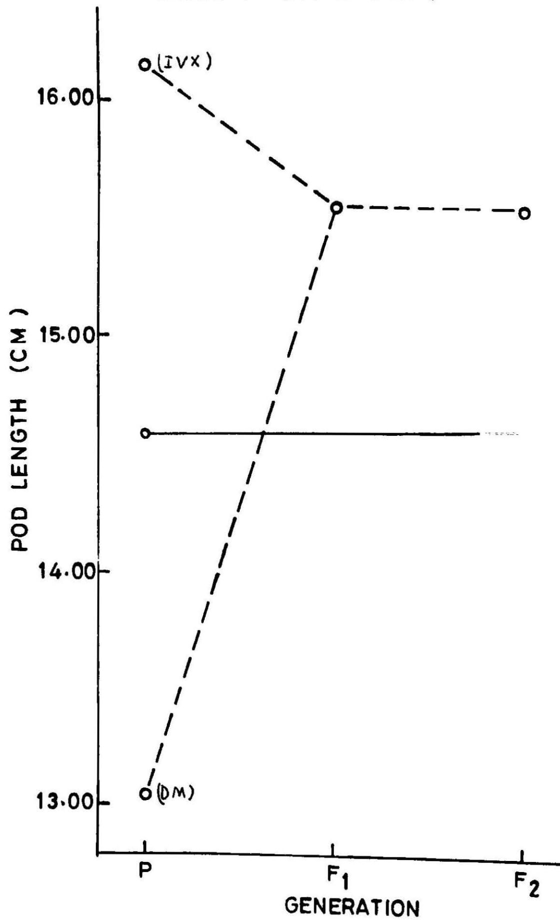

Fig. 2. The points show the mean values of the two parent strains, the F_1 and the F_2 generations. The midparent value is shown by horizontal line.

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b. Percentage Seed set

The means of the parental, F_1 and F_2 populations are presented in Table 7. There was heterosis in the F_1 and F_2 generations for the cross: 4557 x LS (figure 3).

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TABLE 7

Means for parental, F_1 and F_2 populations with their standard errors and midparent value for percentage seed set for the cross: 4557 x LS.

Population/midparent	Mean/midparent value (%)
P_1 (LS)	97.50 ± 1.14
P_2 (4557)	69.16 ± 2.09
Midparent	83.33
F_1	78.94 ± 2.84
F_2	69.90 ± 3.61

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From the figure, the F_1 and F_2 are lower in value than the midparent, and the heterosis is consequently negative in sign. The extent of the F_2 heterosis is -13.43% whilst the F_1 heterosis is -3.39%. This character is conditioned by 4.76 pairs of polygenes as shown in Table 11. The broad-sense heritability estimate was 64.87% which compares favourably with the estimate of 69.52% for number of seeds per pod as shown in Table 12.

c. **Seed Weight**

The means of the parental, F_1 and F_2 populations based on 100-seed weight for the cross: DM x IVX are presented in Table 8. A comparison of the midparent value with the F_1 and F_2 means shows that there is additive effect of the loci conditioning seed size (figure 4) and F_1 heterosis of -0.006g for small seed size. The number of pairs of polygenes for seed size was 6.01 (Table 11) and broad-sense heritability estimate was 84.94%. (Table 12)

d. **Number of seeds per pod**

Mean values of the parental, F_1 and F_2 populations for the cross: DM x I.VX are presented in Table 9. There is complete dominance for large number of seeds per pod by a comparison of midparent value with the F_1 mean whilst the F_2 mean is very close to the lower parental value, as illustrated in figure 5. This result shows the additive nature of the loci responsible for the trait. The number of pairs of polygenes for number of seeds per pod was 7.12 (Table 11). The broad-sense heritability estimate was 69.52% (Table 12). This trait, number of seeds per pod, was highly and positively associated with the logarithm of percentage seed set per pod (Table 13).

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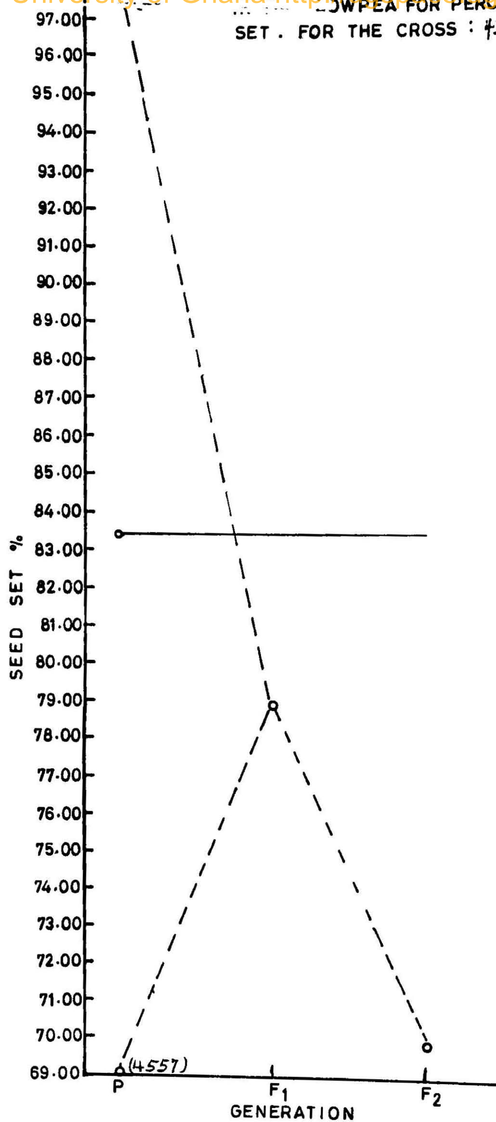

Fig. 3. The points show the mean values of the two parent strains, the F_1 and the F_2 generations. The midparent value is shown by horizontal line.

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TABLE 8

Means for parental, F_1 and F_2 populations with their standard errors and midparent value for seed weight(g) for the cross: DM x IVX.

Population/midparent	Mean/midparent value (g)
P_1(IVX)	0.148 ± 0.0004
P_2 (DM)	0.117 ± 0.0003
Midparent	0.133
F_1	0.127 ± 0.004
F_2	0.139 ± 0.006

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ILLUSTRATION OF MODE OF DOMINANCE IN THE COWPEA FOR SEED WEIGHT (g). FOR THE CROSS: DM x IVX.

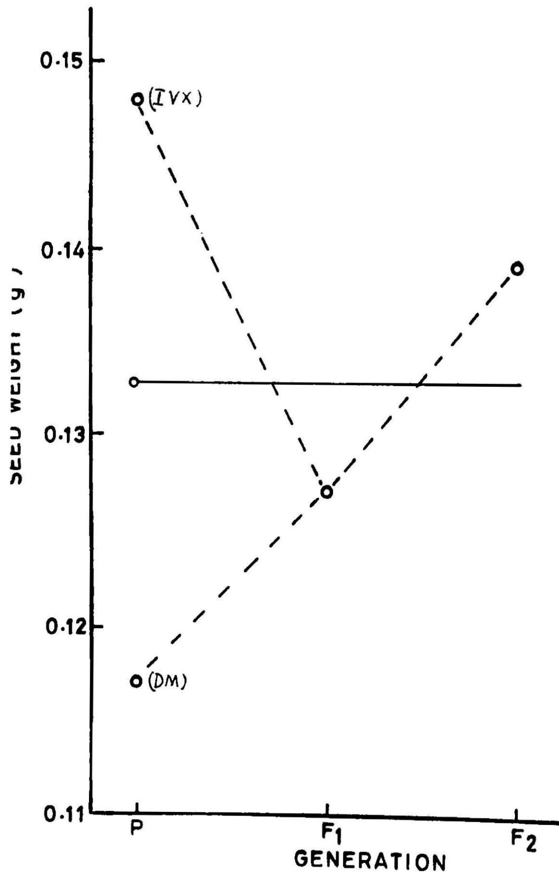

Fig. 4. The points show the mean values of the two parent strains, the F_1 and the F_2 generations. The midparent value is shown by horizontal line.

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TABLE 9

Means for parental, F_1 and F_2 populations with their standard errors and midparent value for number of seeds per pod for the cross: DM x IVX.

Population/midparent	Mean/midparent value
P_1 (IVX)	14.40 ± 0.19
P_2 (DM)	10.80 ± 0.34
Midparent	12.60
F_1	14.30 ± 0.81
F_2	10.42 ± 0.94

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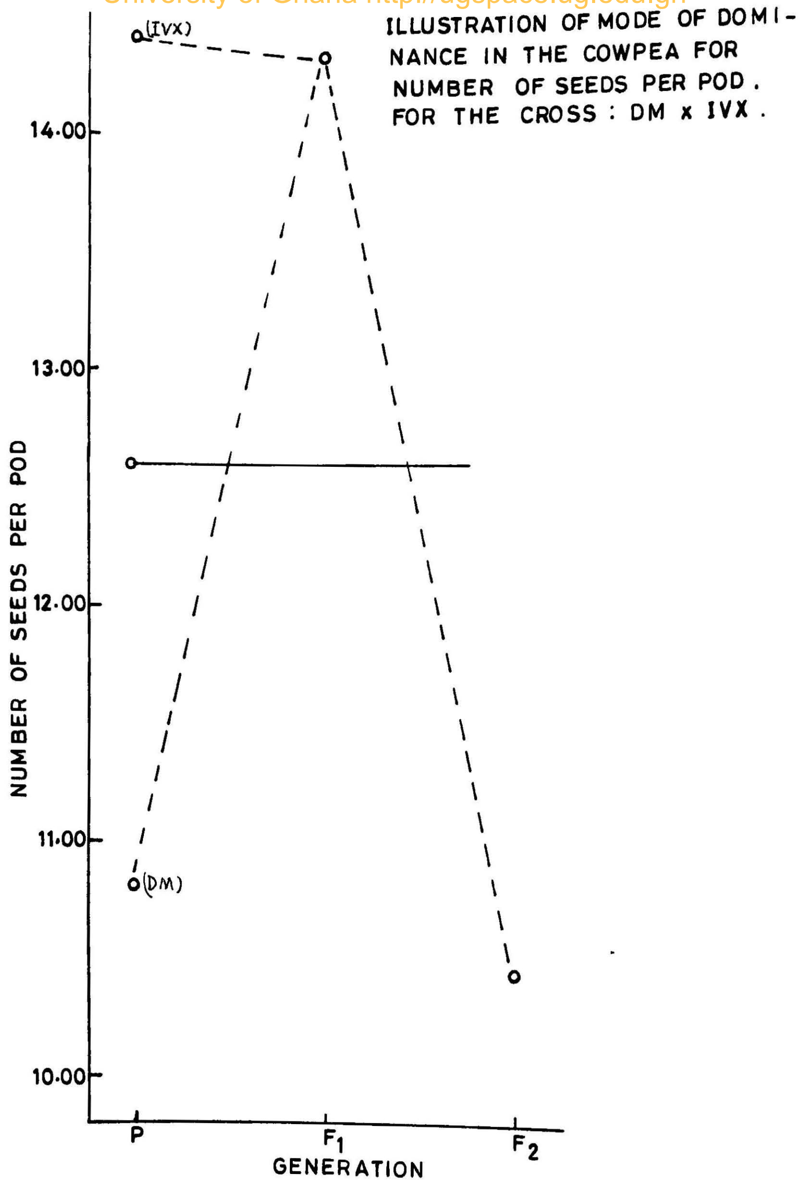

Fig. 5 . The points show the mean values of the two parent strains, the F_1 and the F_2 generations. The midparent value is shown by horizontal line.

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e. **Leaf Length (median leaf)**

The means of the parental, F_1 and F_2 populations for the cross: 1977 x LS are presented in Table 10. A comparison of the midparent value with F_1 and F_2 means shows heterosis for large leaf length as illustrated in figure 6. The extent of the F_2 heterosis was 1.40cm whilst that for the F_1 was 1.54cm. The number of pairs of polygenes conditioning leaf length was 1.75 (Table 11). The broad-sense heritability estimate was 46.69% (Table 12).

f. **Seed-coat pattern**

The following three crosses were used to study seed-coat pattern:

(i) brown eye x solid black (1977 x IM)

(ii) brown eye x solid brown (1977 x LS)

(ii) dark mottled x Watson (brown) (DM x IVX)

Table 14 gives a description of the six seed-coat patterns mentioned in this investigation. The F_1's of all the crosses gave solid seed-coat patterns except dark mottled x watson (brown) which gave mottled (dark) seed-coat pattern. The F_2's however, gave different classes of seed-coat patterns, suggesting genetic segregation as presented in Table 15.

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TABLE 10

Means value for parental, F_1 and F_2 populations with their standard errors and midparent for median leaf length (cm) for the cross: 1977 x IM.

Population/midparent	Mean/midparent value (cm)
P_1 (IM)	10.91 ± 0.57
P_2 (1977)	9.27 ± 0.22
Midparent	10.09
F_1	12.63 ± 0.38
F_2	11.49 ± 0.59

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N LEAF LENGTH (CM).

FOR THE CROSS: 1977 x IM.

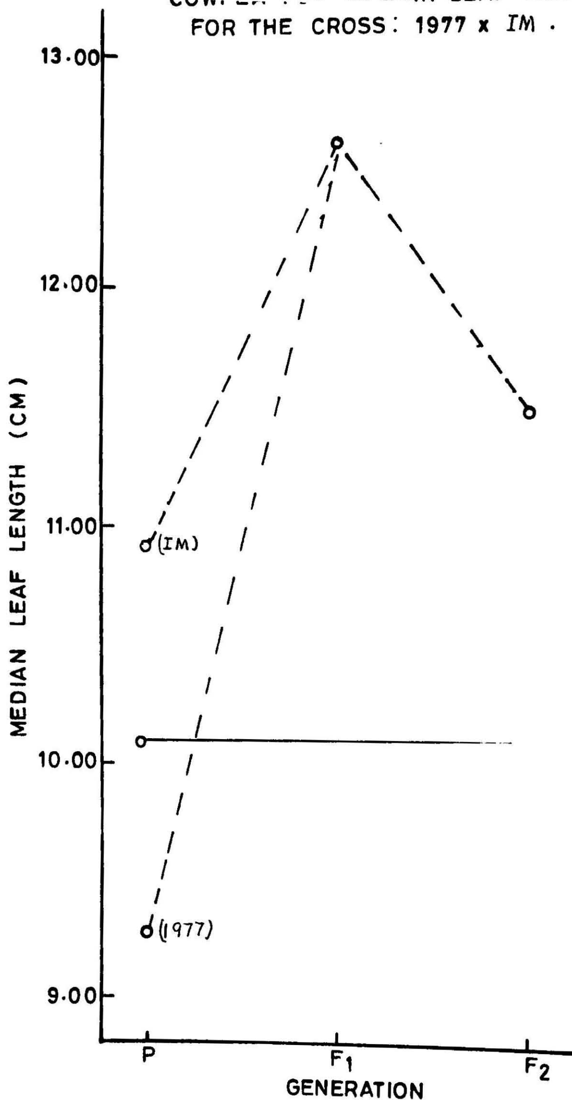

Fig. 6. The points show the mean values of the two parent strains, the F_1 and the F_2 generations. The midparent value is shown by horizontal line.

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TABLE 11

Estimates of number of pair of polygenes for pod length, percentage seed set, seed weight, number of seeds per pod and leaf length.

Character	Number of pairs of polygenes
Pod length	3.82
Percentage seed set	4.76
Seed weight	6.01
Number of seeds per pod	7.12
Leaf length	1.75

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TABLE 12

Heritability percentages (broad-sense) for pod length, percentage seed set, seed weight, number of seeds per pod and leaf length.

Character	Heritability (%)
Pod length	88.00
Percentage seed set	64.87
Seed weight	84.94
Number of seeds per pod	69.52
Leaf length	46.69

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TABLE 13

Phenotypic correlation coefficients between yield components in parental and F_1 populations

	Number of seeds per pod	Log. of percentage set per pod	Pod length
Number of seeds per pod		0.65** (F_1) 0.53** (P)	
Log of percentage seed set per pod			
Pod length	0.80** (F_1) 0.58** (P)		

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TABLE 14

Description of the five seed-coat patterns mentioned in the investigation.

Seed-coat pattern	Description
Holstein	seed colour has definite eye margin which extends over a large portion of the seed-coat.
Small eye	colour around the hilum is discontinuous consisting of two separate elongated coloured areas on either side of, and parallel to, the hilum (Saunders, 1959).
Solid	seed colour extends more or less evenly over the entire seed coat (Saunders, 1959).
Watson	edges of coloured area around hilum are not sharply demarcated but are broken up into separate fine spots especially towards micropylar end of seed (Saunders, 1959).

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Whippoorwill	Seed-coat has irregular areas of dark shade separated by lighter area (Singh and Rachie, 1985).

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TABLE 15

Seed-coat patterns for F_1 and F_2 of intervarietal crosses

Cross(i): P 1977 (brown eye) × IM (solid black)

F_1 solid black

F_2	solid black	whippoorwill mottled (brown)	Watson (black)	Holstein (black) eye	Small black
	(212)	(60)	(32)	(14)	(159)

Cross(ii): P 1977 (brown eye) × LS (solid red)

F1 solid brown

F2	solid brown	solid black	holstein	small eye brown	solid red
	(86)	(22)	(38)	(8)	54

Cross(iii): P DM (dark mottled) × IVX (watson (brown))

F_1 dark mottled

F_2	dark mottled	solid brown	small eye (brown)	watson(brown)
	(332)	(89)	(44)	(204)

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The F_1 of the cross: brown eye (1977) x solid black (IM) produced seeds with solid black coat. This result taken together with those of the F_2,s showed that solid (i.e. black) seed-coat pattern was dominant to eyed pattern. The extension patterns, whippoorwill mottled (brown), watson (black) holstein (black) and small eye (black) showed that there was complementary interaction of two dominant genes, H and W, conditioning seed-coat pattern on a background of brown (blbl). It may however, be proposed that three mendelian factors, by their interactions, produced seed-coat patterns in the progeny of this cross (Table 16). Bl- interacting with the combination H-and W-produced solid black, whilst the double recessive loci blbl interacted with H-and W-to produce Whippoorwill mottled (brown) pattern. The parentals differed from each other by one locus in the following seed-coat patterns: solid black : whippoorwill mottled (brown); whippoorwill mottled (brown) : holstein (black); whippoorwill mottled (brown): small eye black (see Table 17A).

However, the three patterns small eye (black), watson (black) and holstein (black) segregated in the ratio 12:3:1 (see Table 17B).

The F_1 of the cross: brown eye (1977) x solid red (LS) produced solid brown coat seeds. From the F_2 progeny, we can suggest that solid brown seed-coat pattern was epistatic to both eye and solid red seed-coat patterns. The parentals differed by one locus in the following seed-coat patterns:

Solid black : small eye; holstein : small eye;
solid black : small eye; holstein : small eye; solid red : solid black; solid brown : solid red, (see Table 17A).

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TABLE 16

Suggested genotypes for the F_2 progeny of the cross:brown eye (1977) x solid black (IM)

	blbl W_	*blbl* ww		*Bl_* W_	*Bl_* ww
H-	*blbl H_W_* (whippoorwill mottled) (brown)	**blblH_ww* (holstein) (brown)	H-	*Bl_H_W_* (solid black)	*BlH_ww* (holstein) (black)
hh	**blblhhW* (watson (brown)	**blblhhww* (small eye) (brown)	hh	*Bl_hh W_* (watson) (black)	*Bl_hhww* (small eye) (black)

* Not recovered in experimental results.

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TABLE 17A

F_2 seed-coat pattern 3:1 segregation.

Seed-coat pattern	$\chi^2_{1(3:1)}$ value	P
Solid black : whippoorwill mottled (brown)	1.2549	0.30-0.20
Whippoorwill mottled (brown) : holstein (black)	1.4595	0.30-0.20
Whippoorwill mottled (brown) small eye (black)	0.6732	0.50-0.30
Solid : small eye	0.9231	0.50-0.30
Holstein : small eye	1.4254	0.30-0.20
Solid black : small eye	0.0778	0.80-0.70
Solid red : solid black	0.6056	0.50-0.30
Solid brown : solid red	1.2345	0.30-0.20

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TABLE 17B

F_2 seed-coat pattern for complementary interaction

Seed-coat pattern	Expectation	χ^2 value	P
Holstein : solid black	9:7	1.2233	0.30-0.20
Solid brown : solid red : small eye	9:6:1	2.6495	0.20-0.01
Solid brown : solid black : small eye	12:3:1	0.0919	0.80-0.70
Small eye (black) : watson (black) : holstein (black)	12:3:1	1.8745	0.20-0.10

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However the following showed complementary gene action:

Solid brown : solid red : small eye;

Solid brown : solid black : small eye; small eye (black) : Watson (black) : holstein (black); holstein: solid black (see Table 17B).

The various seed-coat patterns obtained from this cross showed that there was complementary interaction of two dominant genes on a background of brown eyed (blblww).

It may, however, be proposed that four mendelian factors by their interactions produced seed-coat patterns in the progeny of this cross as shown in Table 18. The interaction of RR with Bl-- gave solid red seed-coat pattern, rr interaction with Bl produced solid black seed-coat pattern, whilst the interaction of Rr and bb produced solid brown seed-coat pattern. Thus:

RRBl	solid red
Rrblbl	solid brown
rrBl	solid black.

The F_1 individuals of the cross: dark mottled (DM) x Watson (brown) (IVX) were all dark mottled. This result taken together with those of the F_2's showed that dark mottled seed-coat pattern was dominant to the watson (brown) seed-coat pattern and also the extension products were due to the complementary interaction of two dominant genes, H and W, on a background of non-mottle ($m_v m_v$). Therefore it may be proposed that three mendelian factors interacted to produce seed-coat patterns in the progeny of this cross, as shown in Table 19. Combination of the two dominant genes, H and W, in the presence of M_v , the gene for mottling, resulted in dark mottling, whilst watson (brown) resulted from the interaction of $M_v M_v$ and the combination of hh and WW.

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For a solid seed-coat pattern $m_v m_v$ should interact with the combination of H and W.

The expected classes for seed-coat pattern by the proposed scheme are outlined below (figure 7A-7C) for the three crosses.

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TABLE 18

Suggested genotypes for the F_2 progeny of the cross: brown eye(1977) solid red(LS).

	blblww			Bl_ W_	
	R_	rr		R_	rr
H_	blblH_wwR_ (holstein (brown))	*blblH_wwr (holstein (black))	H	Bl_H_W_R_	Bl_H_W_rr
hh	blblhhwwR_ (solid brown	blblhhwwrr smallege brown	hh	*BlhhW_R_ (watson (red)	*Bl_hhW_rr (watson

* Not recovered in experimental results

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TABLE 19

Suggested genotypes for the F_2 progeny of the cross: dark mottled(DM) x watson(brown)(IVX).

	M_{v-}			m_vm_v	
	W-	ww		W	ww
H-	$M_v_H_W$ (dark mottled)	* M_vH_ww (holstein dark mottled)	H-	$m_vm_vH_H_$ (solid brown	* $m_vm_vH_W_$ (holstein brown).
hh	*$M_v_W_hh$ (watson (dark mottled)	*M_v_wwhh (small eye dark mottled)	hh	$m_vm_vW_hh$ watson brown)	$m_vm_v$hhww (small eye

* Not recovered in experimental results, probably due to small sample size bred.

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Figure 7A Suggested genotypes for the parents, F_1 and F_2 populations for the cross: brown eye x solid black.

	1977 (brown eye)		IM (solid black)
P	*blblhhww*	x	*BlBlHHWW*

F_1 *BlblHhWw* (solid black)

F_2	*BlBlH_W_*	*BlBlhhww*	*blblW_h_*	*BlblhhWW*	*BlblHHww*
	(solid black)	(small eye black)	(whippoorwill mottled (brown)	(watson (black))	(holstein (black))
	212	159	60	32	14

Figure 7B Suggested genotypes for the parents, F_1 and F_2 populations for the cross: brown eye x solid red.

	1977 (brown eye)		LS (solid red)
P	*rrblblhhww*	x	*RRBlBlHHWW*

F_1 *RrblblHhWw*

(solid brown)

F_2	*RrblblHhWw*	*RRblblHHWW*	*rrBl_W_H_*	*RrblblHhww*	*rrblblhhww*
	(solid brown)	(solid red)	(solid black)	(holstein (brown)	(small eye brown)
	80	54	22	38	8

Figure 7C Suggested genotypes for the parents, F_1 and F_2 populations for the cross: dark mottled x watson brown)

	DM (dark mottled)		IVX (watson (brown))
P	M_vM_vHhWW	x	$m_vm_vW\text{-}hh$

F_1 M_vm_vHhWw (dark mottled)

F_2	$M_vM_vH_W_$	$m_vm_vW\text{-}hh$	$m_vm_vH_W_$	m_vm_vhhww
	(dark mottled)	(watson (brown)	(solid brown)	(small eye (brown)
	332	204	89	44

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In the cross: brown eye (977) x solid black (Im) the gene for black seed-coat colour exhibits itself in the following patterns: solid, watson, holstein and small eye. The parental brown eye was not recovered in the F_2 progeny, due possibly to an inhibitory effect of the black gene. The absence of the brown eye type could also be due to small sample size. Alternatively, black small eye may be due to a recessive suppressor interaction between *Bl/bl* and *bl/bl* such that all the following genotypes result in black eye phenotype,

*Bl_*

blbl

4.4 Linkage

a. Two major genes

(i) Pigmented bud tip and red calyx

F_2 phenotypic frequencies for the cross,pigmented bud tip, red calyx and non-pigmented bud tip, green calyx are presented in Table 20A. There is significant linkage between the two characters as shown in Table 20B. Chisquared value for one degree of freedom = 52.9412, P < 0.001. The percentage crossing over value was 10.92 ± 4.06 which deviates highly significantly from independent segregation, P< 0.001 Table(26).

(ii) Solid black seed-coat pattern and small eye seed-coat pattern

Table 21A shows the data for the F_2 phenotypic frequencies of the F_2 progeny for the cross: solid black seed-coat pattern x small eye seed-coat pattern. Table 21B shows that the gene for the seed-coat colour solid-black and its allele segregate in a mendelian fashion and similarly

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TABLE 20A

F_2 phenotype frequencies for the cross: red bud tip, red calyx x green bud tip, green calyx in coupling.

Phenotype	Frequency
pigmented bud tip, red calyx (B^R *Rcy*)	45
pigmented bud tip, green calyx (B^R *rcy*)	5
non-pigmented bud tip, red calyx (b^R *Rcy*)	1
non-pigmented bud tip, green calyx (b^R *rcy*)	17
	68

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TABLE 20B

Test for primary segregation and linkage for the loci red bud tip (B^R)/green bud tip (b^R) and red calyx (*Rcy*)/green calyx (*rcy*).

Sources of variation	Degrees of freedom	χ^2	P
Segregation B^R/b^R	1	0.0784	0.8-0.70
Segregation *Rcy/rcy*	1	1.9608	0.20-010
Linkage	1	52.9412	<0.001
(Total)	(3)	(54.9804)	

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TABLE 21A

F_2 phenotypic frequencies for the cross solid black seed-coat x brown small eye seed-coat pattern.

Phenotype	Frequencies
Solid black	161
Holstein (black)	21
Small eye (black)	25
Small eye (brown)	28
	235

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TABLE 21B

Test for primary segregation and linkage for the cross: solid black seed-coat x brown small eye seed-coat pattern

Sources of variation	Degrees of freedom	χ^2	P
Segregation: seed coat colour	1	0.6255	0.50-0.30
Segregation: seed coat pattern	1	2.1575	0.20-0.10
Linkage	1	33.2126	<0.001
Total	(3)	35.9955	

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for the seed-coat pattern, small eye and its allele holstein, chisquared for one degree of freedom = 0.6255 with P= 0.50-0.30 and 2.15744 with P= 0.20-0.10 respectively. The two genes do not segregate independently of each other therefore there is strong linkage between them. (Chisquared for 1 d.f. = 333.2126 with $P < 0.001$.) (Table 21B) The percentage crossing-over value was 36.07±4.08 which deviates significantly from independent segregation, $P < 0.001$ (Table 30)

(iii) **Red pod tip and red calyx**

F_2 phenotypic frequencies for the cross: red pod tip, red calyx x green pod-tip, green calyx are presented in Table 22A. The gene for red pod tip and its allele segregate in a mendelian fashion and similarly for the gene for red calyx and its allele (Table 22B).

There is a highly significant linkage between these two loci, chisquared for 1.d.f. = 19.5800, $P < 0.001$. The percentage crossing-over value was 20.08 ± 7.15 (Table 30) which deviates significantly from independent segregation ($P < 0.001$; Table 30).

(iv) **Brown seed-coat and streakless seed**

F_2 phenotypic frequencies for the cross: streakless, brown seed-coat x streaked, red seed-coat are presented in Table 23A. The gene for streakless seed-coat and its allele segregate in a mendelian fashion and similarly for the gene for brown seed-coat and its allele (Table 23B).

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TABLE 22A

F_2 phenotypic frequencies for the cross: red pod tip, red calyx x light green pod tip, green calyx in coupling.

Phenotype	Frequencies
red pod tip, red calyx (P^b *Rcy*)	25
red pod tip, green calyx (P^b *rcy*)	5
light green pod tip, red calyx (*pb Rcy*)	2
light green pod tip, green calyx (*pb rcy*)	9
	41

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TABLE 22B

Test for primary segregation and linkage for the loci red pod tip(P^{t})/light green pod tip (p^{t}) and red calyx(*Rcy*)/green calyx (rcy)

Sources of variation	Degree of freedom	χ^2	P
Segregation red pod tip P^{t}/p^{t}	1	0.0732	0.80-0.70
Segregation red calyx Rcy/rcy	1	1.8293	0.20-0.10
Linkage	1	19.5800	<0.001
(Total)	(3)	(21.4825)	

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TABLE 23A

F_2 phenotypic frequencies for the cross, streakless, brown seed-coat x streaked, red seed-coat in coupling

Phenotype	Frequencies
Streakless, brown seed-coat (S_l Br)	74
Streakless, red seed-coat (S_l br)	14
Streaked, brown seed-coat (s_l Br)	12
Streaked, red seed-coat (s_l br)	16
	116

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TABLE 23B

Test for primary segregation and linkage for the loci streakless/streakedseed-coat pattern and brown seed-coat(*Br*)/red seed-coat(*br*)

Sources of variation	Degrees of freedom	χ^2	P
Segregation/Streakless/streaked(S_1/s_1)	1	0.04598	0.90-0.80
Segregation/Brown/red seed-coat (Br/br)	1	0.04598	0.90-0.80
Linkage	1	18.77395	<0.001
Total	3)	(18.86591)	

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There is a highly significant linkage between these two loci. Chisquared for one degree of freedom = 18.77395, P<0.001, percentage crossing-over value was 25.72 ± 4.84 (Table 30) which deviates significantly from independent segregation.

The following pairs of loci were found to segregate independently of each other, thus no linkage was established (Table 31):

(i) pale green patch and red bud tip (Table 24)

(ii) pale green patch and red calyx (Table 25)

(iii) red calyx and purple flower (Table 26)

(iv) red bud tip and purple flower (Table 27)

b. **Disturbed linkage**

(i) **pale green patch and purple flower**: It was shown in section 4.2 (a) that the pale green patch factor is controlled by a pair of complementary genes. This presents a case of linkage between a gene and a second one which is a member of a pair of complementary factors (see data in Table 28A). Treating this 9:7 segregation as a disturbed 3:1 segregation a χ^2 contingency table analysis gives a χ^2 = 6.2375 for one degree of freedom and P<0.02-0.01. However, the true value obtained using the 9:7 expectation is χ^2 = 5.7755 for 1.d.f. and P = 0.05-0.02 (Table 28B). The difference between the linkage chisquares as calculated in these two ways is negligble. Estimation of linkage by the product formula gave a crossing-over percentage value of 30.32 ± 6.91 with P< 0.001 (Table 30).

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TABLE 24

F_2 phenotypic frequencies for the cross: pale green patch, red bud tip x normal, green bud tip

Phenotype	Frequencies
pale green patch, red bud tip (Pgp B^R)	24
pale green patch, green bud tip (Pgp b^R)	10
normal, red bud tip (pgp B^R)	18
normal, green bud tip (pgp b^R)	2
	54

$\chi^2_{1(3:1)}$ Pgp/pgp = 4.1728 P = 0.05-0.02

$\chi^2_{1(3:1)}$ B^R/b^R = 0.2222 P = 0.70-0.50

$\chi^2_{1\,\text{Linkage}}$ = 2.7454 P = 0.10-0.05

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TABLE 25

F_2 phenotypic frequencies for the cross: pale green patch, red calyx *x* normal, green calyx.

Phenotype	Frequencies
pale green patch, red calyx (*Pgp Rcy*)	42
pale green patch, green calyx (*Pgp rcy*)	11
normal, red calyx (*pgp Rcy*)	13
normal, green calyx (*pgp rcy*)	6
	72

$\chi^2_{1(3:1)}$	*Pgp/pgp*	= 0.07407	P=0.80-0.70
$\chi^2_{1(3:1)}$	*Rcy/rcy*	= 0.07407	P=0.80-0.70
$\chi^2_{Linkage}$		= 0.8889	P=0.50-0.30

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TABLE 26

F_2 phenotypic frequencies for the cross: purple flower, red calyx *x* white flower, green calyx.

Phenotype	Frequencies
purple flower, red calyx (*Pf Rcy*)	27
purple flower, green calyx (*Pf rcy*)	14
white flower, red calyx (*pf Rcy*)	7
white flower, green calyx (*pf rcy*)	3
	51

$\chi^2_{1(3:1)}$ *Pf/pf* = 0.7908 P= 0.50-30

$\chi^2_{1(3:1)}$ *Rcy/rcy* = 1.8889 P= 0.20-0.10

$\chi^2_{Linkage}$ = 0.1765 P= 0.70-0.50

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TABLE 27

F_2 phenotypic frequencies for the cross: red bud tip, purple flower x green bud tip, white flower

Phenotype	Frequencies
red bud tip, purple flower (B^R Pf)	31
red bud tip, white flower (B^R pf)	9
green bud tip, purple flower (b^R Pf)	10
green bud tip, white flower (b^R pf)	2
	52

$\chi^2_{1(3:1)}$ B^R/b^R = 0.4103 P = 0.70-0.50

$\chi^2_{1(3:1)}$ Pf/pf = 0.4103 P = 0.70-0.50

$\chi^2_{Linkage}$ = 0.1368 P = 0.80-0.70

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TABLE 28A

F_2 phenotypic frequencies for the cross: pale green patch, purple flower x normal, white flower in coupling.

Phenotype	Frequencies
pale green patch, purple flower (*Pgp Pf*)	38
pale green patch, white flower (*Pgp pf*)	5
normal, purple flower (*pgp Pf*)	15
normal, white flower (*pgp pf*)	9
	67

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TABLE 28B

Test for linkage between the genes for pale green patch and purple flower colour.

(i) 2x2 table (contingency table) method.

	Purple	white	Total
pale green patch	38	5	43
normal	15	9	24
Total	53	14	67

$\chi_1^2 = 6.2375$ P = 0.02-0.01

(ii) χ^2 analysis by orthogonality.

$$\chi_1^2 = \frac{(7a_1 - 21a_2 - 9a_3 + 27a_4)^2}{189n}$$

$\chi_1^2 = 5.7755$ P = 0.05 -0.02

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The test for linkage, admitting partial manifestation of the chlorophyll factor or the pale green patch (*Pgp/Pgp*) individuals gives a chisquare value of 5.2784 for one degree of freedom, $P = 0.05\text{-}0.02$. Estimation of linkage in the face of partial manifestation gives a percentage crossing-over value of 24.32 ± 6.62, which deviates significantly from the free segregating value of 50.00 per cent; $\chi_1 = 3.8792$ and $P < 0.001$ (Table 30). The former crossing-over value of 30.32 ± 6.91 is misleading, that is when the disturbance is considered as incomplete manifestation.

The proportion of *Pgp Pgp* phenotypes which are misclassified is 0.18 ± 0.075 which shows a significant departure from unity; $d = 10.8269$ and $P < 0.0001$.

(ii) **purple branch-base and red leaflet base**: In section 4.2(ii),

it was shown that the purple branch-base factor is controlled by a pair of complementary genes. Therefore the linkage system here comprises a gene and a second one which is a member of a pair of complementary factors (Table 29A). The χ^2 orthogonality test for linkage gives a $\chi^2 = 28.5923$ for one degree of freedom and $P < 0.001$ (Table 29B). Estimation by the product formula gave a percentage crossing-over value of 13.02 ± 3.97 which deviates significantly from the free segregating value of 50.00 per cent ($P < 0.001$; Table 30).

Measurement of linkage involving a member of a complementary or duplicate pair however needs further work: by raising progenies to identify the double heterozygotes and by progeny testing the F_2 families available.

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TABLE 29A

F_2 phenotypic frequencies for the cross: purple branch base, red leaflet base *x* green branch base, green leaftlet base in coupling.

Phenotype	Frequencies
purple branch base, red leaflet base (*Pbr Lrb*)	33
purple branch base, green leaftlet base (*Pbr lrb*)	3
green branch base, red leaflet base (*pbr Lrb*)	5
green branch base, green leaftlet base (*pbr lrb*)	16
	57

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TABLE 29B

Test for linkage between the factors purple branch base and red leaflet base by the χ^2 orthogonality analysis.

$$\chi_1^2 = \frac{(7a_1 - 21a_2 - 9a_3 - 27a_4)}{189n}$$

(where a_1, a_2, a_3 and a_4 are observed numbers and n the total observed number).

$\chi_1^2 = 28.5923$.

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TABLE 30

Summary of linkage analysis for two major genes

Linkage system	Percentage crossing over value	Test of significance for deviation from 0.5 (d)	P
Black seed-coat pattern ------ Brown small eye seed-coat pattern	36.07±4.08	3.4117	< 0.001
Brown seed-coat --streakless seed	25.72±4.84	5.0165	< 0.001
*Pale green patch---purple flower	*30.32±6.91	2.8497	< 0.01
	+24.32±6.62	3.8792	< 0.00
Red bud tip ---- Red calyx	10.97±4.06	9.6157	< 0.0010
*Purple branch base - Red leaflet base	⊕ 13.02±3.97	9.3149	< 0.001
Red bud tip - Red caylx	20.08±7.15	4.1870	< 0.001

* Disturbed systems ⊕ Treated as partial manifestation disturbance.

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c. **Major gene and polygene**

In this investigation F_2 individuals were sorted out into their quantitatively different classes, the mean values and their standard errors of the quantitatively variables for each class were calculated, and the differences between the means were examined for significance using the d-test.

(i) **Chlorophyll factor and median leaf length**

Two families were studied in this investigation as presented in Table 32. In the F_2 of family I, the pale green patch individuals gave a mean leaf length of 9.87 $\pm$ 0.204 cm and the normal individuals 8.97 $\pm$ 0.229 cm. The difference between the two classes was significant (d/σ = 2.9345, P = 0.01-0.001 as shown in Table 35). Pale green patch individuals are larger than the individuals of the other class. However the difference is smaller than that between the parents. Similarly the difference for family 2 is significant (d/σ = 2.9199, P = 0.01-0.001 as shown in Table 35). Again the difference is smaller than that between the parents.

Linkage between these two loci is possible since out of the 11 pairs of chromosomes in the cowpea, 2 pairs of polygenes are segregating for leaf length. It is therefore likely that these 2 pairs of polygenes might also carry the chlorophyll factor.

(ii) **Seed size and seed-coat pattern**

Two families were investigated as shown in Table 33. Individuals with solid pattern (black) gave a mean weight of 0.181 $\pm$ 0.025g

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TABLE 31

Chisquared test for linkage of the non-linked factors.

System	χ^2 value for linkage	Degrees of freedom	P
Pale green patch——Red bud tip	3.1296	1	0.10-0.05
Pale green patch——Red calyx	0.8889	1	0.50-0.30
Red calyx——Purple flower	0.1765	1	0.70-0.50
Red bud tip——Purple flower	0.1368	1	0.80-0.70

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TABLE 32

Leaf size and pale green patch linkage in the cowpea

Means and their standard errors of leaf length for F_2 plants

Family	Pale green patch *Pgp*	Normal *pgp*	Leaf length difference *Pgp-pgp*	P
1	9.87±0.204 (n=43)	8.97±0.229 (n=27)	0.90	0.01-0.001
2	10.84±0.253 (n=60)	9.56±0.358 (n=25)	1.28	0.01-0.001

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TABLE 33

Seed size and seed-coat pattern linkage in the cowpea.

Means and their standard errors of F_2 plants

Family	Solid pattern (black) *Bl*	Whippoorwill mottle *Wh*	Seed weight difference *Bl - Wh*	P
1	0.181 ± 0.025 (n = 84)	0.164 ± 0.031 (n = 128)	0.017	0.0001-00001
2	0.139 ± 0.034 (n = 58)	0.133 ± 0.002 (n = 181)	0.006	0.07-0.08

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whilst those with the whippoorwill mottle pattern gave a mean weight of 0.164 ± 0.031g. This shows a significant difference (d/σ = 4.007, P = 0.0001-0.00001 as shown in Table 35). In family 2, individuals with solid pattern (black) gave a mean weight value of 0.139 ± 0.0349 and those with whippoorwill mottle pattern gave a mean weight of 0.133 ± 0.002g. The values show non-significant difference between the two classes (d/σ= 1.7616, P = 0.07-0.08; Table 35). In both families, the differences were less than that of the parental difference, however the solid pattern (black) individuals seemed to be greater in weight than the whippoorwill mottle pattern. In family 1 there was a possible incomplete linkage. Probably the seed-coat genes (polygenes) are linked to some of the 6 pairs of polygenes for seed size.

(iii) **Flowering-time and chlorophyll factor**

Table 34 gives a presentation of the data for these two factors. The pale green patch individuals gave a mean flowering time of 33.70 ± 0.46 days whilst the normal individuals gave an average of 35.18 ± 0.62 days. There seems to be an incomplete linkage. However the number of pairs of segregating polygenes for flowering-time could not be calculated for lack of time.

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TABLE 34

Flowering-time and chlorophyll factor linkage in the cowpea
Means and their standard errors for
flowering-time of F_2 plants in days

Pale green patch *Pgp*	Normal *pgp*	Flowering-time difference Pgp-pgp	P
33.70 + 0.46 (n = 41)	35.18 + 0.62 (n = 27)	1.48	0.05-0.06

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TABLE 35

Significant differences for major gene and polygene linkage by the d-test.

Leafsize and chlorophyll factor

	d/σ	P
Family 1	2.9345	0.01-0.001
Family 2	2.9199	0.01-0.001

Seed-size and seed-coat pattern

	d/σ	P
Family 1	4.007	0.0001-0.00001
Family 2	1.7616	0.07-0.08

Flowering-time and chlorophyll factor

	d/σ	P
Family 1	1.9171	0.05-0.06

* d -> mean difference

* σ -> standard error

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4.5 Parental Genotypes

The parental genotypes for the two varieties of the crosses are as follows:

(1) DM X IM

Factor	DM	IM
Seed coat pattern	$Y_{br}Y_{br}$	BlBl

(2) DM X TVX

Factor	DM	IVX
Seed weight	$s^w s^w$	$S^W S^W$
Pod length	$l^p l^p$	$L^P L^P$
Seeds per pod	$s_p s_p$	$S_p S_p$
Seed coat pattern	$Y_{br}Y_{br}$	W W

(3) 1977 X IM

Factor	1977	IM
Leaf base patch	pgppgp	PgpPgp
Bud tip colour	$b^R b^R$	$B^R B^R$
Pod tip colour	$p^t p^t$	$P^t P^t$
Sepal colour	rcyrcy	RcyRcy
Flower colour	pf pf	Pf Pf
Branch base pigmentation	$pbr_1 pbr_1 pbr_2 pbr_2$	$Pbr_1 Pbr_1 Pbr_2 Pbr_2$
Seed coat	blbl	BlBl
Seed coat pattern (eye)	ybrybr	YbrYbr

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(4) 4557 x LS

Factor	4557	LS
Base of branch pigmentation	$p^{br}p^{br}$	Pbr Pbr
Base of peduncle pigmentation	$p^{b}p^{b}$	$P^{b}P^{b}$
Base of petioled pigmentation	$p^{l}p^{l}$	$P^{l}P^{l}$
Whole plant pigmentation	$p^{w}p^{w}$	PwPw
Flower colour	pfpf	$P^{f}P^{f}$
Leaflet base pigmentation	lrblrb	LrbLrb

(5) 1977 x LS

Factor	1977	LS
Seed coat pattern	brbr	BrBr
Leaf length	llfllf	LlfLlf

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CHAPTER 5

DISCUSSIONS AND CONCLUSIONS

5.1 Cowpea Gene Index

To construct a set of rules for the gene nomenclature of Cucurbitaceae, Robinson *et. al.* (1976, in Singh and Rachie, 1985) followed the recommendations of both the International Committee on Genetic Symbols and Nomenclature (Tanaka et. al., 1957 in Singh and Robinson, 1985) and the Tomato Genetics Cooperative (Barton *et. al.*, 1955; Claybery *et. al.*, 1960, 1966, 1970, in Singh and Rachie, 1985). Fery (1980, in Singh and Rachie, 1985) adapted these rules as outlined in Appendix 1.

In the present work these rules were carefully followed and the following cowpea gene symbols have been suggested as defined in Table 1:

B^{R}	(red bud tip)
Lrb	(red leaflet base)
Pgp	(pale green patch)
P_{w}	(whole plant non-pigmented)
Rcy	(red calyx)
S_{l}	(streakless seed-coat)
Y_{br}	(brown small eye seed-coat pattern).

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5.2 Primary segregation for major genes

5.2.1 Pigmentation

Spillman was among the first investigators of the inheritance of discontinuous characters in cowpea especially the seed-coat pattern referred to as "eye" (Agble, 1969). He reported that all varieties having coffee-coloured or white- or cream-coloured seeds

had white flower and were devoid of anthocyanin in stems and leaves (Agble, 1969). Spillman's conclusion needs further investigation because in the present work two cowpea varieties gave different results. In the variety 1977 the seeds were cream coloured but there was the presence of anthocyanin in the stem, though the flower colour was white. In another variety, West Bred, the seeds were white but the flowers were purple and anthocyanin was present in the stem. Harland (1920) suggested that the presence of anthocyanin pigment in the vegetative parts of the plant was due to a factor X, dominant to its absence. Spillman and Sando (1930) reported that *N* was the general pigment factor, which determines the anthocyanin in stems and leaves, and can be expressed only in the presence of the general colour gene, R. Saunders (1960a) working with over fifteen different varieties in South Africa reported that purple plant colour is digenic in inheritance. The purple plant colour and anthocyanin pigment mentioned by the various writers may be the same as the red pigmentation reported of in the present work. The result of the cross carried out between pigmented plants and unpigmented plants suggests that plant pigmentation is monogenic in inheritance. Plants with the pigment gene, ***P***, have red pigment and those with the recessive allele, *p*, in the homozygous state are devoid of the pigment. The present results agreed with the "one factor" control reported by Harland (1920). The digenic inheritance reported by Saunders (1960a) and Spillman and Sando (1930a, in Agble, 1969) may be true of some varieties but this cannot be the case in this investigation since a few varieties were studied. The basic colour gene reported by the various workers may not be present in some varieties while in other varieties it may be present.

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a. Flower colour

Anthocyanin is responsible for the purple or violet flowers that are characteristic of many cowpea cultivars. There are four major flower colours: dark, pale, tinged, and white. Dark flowers contain a high concentration of anthocyanin in all of the principal flower parts, pale flowers contain small amounts in the wings, tinged flowers have a faint narrow band of pigmentation along the outer edge of the standard, and white flowers are completely devoid of anthocyanin. Flower colour is associated with seed-coat colour and pattern (Spillman, 1913; Harland, 1919a; Saunders, 1960a) dark flowers are characteristic of cultivars with self-coloured or Watson-eye seeds; pale flowers with all eye and holstein seed-coat pattern; tinged flowers with the hilum ring seed-coat pattern and white flowers with white or cream seed-coats. In the present work all the four main flower colours and their associated seed characteristics were observed with exception of white flower and white or cream seed-coat association in 1977 which disagreed with results of earlier workers.

As originally observed by Spillman (1911, 1913), the presence of pigment in the flower is dependent upon the general colour factor *C* and the anthocyanin factor *N*. Harland (1919a) noted that the presence of anthocyanin in flower tissue is the result of an interaction of the two dominant factors *L* and *D*. The *L* factor conditions the pale colour; the *D* factor increases the intensity of the colour but has no effect except in the presence of *L*. Later, Harland (1920) reported that the tinged colour is governed by a single dominant gene, *G*. He noted that *G* produces tinged flowers in white-seeded plants. Harland (1919a) speculated that the dark flowers and the watson seed-coat pattern are controlled by the same factor. In the inheritance of the three flower colours violet, tinged and white, Sen and Bhowal (1961) observed ratios which supported Harland's conclusion that violet is monogenically dominant over tinged,

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and tinged over white. But in the cross:

voilet x white

while Harland (1920) got 3 violet: 1 white in one cross and 12 violet: 3 tinged: 1 white in another, segregation of 9 violet: 3 tinged: 4 white was observed by Sen and Bhowal (1961). Saunders (1960) also reported a 3:1 ratio in each of the crosses:

white x dark

white x tinged

and white x pale

but observed a 9:3:4 ratio in the cross:

tinged x pale.

He concluded that there might be two kinds of white flowers, one due to the absence of a basic colour gene, *R*, and the other the absence of certain complementary genes for seed-coat pattern. In the present work the results of F_2 segregations agreed with a 3:1 ratio which suggests that flower colour is monogenic in inheritance but the gene for flower colour, *C*, may exist in different allelic forms and when present in the homozygous recessive state gives white colour. The allelic forms suggested are Dark (*Cd*); Pale (*Cp*); Tinged (*Ct*) and white (*C*). The results of the present work only agreed with the 3:1 ratio reported by some workers. However, Harland's 9:3:4 and 12:3:1 ratios and Saunder's of 9:3:4 were not observed. This discrepancy may be due to differences in varieties used by the different workers.

b. **Foliage chlorophyll factor**

Pale green arose in 1932 as a mutant in pure line of Red and is characterized by a noticeable degree of chlorophyll deficiency especially in the youngest leaves (Saunders 1960b). Saunders(1960a) proposed the symbol *g* for the recessive gene that conditions this trait. This

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gene was later redesignated as pg by Fery (1980, in Singh and Rachie, 1985). Kolhe (1970, in Singh and Rachie, 1985) found that light-green foliage is dominant to green foliage and is conditioned by two complementary genes that he designated *Lg-a* and *Lg-b*. These were later redesignated by Fery (1980, in Singh and Rachie, 1985) as *Lg-1* and *Lg-2* respectively. Sen and Bhowal (1961) reported that the allelic series Gn^d, Gn, and gn^Y for dark green, green, and yellow-green pod colours respectively, condition similar colour response in the leaf, calyx, and dorsal surface of the standard. Singh and Tindla (1972, in Singh and Rachie, 1985) assigned the symbol *Gr* to a gene that conditions green buds over white. Premsekar and Raman (1972, in Singh and Rachie, 1985) reported that dark-green calyx is dominant over pale green and the segregation pattern observed in an F_2 population suggested monogenic inheritance.

In the present work pale green patches were observed at the leaflet bases, which were designated *Pgp*; the pale green patch factor was found to be dominant over dark green or green. With reference to the present work and those of Kolhe and, Premsekar and Raman it is likely that the state of dominance of pale green is determined by the position in the plant where the character is observed. The segregation pattern observed in the F_2 population for the cross: 1977 x [illegible] suggested monogenic inheritance. However, in one of the four families observed there was one case of disturbed segregation where a 9:7 segregation was observed, possibly as a result of gene interaction, a case which needs futher investigation. Apart from the pale green patch pattern at the leaflet base there was another inverted 'V' shaped pale green patch present in the middle part of the leaflet lamina which will probably show monogenic inheritance. This therefore suggests that the gene for chlorophyll factor (*Pgp*) in the leaflets may exist in different allelic states and needs to be investigated.

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5.3 Quantitative Inheritance

a. Pod length

Several studies have suggested that pod length is moderately to highly heritable. Published broad-sense heritabilty estimates average 75.2 per cent (Singh and Rachie, 1985). Additive gene action is important, and higher heritability is often accompanied by high genetic advance (Veeraswamy *et. al.*, 1973; Tikka *et. al.*, 1977, in Singh and Rachie, 1985). Long pod is usually dominant or partially dominant over short pod (Fennel, 1948; Roy and Richharia, 1948; Brittingham, 1950; Capinpin and Irabagon, 1950; Jindla and Singh, 1970; Aryeetey and Laing, 1973), but there have been some reports of short pod being partially dominant (Leleji, 1975; Bhowal, 1976)). Aryeetey and Laing (1973) estimated that 0.44 effective factors condition pod length, though most published reports indicate that at least two genes are involved. Aryeetey and Laing (1973) showed that pod length was highly and positively correlated with number of seeds per pod. They suggested that the F_2 showed trangressive segregation for long pod, results which differed from those of Brittingham (1950), who reported that there was a tendency for the F_1 and F_2 values to be closer to the values of the short-podded parent and observed a transgressive segregation in the F_2.

In the present work long pod was found to be partially dominant over short pod as already reported by Aryeetey and Laing (1973) and other early workers. The broad-sense heritability estimate of 88.00% differs from the average of 75.2% reported by earlier workers. The difference may be due to the fact that only one family was studied in the present work. The number of segregating factors of 3.82 deviates from already reported ones of 0.44 (Aryeetey and Laing, 1973) and 2.00 (Singh and Rachie, 1985). This might be due to the materials used for the present work. The present result was base on Wright's formula (Wright, 1968),

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which did not take into account the backcrosses. Pod length correlation with number of seeds per pod is in agreement with the report by Aryeetey and Laing (1973). In view of this work and earlier ones, it can be suggested that selection based on pod length is likely to be effective in increasing yield (number of seeds), although negative correlation has been found between pod length and certain yield components, a difference which might be due to the use of different varieties by different workers.

b. **Seed weight**

Large seed size is normally partially dominant over small seed size (Aryeetey and Laing, 1973), with no transgressive segregation.

Reported broad-sense heritability estimates include 63.0% (Aryeetey and Laing, 1973) and 80.0% (Sène, 1968, in Aryeetey and Laing, 1973). Aryeetey and Laing (1973) suggested 10.05 effective factors for seed size, whilst Sene (1968, in Aryeetey and Laing, 1973) suggested an estimate of 6.27.

In the present work the state of dominance agrees with the report of Aryeetey and Laing (1973) and an F_1 heterosis of -0.006g for small seed size was obtained. The latter findings could be due to different cowpea varieties used and sample size difference. The number of segregating factors of 6.01 agrees with that of Sene (1968, in Aryeetey and Laing, 1973). The present work did not report on narrow-sense heritability estimates since backcross generations were not raised. However it has been reported that, the narrow-sense heritability estimates for seed size is fairly high. This is an indication that, initially, at least, selection for seed size is likely to be successful (Aryeetey and Laing, 1973).

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c. **Number of seeds per pod**

Number of seeds per pod is moderately heritable under most environmental conditions. Published heritability estimates average 52.8 per cent (Singh and Rachie, 1985). Non-additive gene action accounts for much of the variation. Singh and Jain (1972, in Singh and Rachie, 1985), for example, demonstrated that specific combining ability was important but that general combining ability was not. Tikka *et. al.*, (1977, in Singh and Rachie, 1985) observed that the high heritability was accompanied by a comparatively low genetic advance. Kheradnam and Niknejad (1977, in Singh and Rachie, 1985), however, reported that both general and specific combining abilities were important. Leleji (1975, in Singh and Rachie, 1985) reported that a small number of seed per pod is partially dominant over a larger number. Aryeetey and Laing (1973) reported that a single effective factor conditions seed number per pod. They suggested partial dominance for high number of seeds per pod and transgressive segregation in F_2. In the present work the F_1 showed full dominance for large number of seeds per pod, whilst the F_2 means fell closely to the smaller parent value. This compares with Kheradnam and Niknejad's (1971, in Singh and Rachie, 1985) suggestion about combining abilities. The broad-sense heritability estimate was 69.52% as compared with Aryeetey and Laing's 47.8% and 68.4% of Sohoo *et al.* (Singh and Rachie, 1985). The number of segregating loci for number of seeds per pod was 7.12 as compared with 1.00 of Aryeetey and Laing's (1973). This difference in results may be due to the fact that the present work was based on Wright's formula (Wright, 1968). The narrow-sense heritability estimate of 37.8% suggested by Aryeetey and Laing (1973) was an initial indication that selection for number of seeds per pod is likely to be successful. The differences observed by different workers in comparison with the present work may be due to the use of different cowpea varieties.

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d. Leaf length

It has been reported that six different genes condition leaf size or leaf shape in cowpea. Small leaf, *ls*, is recessive to large leaf (Krishnaswamy *et. al.*, 1945, in Singh and Rachie, 1985); long leaf, *Llf*, is dominant to short leaf (Kolhe, 1970 in Singh and Rachie, 1985). In the present work, large leaf was found to be dominant to small leaf and 1.75 pairs of polygenes condition this leaf trait. F_2 and F_1 heteroses were observed to be 1.40cm and 1.54cm respectively.

e. Seed-coat pattern

Seed-coat patterns are generally inherited independently of solid colour, but the appearance of any pattern is dependent upon the presence of the general colour factor C (Singh and Rachie, 1985). However, the present work suggests linkage between solid colour (black) and eye pattern, though further work must be done for confirmation. Spillman (1911) was the first to attempt an explanation of the inheritance of the eye patterns. He proposed the symbols *w* and *h* for genes conditioning the holstein eye and watson patterns, respectively. Both patterns are recessive to solid pigmentation, a situation that agrees with the present work.

The genotype for the ordinary or small eye is *hhww*; the large eye is the heterozygote between the holstein and small eye patterns *hhww*. However, Spillman and Sando (1930) later concluded that the big eye genotype was homozygous at the *h* locus and heterozygous at either or both the *w* and *Na* loci. Harland (1919a, 1920, 1922) suggested nothing is indicative of the heterozygous condition at the *Bl* locus. Saski (1922) studied an intermediate between large eye and holstein

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patterns and concluded that it is conditioned by a single recessive gene. Spillman and Sando (1930) assigned the gene *W*, to the whippoorwill mottle pattern but Fery (1980, in Singh and Rachie, 1985) suggested *Wh* instead, since the former gene designation had been assigned to a different character already. Franckowiak and Barker (1974, in Singh and Rachie, 1985) concluded that several of the genes are allelic to the gene governing black seed-coat, *Bl*. Using Harland's (1919a, b, 1920) they proposed the following: B^e for New Era pattern; Bl^f, blue; Bl^l black with light spots; Bl^s, black spots; bl^t, Taylor pattern (thinly scattered bluish-purple dots); and Bl^x, modifier of Bl^f. The dominant gene *Mu* conditions mottling in the seed-coat. Fery (1980, in Singh and Rachie, 1985) suggested that several of these *Bl* alleles are most likely genes described by earlier researchers. However, due to the use of different varieties in the different studies the results are difficult to reconcile.

Franckowiak and Barker's (1974, in Singh and Rachie, 1985) *Bl* alleles should be kept separate from the genes described earlier by Fery (1980, in Singh and Rachie, 1985). In the present work about ten different seed-coat patterns appeared from the crosses. Though the small sample size could not allow for a clear-cut mendelian analysis of the results, it is evident from the number of classes obtained in the F_2's that seed-coat pattern is conditioned by about five mendelian factors namely: *Bl*, *H*, *Mv*, *R* and *W*. These factors interact to produce the following seed-coat patterns:

Genotype	Phenotype
*Bl_H_W_*	Solid black
BlHHww	holstein (black)
BlhhWW	watson (black)
Bl_hhww	small eye (black)
*blbl H_W_*	whippoorwill (brown)

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*R_Bl_H_W_*	solid red
*rrBl_H_W_*	solid black
R_blblH_ww	holstein (brown)
Rrblblhhww	solid brown
rrblblhhww	small eye
$M_v_H_W$	dark mottled
$M_vM_v H_W_$	solid brown
$M_vM_v hhWW$	watson (brown)
$m_vm_v hhww$	small eye

However, Agble (1969) in his work suggested three mendelian factors. The combination of the two dominant genes *H* and *W* results in self-colour or solid seed-coat pattern (Spillman and Sando, 1930). This report agrees with the findings in the present work. In the present work, the following gene interactions gave solid seed-coat patterns:

Genotype	Phenotype
Rrblblhhww	solid brown
$m_vm_vH_W_$	solid brown

It is therefore possible that the presence of the gene *R* (in its dominant state) suppresses the recessive character of the combination *hhww*. The combinations *Bl_H_W_* and *rrBl_H_W* produce the same seed-coat pattern, solid black. By the present model, the combination of the two recessive genes *h* and *w* results in small eye pattern which agrees with Spillman's (1911) proposal but *Rrblblhhww* produces a solid seed-coat pattern as a result of gene interaction. It is likely that the presence of *Rr* suppresses the effect of *hhww* thus modifying this combination to give a solid seed-coat pattern.

The present work explains the different opinions expressed by various workers over

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the number of factors involved in seed-coat pattern determination because from Table 19, it is seen that in some of the patterns the parentals differ at one locus whilst in some they differ at two loci.

5.4 Linkage

5.4.1 Two major genes

Linkage analysis in cowpea has been minimal and many of the reported findings as listed in Table 37 need further verification. Some genes may be so tightly linked that they might be allelic rather than linked as observed by Harland (1920) for the following genes *Bl*, *P* and *E*. Spillman and Sando (1930) suggested linkage as the probable explanation for the association between traits conditioned by *Pr*, *Br*, *De*, *T*, *F* and probably *S* genes. Saunders (1960b) suggested that the association between the colour factor *C*, pod length, and seed size reflects the multiple effects of the *C* gene rather than linkage. Roy and Richharia (1948) suggested

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TABLE 36

Reported genetic linkage in the cowpea (Source: Singh and Rachie, 1985)

Observed pair of loci	Crossing-over	Reference
Bf — *V*	25.5	Saunders, 1959
Bg — *Pf*	20.3	Kolhe, 1970
Bg — *Ystp*	39.5	Kolhe, 1970
Bl — *Bp*	----+	Saunders, 1960b
Bl — *Ce*	34.4	Saunders, 1960b
Bl — *E*	----+	Harland, 1920
Bl — *P*	----+	Harland, 1920
Bp — *Spk*	20.0	Saunders, 1960a,b
C — *V*	20.0	Saunders, 1960b
Cm — *Tr*	25.0	DeZeeuward Crum,1963
E — *P*	----+	Harland, 1920
F — *T*	----+	Spillman and Sando, 1930
o — *P*	15.4	Saunders, 1960b
P — *sh*	34.6	Saunders, 1960b
Pb — *Pb*	19.9	Sen and Bhowal, 1961
pb — *Pbr*	13.5	Sen and Bhowal, 1961
Pf — *Ystp*	20.4	Kolhe, 1970
pg — *w*	23.4	Saunders, 1960b
Sk —*Spk*	----+	Saunders, 1960a
Wp-a- *Dd-a*	5.8	Kolhe, 1970

Note: Preferred gene symbols used (see Table 1) *Bg* (Brown grain), *pt* (purple pod tip)
+ Tightly linked.

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linkage between the gene systems governing pod length and the fibre in pod wall. Kuhn *et. al.*, (1981, in Singh and Rachie, 1985) speculated that the *Mvi* gene that conditions the movement of cowpea chlorotic mottle virus within the plant is closely linked to one of the genes that controls the replication of the virus.

In the present investigation, six instances of linkage each involving different genes, have been found. The suggested linkage systems are (discounting pleiotropy for (i), (ii) and (iii)):

(i) red bud tip —— 10·97% —— red calyx

(ii) pale green patch —— 30·32% —— purple flower

(iii) purple branch base —— 13·02% —— red leaflet base

(iv) black seed-coat —— 36·07% —— brown small eye seed-coat pattern

(v) red pod tip —— 20·08% —— red calyx

(vi) brown seed-coat —— 25·72% —— streakless

Sen and Bhowal (1961) observed linkage between the genes controlling purple pod tip, stems with purple at the internodes and purple petiole base. In the present work red pod tip was found to be linked with red calyx. Sen and Bhowal (1961) found that the gene conditioning purple branch was also linked with the gene conditioning red leaflet-base. Kolhe (1970, in Singh and Rachie, 1985) also found that the gene conditioning purple flower, was linked with the gene conditioning yellow stripes on petals and this latter gene was linked to the gene controlling brown grain. In the present investigation the gene controlling purple flower was also found to be linked with the gene controlling pale green patches at the leaflet base. Saunders (1960b) in his investigation found linkage between the gene conditioning pale green colour in the plant and the gene conditioning watson seed-coat pattern. In the present investigation, however the pale green patch was limited to the base of the leaflets.

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Combining the already observed linkage systems and those of the present work the following arbitrary linkage groups could be suggested:

(a) Purple pod tip, Purple branch base and Red leaflet base

(i) *Pt* ——————— *Pbr* ——————— *Lrb*

(ii) *Pbr* ——————— *Lrb* ——————— *Pt*

(iii) *Pbr* ——————— *Pt* ——————— *Lrb*

(b) Brown grain, Yellow stripes on petals, Purple flower, Pale green patch and Watson seed-coat.

(i) *Bg* ——— *Ystp* ——— *Pf* ——— *Pgp* ——— *w*

(ii) *Bg* ——— *Pf* ——— *Ystp* ——— *Pgp* ——— *w*

(iii) *Bg* ——— *Pf* ——— *Pgp* ——— *Ystp* ——— *w*

(iv) *Bg* ——— *Pf* ——— *Pgp* ——— *w* ——— *Ystp*

(v) *Bg* ——— *Pgp* ——— *Pf* ——— *w* ——— *Ystp*

(vi) *Bg* ——— *Pgp* ——— *w* ——— *Pf* ——— *Ystp*

(vii) *Bg* ——— *w* ——— *Pgp* ——— *Pf* ——— *Ystp*

(viii) *Ystp* —— *Bg* ——— *Pf* ——— *Pgp* ——— *w*

e.t.c

The loci for pale green patch/normal and purple/white flower appeared to show disturbed linkage as a result of partial manifestation, with a proportion of 0.1869 ± 0.075 partial penetrance of the pale green patch individuals. However this needs further investigation due to the low F_2 sample size of sixty-seven. Similarly the purple branch base individuals seemed to show an incomplete viability with a proportion of 0.5714 ± 0.157 of these individuals not being viable. Further families must be studied and the sample size be increased so as to establish inviability disturbance, since only fifty-seven seedlings out of the ninety-six F_2 seeds sown, survived to maturity.

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5.4.2 Polygene and major gene

The first case of apparent linkage between polygenes and a major gene was reported by Sax (1923, in Mather and Jinks, 1970) when he studied crosses between strains of *Phaseolus vulgaris*, with large coloured seeds, and those with small white seeds. He found linkage between seed colour with an F_2 ratio of 3:1 and seed size which proved to be a continuously variable character. Later Rasmusson (1935) investigating the variation of flowering-time in the garden pea observed that one or more flowering-time genes were linked with the major gene governing flower pigmentation. Many cases of linkage between major genes and polygenes have subsequently been reported, although in the majority of them the possibility of pleiotropic action of the major gene has not been fully excluded (Mather and Jinks, 1970). Brittingham (1950) reported the quantitative - qualitative linkage for several genes in the cowpea: the genes controlling vining and anthocyanin coloration in the vegetative parts; the genes controlling buff seed-coat and pod length; and the genes conditioning general colour factor and seed size. However, Saunders (1960b) suggested that the association between colour factor, pod length and seed size reflects the multiple effects of the colour factor gene rather than linkage. Additionally, she suggested that seed-coat colour and date of maturity are associated in a quantitative-qualitative linkage.

In the present investigation there was the possibility of two major gene and polygene linkage systems. The major gene conditioning pale green patch was likely to be linked with the gene conditioning leaf length. Two families were studied and linkage of these two genes were consistent in both. The difference in leaf length between pale green patch leaflets and normal was significant and the patched were greater than the normal as would be expected from the parents. The difference, however, was smaller than that between the parents. The gene governing flowering-time was also found to be linked to the gene conditioning pale green patch.

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Only one family was studied for these two characters. The difference in flowering-time between pale green patch leaflets and normal was significant and the patched individuals showed longer flowering-time period. The difference, however, was smaller than that of the parentals.

The conclusions drawn from the present work needs further investigation in order to establish the absence of pleiotropic action of the two major genes.

5.5 The combination of multiple recessive

(a) The combination of two recessive loci.

The observation of a significantly low fraction of double recessives as compared with the 1/16 expected on the basis of independent assortment is the first clear indication of linkage. However, it is not desirable to derive linkage data entirely from double intercross matings - or indeed from single intercrosses but from double backcrosses for the following reasons:

(i) a proportion of the recombinant genotypes in intercross progeny has the same phenotype as some of the non-recombinant genotypes and can therefore not be easily indentified by breeding test.

(ii) from double backcrosses, each genotype of the progeny has a distinct and individual phenotype, consequently the exact number of recombinants can be counted.

A double recessive of each sex can be produced from the double intercross by the two generation method. Each such recessive requires the occurrence of a crossover in one parent simultaneously with one from the other, hence the closer the linkage, the rarer will this genotype be and the less efficient this method of obtaining it.

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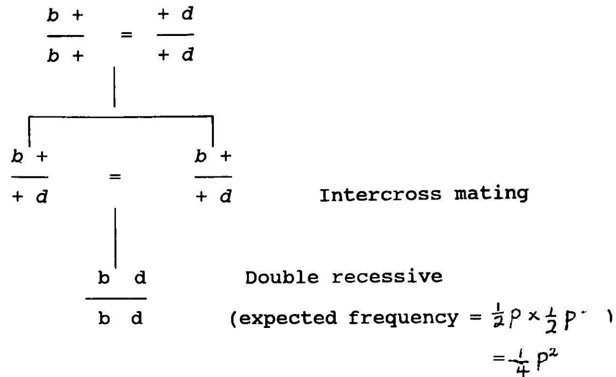
Assuming we have a hypothetical stock A_b_C and we want to include a fourth point d where A and C are used as dominants, and b and d are known to be linked with a recombination fraction p. The following plan is followed:



The way in which the genotypic and mating frequencies involved can be calculated is shown in appendices 3A and 3B.

In the present investigation the expected frequencies (based on the calculated recombination fractions) for the double recessive classes are shown in Table 37. The expected genotypic frequencies for the various matings are presented in Tables 38-42. The observed numbers for the ten genotypic classes could not be presented since F_3 generation was not raised.

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TABLE 37

Expected frequencies for the double recessive classes

Double Recessive	Expected frequency
$b^R b^R$ rcy rcy	$\frac{1}{324}$
pbrpbrrcyrcy	$\frac{1}{100}$
pbrpbrlrblrb	$\frac{1}{256}$
blblybrybr	$\frac{1}{36}$
pgppgppfpf	$\frac{1}{64}$

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TABLE 38

Expected genotypic frequencies for the mating ;
Pgp/pf = *Pgp/pf* (p = 1/4 and q = 3/4)

FIRST LOCUS

SECOND LOCUS	*Pgp Pgp*	*Pgp pgp*	*pgp pgp*	Total
Pf Pf	1	6	9	16
Pf Pf	6	18/2	6	32
pf pf	9	6	1	16
Total	16	32	16	64

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TABLE 39

Expected genotypic frequencies for the mating: $b_{.}^{R}/rcy = b_{.}^{R}/rcy$
(p = 1/9 and q = 8/9)

FIRST LOCUS

SECOND LOCUS	$B_{.}^{R}B_{.}^{R}$	$B_{.}^{R}b_{.}^{R}$	$b_{.}^{R}b_{.}^{R}$	Total
RcyRcy	1	16	64	81
Rcyrcy	16	128/2	16	162
rcyrcy	64	16	1	81
Total	81	162	81	324

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TABLE 40

Expected genotypic frequencies for the mating: *rcy/pbr* = *rcy/pbr*
(p = 1/5 and q = 4/5)

FIRST LOCUS

SECOND LOCUS	*RcyRcy*	*Rcyrcy*	*rcyrcy*	Total
Pbrpbr	1	8	16	25
Pbrpbr	8	32/2	8	50
pbrpbr	16	8	1	25
Total	25	50	25	100

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TABLE 41

Expected genotypic frequencies for the mating: *pbr/lrb=pbr/lrb*
(p = 1/8 and q = 7/8)

FIRST LOCUS

SECOND LOCUS	*Pbrpbr*	*Pbrpbr*	*pbrpbr*	Total
LrbLrb	1	14	49	64
Lrblrb	14	98/2	14	128
Lbrlrb	49	14	1	64
Total	64	128		256

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TABLE 42

Expected genotypic frequencies for the mating: Bl/Ybr = Bl/Ybr
(p = 1/3 q = 2/3)

FIRST LOCUS

SECOND LOCUS	BlBl	Blbl	blbl	Total
YbrYbr	1	4	4	9
Ybrybr	4	8/2	4	18
ybrybr	4	4	1	9
Total	9	18	9	36

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SUMMARY

1. Six varieties of cowpea were used for the investigation. Inheritance and linkage were based on F_2 data.

2. The phenotypes of the parent varieties are:

DM: normal leaflet base; purple flower colour; dark mottled seed coat; pigment at bases of branch, peduncle, petiolet; whole plant pigmentation; red sepal; red pod tip; red flower bud tip; late flowering time; small median leaf length; long number of seeds per pod; high percentage seed set; short pod and small seed.

IM: light green patch at leaflet base; purple flower; black seed coat; pigment at bases of branch, peduncle, petiolet; whole plant pigmentation; red sepal; red pod tip; red flower bud tip; early flowering time; large median leaf length; high number of seeds per pod; low percentage seed set; long pod and large seeds.

IVX: normal leaflet base; purple flower; holstein seed coat pattern; pigment at bases of branch, peduncle, petiolet; whole plant pigmentation; red sepal; red pod tip; red flower bud tip; early flowering time; large median leaf length; high number of seeds per pod; high percentage seed set; long pod and large seeds.

LS: normal leaflet base; purple flower; red seed coat with streaks; pigment at bases of branch, peduncle, petiolets; whole plant pigmentation; green sepal; light green unripe pod tip; light green flower bud tip; late flowering time; large median leaf length; high number of seeds per pod; high percentage seed set; long pod and large seed.

1977: normal leaflet base; white flower; brown small eye seed coat pattern; pigment at bases of branch, peduncle, petiolets; whole plant pigmentation; green sepal; light green unripe pod tip; early flowering time; small median leaf length; small number of seeds

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per pod; high percentage seed set; short pod length and small seed.

4557: normal leaflet base; white flower, Watson seed coat pattern; no pigment at bases of branch, peduncle, petiolet; whole plant non-pigmentation; green sepal; light green unripe pod tip; late flowering time; small median leaf length; small number of seeds per pod; high percentage seed set; short pod length and small seed.

3. In assigning cowpea gene symbols the recommendations of both the International Committee on Genetic Symbols and Nomenclature and the Tomato Genetics Cooperative were followed. Seven cowpea gene symbols have been suggested:

B^R (red bud tip)

Lbr (red leaflet base)

Pgp (pale green patch at leaflet base)

P_w (whole plant non-pigmented)

Rcy (red calyx)

S_1 (streakless)

Y_{br} (brown small eye seed-coat pattern).

4. With respect to the factors studied in this investigation the following were observed in the F_1 plants:

(a) The pale green patch at leaflet base was dominant to normal patch.

(b) The purple flower colour was dominant to white.

(c) The black seed coat was dominant to small brown eye.

(d) The Pigmentation at the base of branch was dominant to non-pigmentation.

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(e) The red colour at the tip of the unripe pod was dominant to light green colour.

(f) The red colour at the tip of the flower bud was dominant to light green colour.

(g) The pigmentation at the base of the peduncle was dominant to non-pigmentation.

(h) The pigmentation at the base of the petiolet was dominant to non-pigmentation.

(i) The red colour of the sepal was dominant to light green colour.

(j) The whole plant pigmentation was dominant to whole plant non-pigmentation.

(k) Early flowering was dominant to late flowering.

(l) The greater leaf length was dominant to smaller leaf length.

(m) The greater number of seeds per pod was dominant to smaller number of seeds per pod.

(n) The smaller percentage seed set was dominant to greater percentage seed set.

(o) The greater pod length was dominant to smaller pod length.

(p) The greater seed weight was dominant to smaller seed weight.

5. Disturbed segregation was observed in

(i) chlorophyll factor and branch base pigmentation and

(ii) chlorophyll factor and purple flower colour.

6. Transgressive segregation was observed for long pod, large seed size, small number of seeds per pod, large leaf length and low percentage seed set. F_2 heterosis of -13.43% and F_1 heterosis of -3.39% were observed for the trait percentage seed set, for seed weight there was an F_1 heterosis of -0.006g. Considering leaf length, the F_2 and F_1 values were 1.40cm and 1.54cm respectively.

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7. Pod length was highly and positively correlated with number of seeds per pod.

8. Number of seeds per pod was highly and positively correlated with the log of percentage seed set per pod.

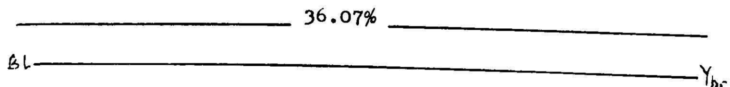
9. The broad-sense heritability estimate was observed to be more than 50% for the following traits: pod length, (88.0%) seed weight (84.94%), number of seeds per pod (69.52%), percentage seed set per pod (64.87%); the estimate for leaf length however, was 46.69%.

10. The number of polygenes(n) segregating for the following traits were greater than unity: pod length (n = 3.82), seed weight (n = 6.01), number of seeds per pod (n = 7.12), percentage seed set per pod (n = 4.76) and leaf length (n = 2).

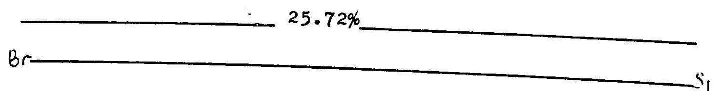
11. Seed-coat pattern was conditioned by about five mendelian factors. Their interactions resulted in different seed-coat patterns in the F_2,s. The combination of the two dominant genes H and W resulted in self-coloured or solid seed-coat pattern, their recessive forms produced small eye.
The presence of R, the gene for red suppressed the effect of hhww, the recessive for H and W.

12. Six 2 loci linkage systems were established:

(i) Black seed-coat pattern and Brown small eye seed-coat pattern.



(ii) Brown seed-coat pattern and streakless seed-coat



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(iii) Pale green patch at leaftlet base and Purple flower

30.32%

P_{gp} ———————— P_f (Treated as disturbed linkage)

24.32%

P_{gp} ———————— P_f (In the face of partial manifestation)

(iv) Red bud tip and Red calyx

10.97%

B^R ———————— R_{cy}

(v) Purple branch base and Red leaflet base

13.02% (Treated as disturbed

disturbed linkage)

P_{br} ———————— L_{rb}

(vi) Red pod tip and Red calyx

20.08%

P^t ———————— R_{cy}

Suggested Linkage Group

(vii) Purple pod tip, Purple branch base and Red leaflet base

P^t ———————— P_{br} ———————— L_{rb}

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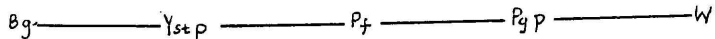
(viii) Brown grain, Yellow strips of petals, Purple flower, Pale green and Watson seed-coat



13. Major gene and polygene linkages were found between the following:

    (i) chlorophyll factor and median leaf length

    (ii) chlorophyll factor and flowering-time and

    (iii) seed size and seed-coat pattern

14. Individuals with pale green patch at leaflet base seemed to have larger leaf length and also tended to flower early.

15. The expected frequencies for the double recessive classes for the linkage systems were rather low and therefore combination for multiple recessives cannot be achieved in the first generation.

16. There seemed to be incomplete penetrance of 0.18 ± 0.075 for the pale green patch individuals.

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SUGGESTED INVESTIGATIONS

1. Combination of multiple recessives which are linked for backcross linkage analysis (constructing genetic map distances).
2. Investigation into the disturbed linkage system of this work.
3. Protein inheritance.
4. Investigations into correlated characters.
6. Inheritance of early anthesis in the cowpea.
7. Linkage relations of the genes involved in the gene interactions of seed-coat colours.

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MATHEMATICAL SYMBOLS

Symbol	Definition
α	Differential contribution of a dominant gene.
a_A	Observed proportion of the A allele.
a_a	Observed proportion of the a allele.
e^L	Likelihood.
L	Logarithm of the likelihood.
m_A	Expected proportion of the A allele.
m_a	Expected proportion of the a allele
μ	Viability of a given phenotype.
$\hat{\mu}$	Maximum likelihood estimate of μ
S_μ	Score for μ
$I_{\mu\mu}$	Information function of μ
$Var(\mu)$	Large-sample variance of the maximum likelihood estimate of μ
p_1	Recombination fraction in male.
p_2	Recombination fraction in female
p	Recombination fraction when $p_1=p_2$
P	The product of $(1-p_1)$ and $(1-p_2)$
$V_{\hat{p}}$	Variance of recombination fraction.
$s_{\hat{p}}$	Standard error of the recombination fraction.

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V_P	Variance of P
S_P	Standard error of P.
Σ	Summation.
σ^2_E	Environmental variance.
σ^2_F	Phenotypic variance of F_1 generation.
σ^2_F	Phenotypic variance of F_2 generation
V_x	Random sampling variance of the linear function X
y	The unknown parameter of the logarithm of the likelihood.
$\hat{y}$	Maximum-likelihood estimate of y.
y_o	Hypothetical value of y.
$I(y_o)$	Amount of information for y.
λ	Proportion of phenotypes misclassified.
$\hat{\lambda}$	Maximum-likelihood estimate of λ
$Var(\hat{\lambda})$	Large-sample variance of the maximum-likelihood estimate of λ

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APPENDICES

APPENDIX 1

Rules for gene nomenclature applied to the genus *Vigna*.

(Source: Fery 1980, in Singh and Rachie, 1985)

(a) The name of a gene should be descriptive of the characteristic phenotype conditioned by the gene. The name should be short and in either English or Latin.

(b) Genes are symbolized by italicized Roman letters, the first letter being the same as that for the name. A minimum number of additional letters is used to distinguish the symbol from other symbols already assigned to the species.

(c) The first letter of the symbol and name is capitalized if the gene is dominant to the normal allele, otherwise, all letters are in lower case. The normal allele is represented by the symbol followed by the superscript '+'. Except for instances in which a symbol has already been established for the normal allele, the primitive form of each species shall represent the '+' allele for each gene.

(d) A symbol shall not be assigned to a gene that is not firmly established by statistically valid segregation data.

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(e) Mimics, that is different genes that condition similar phenotypes, may be assigned distinctive names and symbols or the symbol of the original gene followed by a hyphen and distinguishing Arabic numeral or Roman letter. The suffix '1' is used, or understood, for the original gene in a mimic series. Allelism tests should be made before a new gene symbol is assigned to a mimic.

(f) Multiple alleles are assigned the same symbol, followed by a Roman letter or Arabic number superscript. The allelism test must be made to establish multiple allelism.

(g) Indistinguishable alleles, that is, alleles at the same locus that condition identical phenotypes, preferably should be given the same symbol. However, an allele that is an apparent recurrence of the same mutation can be given a distinctive symbol by adding to the symbol of the original allele superscript Roman letters or Arabic numbers that are enclosed in parentheses. The superscript '(1)' is understood and not used for the original allele.

(h) A modifying gene may be designated using a symbol for an appropriate name, for instance, intensifier, suppressor, or
inhibitor, followed by a hyphen and the symbol of the allele affected. Alternatively, a modifying gene may be given a distinctive name and symbol without reference to the gene modified.

(i) In instances where the same symbol has been assigned to different genes, or the same gene has been assigned different symbols, priority in publication will be primary criterion for establishing the preferred symbol. Incorrectly assigned symbols will be enclosed in parentheses on gene lists.

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APPENDIX 2A

Maximum-likehood method of calculating recombination value for F_2 data involving red bud tip (B^R) and red calyx (R_{cy}).

Class	red bud tip, red calyx (B^R Rcy)	red bud tip, green calyx (B^R rcy)	green bud tip red calyx (b^R Rcy)	green bud tip green calyx (b^R rcy)	Total
Expected number	n(2+P)	n(1-P)	n(1-P)	nP	4
Observed number	45	5	1	17	68

The logarithm likelihood expression is then:

$$L = 45\log(1/2 + 1/4P) + 5\log(1/4 - 1/4\,P) + 1\log(1/4 - 1/4\,P) + 17\log 1/4\,P$$

Maximization leads to the equation

$$\frac{dL}{dP} = \frac{45}{2+P} - \frac{5}{1-P} - \frac{1}{1-P} + \frac{17}{P} = 0$$

$$\Rightarrow \quad nP^2 - (a_1 - 2a_2 - 2a_3 - a_4)\,P - 2a_4 = 0$$

$$= 68P^2 - 11P - 34 = 0$$

giving $P = 0.7926$

Variance of P is given by

$$VP = \frac{2\,P\,(1-P)\,(2+P)}{n(1+2\,P)}$$

Hence $VP = 0.005223$ and $Sp = 0.07227$

Assuming that $p_1 = p_2$ we have

$$(1-p) = \quad P = 0.8903$$

$$p = 0.1097 \text{ or } 10.97 \text{ per cent.}$$

The variance of p is then found from the variance of P by the formula

$$Vp = \frac{VP}{4P}$$

Hence

$$Vp = 0.001647$$

and $Sp = \quad Vp \quad = 0.04059$ or 4.06 per cent.

Test of significance of the deviation of p from the freedom value of 0.5 is given by

$$\frac{d}{Sp} = 9.6157, \quad P<0.001$$

Therefore, recombination fraction for the two factors red bud tip and red calyx is 10.97±4.06%

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APPENDIX 2B

Maximum-likelihood method of calculating recombination value for F_2 data involving the allleles for pale green patch at leaflet base (*Pgp*) and purple flower (*Pf*).

Class	pale green patch, purple flower (*Pgp Pf*)	pale greeen patch white flower (*Pgp pf*)	normal, purple flower (*pgp Pf*)	normal, white (*pgp pf*)	Total
Expected frequency	$\frac{n\mu(2+P)}{3\mu+1}$	$\frac{n\mu(1-P)}{3\mu+1}$	$\frac{n(1-P)}{3\mu+1}$	$\frac{nP}{3\mu+1}$	1
Observed number	38 (a_1)	5 (a_2)	15 (a_3)	9 (a_4)	67

The product formula puts

$$\frac{a_1a_4}{a_2a_3} = \frac{2P + P^2}{1-2P + P^2}$$

Applying to the present situation we find

$$\frac{342}{75} = \frac{2P + P2}{1-2P + P^2}$$

$$(a_1a_4 - a_2a_3)P^2 - 2(a_1a_4 + a_2a_3)\ P + a_1\ a_4 = 0$$

$$267P^2 - 834P + 342 = 0$$

giving $P = 0.48555$

Variance of P is given by

$$VP = \frac{2P(1-P)\ (2+P)}{n(1+2P)}$$

Hence $VP = 0.009264$ and $SP = 0.09625$

Assuming $p_1 = p_2$ we have

$$(1-p) = P = 0.6981$$

$p = 0.3032$ or 30.32 per cent

Variance of p is given by

$$Vp = \frac{VP}{4P}$$

Hence $Vp = 0.004770$

and $Sp = Vp = 0.06906$ or 6.91 per cent.

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Test of significance of the deviation p from the freedom value of 0.5,

$$\frac{d}{Sp} = 2.8497, \quad P<0.001$$

Therefore the recombination fraction in the case of the factors pale green patch at leaflet base and purple flower is 30.32 ± 6.91%

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APPENDIX 2C

Maximum-likelihood method of calculating recombination value for F_2 data involving the alleles for purple branch base (*Pbr*) and red leaflet base (*Lrb*).

Class	purple branch base red leaflet base (*Pbr Lrb*)	purple branch base green leaflet base (*Pbr lrb*)	green branch base red leaflet base (*pbr lrb*)	green ranch base green leaflet base (*pbr lrb*)	Total
Expected frequency	$\frac{n\mu(2+P)}{3\mu+1}$	$\frac{n\mu(1-P)}{3\mu+1}$	$\frac{n(1-P)}{3\mu+1}$	$\frac{nP}{3\mu+1}$	1
Observed number	33 (a_1)	3 (a_2)	5 (a_3)	16 (a_4)	57

The product formula puts

$$\frac{a_1\ a_4}{a_2\ a_3} = \frac{2P + P^2}{1-2P + P^2}$$

$$\frac{528}{15} = \frac{2P + P^2}{1- 2P+P^2}$$

$$513P^2 - 1086P + 528 = 0$$

giving

$$P = 0.7566$$

Variance of P is given by

$$VP = \frac{2P(1-P)\ (2+P)}{n(1+2P)}$$

Hence $Vp = 0.007088$ and $Sp = 0.08419$

Assuming $p_1 = p_2$ we have

$$(1 - p) = P = 0.8698$$

$$p = 0.1302 \text{ or } 13.02 \text{ per cent}$$

Variance of p is given by

$$Vp = \frac{VP}{4P}$$

Hence $Vp = 0.001576$

and $Sp = 0.0397$ or 3.97 per cent

Test of significance of the deviation of p from the freedom value of 0.5,

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$$\frac{d}{Sp} = 9.3147, \quad P<0.001$$

Therefore the recombination fraction for the factors purple branch-base and red leaflet base in the presence of disturbed linkage is 13.02 ± 3.97%

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APPENDIX 2D

Maximum-likelihood method of calculating recombination value of F_2 data involving the alleles for red pod tip (P^b) and red calyx (R_{cy}).

Class	red pod tip red calyx (P^b Rcy)	red pod tip green calyx (P^b rcy)	light green pod red calyx (pb Rcy)	light green pod green calyx pb rcy)	Total
Expected frequency	$\frac{n(2+P)}{4}$	$\frac{n(1-P)}{4}$	$\frac{n(1-P)}{4}$	$\frac{nP}{4}$	1
Observed number	25	5	2	9	41

The logarithm likelihood expression is

$$L = 25\log(1/2 + 1/4P) + 5\log(1/4 - 1/4P) + 2\log(1/4 - 1/4P) + 9\log(1/4)P$$

Maximization leads to the equation

$$\frac{dL}{dP} = \frac{25}{2+P} - \frac{5}{1-P} - \frac{2}{1-P} + \frac{9}{P}$$

$$\Rightarrow \quad 41P^2 - 2P - 18 = 0$$

giving

$$P = 0.6386$$

Variance of P is given by

$$VP = \frac{2P(1-P)\ (2 + P)}{n(1+ 2P)}$$

Hence VP = 0.013045 and Sp = 0.1142

Assuming $p_1 = p_2$ we have

$$1 - p = P = 0.7992$$

$$p = 0.2008 \text{ or } 20.08 \text{ per cent}$$

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Variance of p is given by

$$Vp = \frac{VP}{4P}$$

Hence $Vp = 0.005107$

and $Sp = 0.07146$

Test of significance of the deviation of p from the freedom value of 0.5,

$$\frac{d}{Sp} = 4.1870, \quad P<0.001$$

Therefore the recombination fraction for the factors red pod tip and red calyx is 20.0 ± 7.15%

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APPENDIX 3A

General method for calculating genotypic and mating frequencies

POLLEN

OVULE	++ $\frac{1}{2}p$	*b* + $\frac{1}{2}(1-p)$	+ *d* $\frac{1}{2}(1-p)$	*b d* $\frac{1}{2}p$	
++ $\frac{1}{2}p$	p^2	$p(1-p)$	$p(1-p)$	p^2	$\frac{1}{2}p$
b+ $\frac{1}{2}(1-p)$	$p(1-p)$	$(1-p)^2$	$(1-p)^2$	$p(1-p)$	$\frac{1}{2}(1-p)$
+*d* $\frac{1}{2}(1-p)$	$p(1-p)$	$(1-p)^2$	$(1-p)^2$	$p(1-p)$	$\frac{1}{2}(1-p)$
b d $\frac{1}{2}p$	p^2	$p(1-p)$	$p(1-p)$	p^2	$\frac{1}{2}p$
	$\frac{1}{2}p$	$\frac{1}{2}(1-p)$	$\frac{1}{2}(1-p)$	$\frac{1}{2}p$	1

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APPENDIX 3B

Determination of genotypic frequencies

FIRST LOCUS

SECOND LOCUS	++	+*b*	*bb*	
++	p^2	2pq	q^2	1
+*d*	2pq	$2q^2/2p^2$	2pq	2
dd	q^2	2pq	p^2	1
	1	2	1	4

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