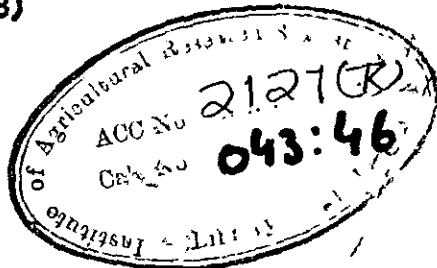


V 95
V 87

**GENETIC
COMPONENTS OF VARIATION
IN PRESENCE OF
GENE-ENVIRONMENT INTERACTIONS.**

By

**T.C. SEETA RAMA SARMA
(1962-63)**



DE-04
②

Dissertation

submitted in fulfilment of
the requirements for the award of Diploma
in Agricultural and Animal Husbandry Statistics of the
Institute of Agricultural Research Statistics
(I.C.A.R.)
NEW DELHI.

ACKNOWLEDGEMENT

I am much indebted to Shri. Prem Narain, Assistant Professor of Statistics, Institute of Agricultural Research Statistics, Indian Council of Agricultural Research, New delhi for his valuable guidance, keen interest and constant encouragement during the course of investigation and of preparation of the thesis.

I am also thankful to Dr. W. G. Panse, Statistical Adviser, Institute of Agricultural Research Statistics, Indian Council of Agricultural Research for providing me with adequate facilities for the thesis work.

J. (T. C. Seeta Rama Sarma) ^{25/7/63}
(T. C. Seeta Rama Sarma.)

CONTENTS.

<u>CHAPTER</u>	<u>Page No.</u>
1. Introduction ...	1
2. Review of literature ...	5
3. Description of the components ...	25
4. Biometrical Analysis ...	49
5. Summary ...	62
REFERENCES. ...	65
<u>APPENDIX</u>	
I. ...	(i)
II. ...	(vi)
III. ...	(xvii)

CHAPTER I

INTRODUCTION

It is well known that an attribute of a living organism is partly determined by the effects of hereditary factors received from parents and partly by the effects of the environment in which it develops. The ultimate part of hereditary factors are genes. The genes do not cause a cell to develop into anything in particular, but they give the cell the capacity to develop in any one of a great many different directions. The particular direction in which one cell develops is then determined by the environment, acting in conjunction with the genes. The genes are located on the chromosomes in the nuclei of the cells of the organism. Their totality constitutes the genotype of an individual. The phenotype, the sum total of an individual's expressed peculiarities of form, size, colour, behaviour... is the result of the interaction of the genotype with a given environment.

In the case of qualitative attributes, usually variations in the environment do not effect the phenotype. Except in cases of dominance and epistascy, the various genotypes can be distinguishable on the basis of their phenotypes. These dominance and epistascy are interactions within genetic material. Few genes control such attributes and so the mode of inheritance of such attributes can be determined by Mendel's laws of inheritance and the principle of linkage.

The attributes show discontinuous variation. So, the analysis of data only require the frequencies with which the different genotypes are represented in the group of individuals under observation.

The situation is different with quantitative characters. Here the genotypes cannot be identified straightaway for, the variations in the environment give the same phenotypic value for different genotypes. The number of genes determining a genotype are quite large, their individual effects being similar and cumulative and small in relation to effects of environment. The large number of genes coupled with environmental modifications produce continuous variation in such characters.

The mode of inheritance of such a character is determined by the biometrical method given by Mather (1949). This method consists of crossing two true breeding strains, raising F_1, F_2, F_3 , and the two back crosses to the true parental forms. The data so gathered allows the estimation of various components of variation, viz., D, the fixable component, H the unfixable component, and E the variation due to non-heritable agencies. D corresponds to variation due to additive effects and H corresponds to variation due to dominance deviations. This analysis is to be carried out of measurements made on a scale satisfying the criteria of scaling so that the variation component

due to genic interaction is eliminated.

One of the important assumptions, apart from others, on which this analysis is based on, is that the differences among the two true breeding strains and their F_1 's are likely to be the same if the experiment is conducted in any other environment. In other words, the variance component due to environment and the heritable components of variance are simply additive. For instance, in F_2 , the total phenotypic variance (V_{F_2}) is expressed as $\frac{1}{2}D + \frac{1}{4}H + E$. This may not always be true. The effect of environment may be interacting with that of genotype so that there may be additional component of variation due to interaction which is not accounted for in this analysis. Jones and Mather (1958) gave a method when genotype - environment interactions are present by introducing terms G_D and G_H which are the components due to interactions of fixable and unfixable variation with the environment.

Since it may not always be possible to choose a scale so as to eliminate genic interactions, a general approach should be to consider the scale suggested by experimental techniques, allowing the allelic and non-allelic interactions to take their own values. In addition to the genetic components of variation, D and H there would be components of variation represented, for the digenic interactions, by I, J and L (additive X additive, additive X dominance, dominance x dominance respectively) ,

[Contd.]

(Hayman and Mather - 1955) When the genotype - environment interactions are present, this would mean more components due to interactions, which may be confounded with the main components.

The object of the present investigation is, therefore, to study and discuss how these various genetic components of variances are affected when gene-environment interactions are present and both allelic and non-allelic interactions are taken into account.

-: 0 :-

CHAPTER 2
REVIEW OF LITERATURE

(a) Genetic components of variation.

In the case of metric characters, it is not possible to follow genes individually and set up a correspondence between the genes under consideration and the characters expressed as can be done in case of qualitative characters. One is interested in estimating the pooled effects of all the genes carried by the individual, together with the pooled effects produced by the various combinations of allelic and non-allelic genes which are carried by the individual. This totality of effects confers a genotypic value on the individual, and associated with a variant (major or minor) of environment in which the individual develops. This determines the phenotypic value of the individual. This in other words, means that the observed phenotypic value of an individual deviates in one direction or the other from the genotypic value depending on the environment in which the development of the individual has occurred. So, the genotypic value may be defined in terms of the average value of the phenotypes that would be evoked in each of the individual environments of a population of environments.

The above defined genotypic value of an individual has, however, further subdivisions. Since,

the genes are transmitted from parents to offspring and not the genotypes, the genotypic value of an individual itself deviates in one direction or another from the value conferred on the individual due to additive effects of genes, depending upon the dominance and epistatic relations which are set up between the genes received by the individual from parents. Thus the genotypic value can be looked upon as composed of value due to additive effects of genes (often spoken of as breeding value), value due to dominance deviations and value due to epistatic deviations.

The differences among individual on the basis of their phenotypic values can be measured by the variance of phenotypic values. This phenotypic variation is capable of resolution by virtue of the above definitions of 'values', into genetic and non-genetic variations. The genetic variation is, by the same reasons capable of further resolution into various components known as genetic components. These are, the additive genetic component and the non-additive genetic component, the latter being capable of subdivision into dominance variance and epistatic variance components.

The concept of value makes it necessary to choose a scale on which the phenotypic measurements are to be taken. Normally it is the scale provided by the instruments which are in use. However, to facilitate

7

the analysis of data and the interpretation and use of resulting statistics, sometimes it is advocated to choose a scale such that the epistatic deviations cancel out whereas the dominance deviations take their own value on the chosen scale (Mather (1949)). In other words, on the chosen scale, the genic effects must be simply additive on the average and the contribution made by non-heritable agents must be independent of the genotype. This choice is, however, perfectly arbitrary and at times it may be quite a hard task to get a scale suiting the above needs. On the contrary some workers like Falconer (1960) even depreciate the use of scaling from a practical point of view, as it distorts the genetic situation existing on the given scale of measurements provided by the instruments in use. Irrespective of the merits or demerits of scaling it helps to adopt the biometrical method when either the scaling tests have shown the absence of epistatic interactions or proper scaling has been done to eliminate these interactions if they are existing.

(i) DESCRIPTION

Fisher, Immer and Tedin (1932) gave a method of determining the contributions of each of the genes involved to the additive genetic variance and dominance variance assuming that the genic interactions,

if found existing are eliminated by choosing a proper scale. The additive effect for the gene A - a denoted by d_a may be defined as half of the difference between the genotypic values of the two homozygotes AA and aa so that the genotypic values for AA and aa may be represented by $+d_a$ and $-d_a$ measured from the midpoint of the two homozygotes, the origin of the scale chosen. The genotypic value of the heterozygote Aa may be represented by $\pm h_a$ as measured from the origin the \pm sign indicating the direction of the dominance. with no dominance Aa would have a genotypic value equal to zero, midway between the values of two homozygotes. Such a representation of main effect and dominance deviation for the gene A-a would be quite consistent with the principles of Mendelian Genetics.

A cross between two true breeding parents P_1 and P_2 results in F_1 generation which shows only non-genetic variations similar to that of the parents. When F_1 is selfed or two F_1 's are crossed, the resulting generation F_2 , shows both genetic and non-genetic variations. According to Mather (1949) the genetic variations in F_2 , with no differential fertilization and viability, can be shown to be equal to $\frac{1}{2}D + \frac{1}{4}H$ where D and H are the fixable and unfixable variations respectively given by

$$D = \sum_a d_a^2 ; \quad H = \sum_a h_a^2$$

The variance due to additive effects of genes, may, therefore be taken as $\frac{1}{2}D$ and that due to dominance deviations as $\frac{1}{4}H$. The F_2 can be selfed to give rise to F_3 families. Pairs of individuals can be drawn at random from F_2 and intercrossed, giving rise to biparental progenies (denoted by S_3). Further, each type of female of F_2 can be crossed to a male picked up at random out of all possible males of F_2 , giving rise to maternal progenies (denoted by M_3).

The various second degree statistics arising from these generations can be expressed in terms of D and H as shown below (Mather (1949)),

1. Variance of F_2 : $H^V_{1F_2} = \frac{1}{2}D + \frac{1}{4}H$
2. Variance of F_3 means : $H^V_{1F_3} = \frac{1}{2}D + \frac{1}{16}H$
3. Mean variance of F_3 progenies : $H^V_{2F_3} = \frac{1}{4}D + \frac{1}{8}H$
4. Covariance of F_2 and F_3 means : $W_{1F_23} = \frac{1}{2}D + \frac{1}{8}H$
5. Variance of BIP means : $H^V_{1S_3} = \frac{1}{4}D + \frac{1}{8}H$
6. Mean variance of BIP's : $H^V_{2S_3} = \frac{1}{4}D + \frac{3}{16}H$
7. Covariance of F_2 and BIP means: $W_{1S_23} = \frac{1}{4}D$

8. Variance of MAT means : $H^V_{1M_3} = \frac{1}{8} D$

9. Near variance of MAT progenies: $H^V_{2M_3} = \frac{3}{8} D + \frac{1}{2} H$

When the scaling tests demonstrate the existence of genic interactions which cannot be removed in the absence of an adequate scale, the above biometrical quantities have got to be modified.

Hayman and Mather (1955) considered the case of genic interactions in continuous variation. With two gene differences, nine genotypes are possible and eight parameters are used to give a complete description of the genotypic values. Four of these parameters will be d's and h's appropriate to the two gene pairs. The other four correspond to non-allelic interaction comparisons. The distribution of these four parameters among nine genotypes is shown in the table below

	AA	Aa	aa
	d_a	h_a	$-d_a$
BB	$d_a + d_b$	$h_a + d_b$	$-d_a + d_b$
	$+ \frac{1}{2} j_{ab/}$		$- \frac{1}{2} j_{ab/}$
d_b	$-\frac{1}{2} j_{a/b} - \frac{1}{2} j_{b/a}$	$+ \frac{1}{2} j_{b/a}$	$+ \frac{1}{2} j_{a/b} - \frac{1}{2} j_{b/a}$
	$+ \frac{1}{4} l_{/ab}$	$-\frac{1}{4} l_{/ab}$	$+\frac{1}{4} l_{/ab}$

(contd.)

f1

	$d_a + h_b$	$h_a + h_b$	$-d_a + h_b$
Bb	$+\frac{1}{2}j_{a/b}$		$-\frac{1}{2}j_{a/b}$
h_b	$-\frac{1}{4}l_{/ab}$	$+\frac{1}{4}l_{/ab}$	$-\frac{1}{4}l_{/ab}$
<hr/>			
	$d_a - d_b$	$h_a - d_b$	$-d_a - d_b$
bb	$-i_{ab/}$		$+i_{ab/}$
$-d_b$	$-\frac{1}{2}j_{a/b} + \frac{1}{2}j_{b/a}$	$-\frac{1}{2}j_{b/a}$	$+\frac{1}{2}j_{a/b} + \frac{1}{2}j_{b/a}$
	$+\frac{1}{4}l_{/ab}$	$-\frac{1}{4}l_{/ab}$	$+\frac{1}{4}l_{/ab}$
<hr/>			

These four parameters fall into three classes. One is homozygote - homozygote interaction represented by $i_{ab/}$ and the second one is homozygote - heterozygote interactions represented by $j_{b/a}$ and $j_{a/b}$ and the last one is heterozygote - heterozygote interaction represented by $l_{/ab}$. The coefficients of $\frac{1}{2}$ and $\frac{1}{4}$ are applied to the j 's and l 's respectively so that equal contributions will be made to the overall differences in an F_2 family by interactions of unit size. All the classical types of genic interactions may be cast in terms of i , j and l . The con-

tribution of the two gene differences A-a, B-b to various second degree statistics are shown as follows:-

$$1. \text{Contribution to } H^V_{1F_2} = \frac{1}{4}d_a^2 + \frac{1}{4}d_b^2 + \frac{1}{4}h_a^2 + \frac{1}{4}h_b^2$$

$$+ \frac{1}{4}i_{ab}^2 + \frac{1}{8}j_{a/b}^2 + \frac{1}{8}j_{b/a}^2 + \frac{1}{16}l_{/ab}^2$$

$$2. \text{Contribution to } H^V_{1F_3} = \frac{1}{2}(d_a - \frac{1}{4}j_{a/b})^2 + \frac{1}{2}(d_b - \frac{1}{4}j_{b/a})^2$$

$$+ \frac{1}{16}(h_a - \frac{1}{4}l_{/ab})^2 + \frac{1}{16}(h_b - \frac{1}{4}l_{/ab})^2 + \frac{1}{4}i_{ab}^2 + \frac{1}{32}j_{a/b}^2$$

$$+ \frac{1}{32}j_{b/a}^2 + \frac{1}{256}l_{/ab}^2$$

$$3. \text{Contribution to } H^V_{2F_3} = \frac{1}{4}(d_a - \frac{1}{4}j_{a/b})^2 + \frac{1}{4}(d_b - \frac{1}{4}j_{b/a})^2$$

$$+ \frac{1}{8}(h_a - \frac{1}{4}l_{/ab})^2 + \frac{1}{8}(h_b - \frac{1}{4}l_{/ab})^2 + \frac{5}{16}i_{ab}^2 + \frac{7}{64}j_{a/b}^2$$

$$+ \frac{7}{64}j_{b/a}^2 + \frac{1}{32}l_{/ab}^2$$

$$4. \text{Contribution to } W_{1F_{23}} = \frac{1}{2}d_a (d_a - \frac{1}{4}j_{a/b})$$

$$+ \frac{1}{2}d_b (d_b - \frac{1}{4}j_{b/a}) + \frac{1}{8}h_a (h_a - \frac{1}{4}l_{/ab})$$

$$+ \frac{1}{8}h_b (h_b - \frac{1}{4}l_{/ab}) + \frac{1}{4}i_{ab}^2 + \frac{1}{16}j_{a/b}^2$$

$$+ \frac{1}{16}j_{b/a}^2 + \frac{1}{64}l_{/ab}^2$$

$$5. \text{Contribution to } H^V_{1S_3} = \frac{1}{4}d_a^2 + \frac{1}{4}d_b^2$$

$$+ \frac{1}{16}h_a^2 + \frac{1}{16}h_b^2 + \frac{1}{16}i_{ab}^2 + \frac{1}{64}j_{a/b}^2$$

$$+ \frac{1}{64}j_{b/a}^2 + \frac{1}{256}l_{/ab}^2$$

6. Contribution to $H V_{2S_3} = \frac{1}{4} d^2_a$

$$+ \frac{1}{4} d^2_b + \frac{3}{16} h^2_a + \frac{3}{16} h^2_b + \frac{3}{16} i^2_{ab/}$$

$$+ \frac{7}{64} j^2_{a/b} + \frac{7}{64} j^2_{b/a} + \frac{15}{256} l^2_{/ab}$$

7. Contribution to $W_{1^2S_3} = \frac{1}{4} d^2_a + \frac{1}{4} d^2_b + \frac{1}{16} i^2_{ab/}$

It can be seen from these results that when extended to more than two gene

differences V_{1F_2} , V_{1S_3} , V_{2S_3} , and $W_{1^2S_3}$

can be expressed in terms of D, H, I, J and L

where $D = \sum d^2_a$; $H = \sum h^2_a$; $I = \sum i^2_{ab/}$

$J = \sum (j^2_{a/b} + j^2_{b/a})$ and $L = \sum l^2_{/ab}$,

the last three being variance components due to digenic interactions. As far as

V_{1F_3} , V_{2F_3} and $W_{1^2F_3}$ are concerned,

j's get confounded with d's, and l's with h's so that the definitions of D and H do not remain the same as before.

(ii) ANALYSIS

In absence of genic interactions Mather (1949) has given method of analysis and demonstrated it in cases of Juisenberry's data on grain length in oats and lettuce species cross. This type of analysis is only applicable in absence of genic interactions. As mentioned earlier, at first scaling is to be done so that the various types of interactions vanish and then only we can apply the analysis given by Mather. There can be no certainty that a scale exists on which all interactions will vanish. There are some evidences in particular cases that scaling may reduce the interactions that are present but it cannot wholly remove them. In those cases Mather's analysis cannot be used. A analysis which takes account of these interactions is to be developed. With the inclusion of these interactions, we see that in F_2 , S_3 , and M_3 generations, the interactions remain unconfounded and so they can be used to help directly in separation of main and interactive effects. But F_3 statistics namely V_{1F_3} , V_{2F_3} and V_{123F_3} show confounding of these interactions and so the definitions of D and H change from $\sum d^2$ and $\sum h^2$ in F_2 , so that the basic constitution of the components of variation changes with generation. In case of linked genes also the definitions of D and H will be changing. The heterogeneity in the definition of D and H poses practical difficulty in the estimation of the components of

variation. Sufficient number of statistics are to be calculated in which the definitions of these components do not change so as to have a fruitful analysis. It may not always be possible to have the statistics, sufficient in number, in all types of situations.

-: 0 :-

(b) Interaction of genotype and environment.

As discussed earlier, the phenotypic value of an individual can be conceived as made up of A , the breeding value, D , the dominance deviation, I , the epistatic deviation and E , the environmental deviation. In other words, we can write $P = A + D + I + E$. In this model we assume that we can associate a certain environmental deviation with a specific difference of environment, irrespective of the genotype on which it acts. When this is not so there is interaction between various components of G and E . Inclusion of this type of G and E interaction known as genotype - environment interaction makes the model complex.

When these interactions exist, the problem of improvement in plants and animals take a new shape. As pointed out by Wright (1939) in such a case, a race would have to be bred for each ecological niche large enough to support one.

Hammond (1947) however, suggested that animals should be bred in a highly favourable environment because a character is best selected for under environmental conditions favouring its fullest expression. This is only true if there are no genotype - environment interactions as shown by Falconer and Letyszewski (1952). The practical side of the relations between genotype and environment has been receiving considerable attention and it is equally desirable to examine it theoretically.

The classification of the types of genotype-environment interactions was first made by Haldane (1946). He put forward four types of interactions between two genotypes and two environments with no ties. He, however, did not give any attention to the types of differences between environments and between genotypes.

As suggested by McBride (1958) environmental differences can be partitioned into two types, micro- and macro-environments. We can consider these two types with regard to intra- and inter-population genotypic differences separately. Different climates and even different management practices are examples of macro-environmental differences in domestic livestock, while micro-environmental differences are those environmental fluctuations which occur even when all individuals are apparently treated alike. The following table classifies the various situations.

Micro-environments Macro-environments

Intra-population genotypes	Type A	Type B
Inter-population genotypes	Type C	Type D

Type A (Intra-population, micro-environmental):

There is no direct evidence available whether this type of interactions exist or not. In biometrical genetics, usually we assume them to be absent. If any genetic variation in aggressiveness exists in species showing this type of effect, genotype-environment interactions of type A may be detected.

Type B (Intra-population, macro-environmental)

This type of interaction is of importance when selection is practised within breeds or strains. The presence of type B interactions necessitates the selection within the environment for which the organism is required.

When Robertson and Mason(1956) compared progeny groups in special testing stations with progeny groups from the same bulls in herds of varying production levels, the variation between sire groups was much greater in the testing stations than that observed in the high yielding herds; the regression of field results on test station values for herds at all levels of production was only about 0.2 for yield and 0.5 for butter-fat percentage. This suggests the presence of type B interaction.

Falconer and Latyszewski (1952) selected for body weight in mice in two lines, one kept on a high plane of nutrition and the other on a low plane. The result of this selection was, however, different in each environment signifying the presence of interaction. Under conditions of low-level feeding, selection operated on the ability to lay down increased body tissues, such as muscle and bone, while leaving unchanged the ability to lay down fat. On the high plane of nutrition, the ability to lay down fat was under selection to such an extent that in eight generations of selection, the fat content of the full-diet strain was about 24% greater than that of the mice on restricted diet when both were reared on the high plane of nutrition.

Falconer (1952) made a considerable advance in handling of this subject when he considered the problem of performance under two environments as a case of two different correlated characters, the correlation between them having a genetic component. If control of the environment involved only a reduction in environmental variance, the genetic correlation would be unity. Falconer advocated that if h_1^2 , and h_2^2 are respectively the heritabilities of performance in the controlled and uncontrolled economic environments and r_G is the genetic correlation between them, then if $h_1 r_G$ is greater than h_2 , selection should be carried out under controlled conditions.

Type C (Inter-population micro-environmental)

In applied genetics this type of interaction is not considered important. Robertson and Reeve (1952) suggested that heterozygous genotypes are competent, to handle a wider range of micro-environments than the homozygous genotypes; and are thus less subject to environmental variation. Under this interpretation, micro-environmental fluctuations cause some populations (the pure breeds) to vary, yet they produce no effects on other populations (the hybrids). In this sense, heterosis is an example of Type C interactions.

Type D (Inter-population, macro-environmental)

The presence of type D interactions influence important decisions in animal and plant breeding. This is the type implied by Wright (1939).

Before a breeder can locate the breeds or strains, that will perform best in his environment, he must first test for the presence of type D interaction. Having found the best strain for his particular conditions, he must then decide whether the conditions under which his selection is to be carried out are important, i.e., whether type B interactions are present.

Breed differences in response to temperature changes were demonstrated by Huston and Jones (1957) for egg size, body weight, and feed consumption in the fowl. They found that the white Leghorn performed as well at a constant temperature 90°F as under uncontrolled temperature conditions, while New Hampshires and White Plymouth Rocks were adversely effected by the high temperature environment.

The existence of highly adapted local races of many organisms suggests that type D interactions may be extremely prevalent.

The presence and importance of Type B interactions may well be brought out by reviewing the paper of Mather and Vines (1952)

In their experiment F_1 , F_2 , F_3 s, BIPs, IBs and 2Bs were available for use in 1946, the F_3 s BIPs being derived from F_2 and 2 Bs from IB plants. Randomised block design was used. In 1947 and 1948, the same type of experiment was repeated except for the omission of BIP and 2B families but with F_4 instead. Thus in each of the three years F_1 , IBs, F_2 s and F_3 s were included. Seventeen second degree statistics were calculated for two characters, height and flowering time. The method used in the analysis of the variability was the same as the method described by Mather (1949). The different variances and covariances were regarded as compounded of the usual three components namely D, H and E, assuming adequacy of scale upon which the character was measured. Estimates of D, H and E were obtained by a least squares technique from the values of different statistics available.

In 1946 experiment there was no evidence of residual interaction in the case of height. It was also found true for 1947 data, whereas for 1948 data, there was evidence of residual interaction. The linkage item was significant in both the years (i.e., in 1947 and 1948), when compared with the duplicates mean square. Regarding

flowering time, the situation was the same as in height analysis in 1947, but in 1948 there was evidence of neither linkage nor residual interaction. Since the results of the two years were conflicting each other a joint analysis of the two years' results was used, which was slightly different from the method given by Mather (1949 b)

In joint analysis, sum of squares due to main effects (linkage and residual interaction), Heterogeneity between years (components, linkage and residual interaction), Heterogeneity within years (components, linkage and residual interaction) were obtained. Regarding height, the three mean square items for Heterogeneity within years and the three mean square items for heterogeneity between years were homogeneous among themselves. The two main effects did not differ significantly. The mean square for heterogeneity between years as a whole was significantly higher than that for heterogeneity within years.

In the experiments considered, interactions are not explicitly appearing in the analyses as components of variation. They may, however, be detected by their effects in causing heterogeneity of the components utilized. There was no evidence, atleast in 1947 and 1948 of variation in the values of D, H and E from one statistic to another and it was not of a kind attributable

to linkage. It must be attributed to interaction not removed and perhaps irremovable by scaling. The analysis which had revealed the interaction had been carried out on the assumption that the gene ratios were undisturbed by selection. Since disturbances attributable to genic and genotype-environmental interactions had been detected in the control of height, it was apparent that new components of variation in addition to D, H and E should be explicitly introduced to cover such situation.

The simplest case of genotype-environment interaction when non-allelic interactions are assumed to be non-existent has been discussed theoretically by Mather and Jones (1958). It is briefly outlined below:

Consider two true breeding lines differing by a single gene substitution, in two environments. Four situations are then possible as shown in the table below and therefore, three parameters are required to describe completely the differences among the four phenotypes.

<u>Genotype</u> <u>Environment</u>	A A	a a	Mean
X	$d_a + e_1 + g_1$	$-d_a + e_1 - g_1$	e_1
Y	$d_a - e_1 - g_1$	$-d_a - e_1 + g_1$	$-e_1$
Mean	d_a	$-d_a$	0

The parameters are d_a , e_1 and g_1 ; d_a is the parameter used to represent the differences between two genotypes and e_1 to represent the differences between two environments. The third comparison g_1 measures the statistical interaction of the genetical and environmental components.

If we include the hetrozygote Aa as well as the two homozygotes AA and aa, six situations are then possible and hence five parameters are needed. Three of these will be the same as in the previous case and the other two will be h_a and g_{h_a} . g_{h_a} represents the interaction of h_a and e_1 comparisons. Considering F_2 of the cross AA X aa, the contribution of interaction to variation can be determined. The variance of F_2 would be given by

$$V_{1F_2} = \frac{1}{2}d^2 + \frac{1}{2}\sum' g_{d_1}^2 + \frac{1}{4}h^2 + \frac{1}{4}\sum' g_{h_1}^2 + \sum' (e_1 + \frac{1}{2}g_{h_1})^2$$

Where the summation is taken over various environmental differences. In absence of epistasis, adding over all the genes under consideration V_{1F_2} can be represented as

$$\frac{1}{2}D + \frac{1}{4}H + \frac{1}{2}G_D + \frac{1}{4}G_H + E \quad \left(\frac{1}{2}\right) \quad \text{where } G_D = \sum\sum' g_{d_1}^2; G_H = \sum\sum' g_{h_1}^2$$

$$E \left(\frac{1}{2}\right) = \sum' (e_1 + \frac{1}{2}\sum g_{h_a})^2. \quad \sum \text{ is the summation over various gene differences and}$$

\sum' is the summation over various environmental differences. In a similar manner the total variance of F_3 generation can also be shown as given below.

$$V_{F_3} = V_{1F_3} + V_{2F_3} = \frac{1}{4}D + \frac{3}{16}H + \frac{1}{4}G_D + \frac{3}{16}G_H + E_{\left(\frac{1}{4}\right)}$$

$$\text{Where } E_{\left(\frac{1}{4}\right)} = \sum (e_1 + \frac{1}{4} \sum g_{ha_1})^2$$

It is thus seen that when gene-environment interactions exist it is possible to introduce components, G_D and G_H in addition to D and H to describe the situation. In the following chapter this description has been investigated in a general case when non-allelic interactions are also present.

--: 0 :-

Chapter 3.

Description of the Components.

Taking into consideration two pairs of genes A-a and B-b, there are nine genotypes, four homozygotes, four single heterozygotes and one double heterozygote. With two environments, eighteen situations are possible and seventeen parameters will be necessary to specify completely the differences among the eighteen phenotypes. For the two gene pairs there will be parameters d_a, d_b, h_a, h_b corresponding to main effects and $i_{ab}, j_{a/b}, j_{b/a}, l_{ab}$ corresponding to digenic interactions in all eight parameters. The ninth parameter e_1 represents the differences between the two environments. The remaining eight more parameters designated by

$g_{d_a}, g_{d_b}, g_{h_a}, g_{h_b}, g_{i_{ab}}, g_{j_{a/b}}, g_{j_{b/a}},$ and $g_{l_{ab}}$, would represent the interactions of the earlier eight parameters with e_1 comparisons. The eight parameters $d_a, d_b, h_a, h_b, i_{ab}, j_{a/b}, j_{b/a}, l_{ab}$ are independent of each other and so will be the eight interaction parameters. Moreover, the two sets of eight parameters will be independent of one another. The description is complete and shown in Table No. 1 (vide Appendix II)

The system can be extended to cover cases of more than two gene pairs, provided digenic interactions are only considered as a first approximation. Another gene difference represented by C-c that is added, brings in a further $d_c, h_c, i_{ac}, j_{a/c}, j_{c/a}, l_{ac}, i_{bc}, j_{b/c}, j_{c/b}, l_{bc}$. To accommodate their interactions with the

environment, a further set of g 's i.e., g_{dc} , g_{bc} , g_{iac} , $g_{ja/c}$, $g_{jc/a}$, $g_{l/ac}$, $g_{lbc/}$, $g_{ju/c}$, $g_{jc/b}$, $g_{l/cb}$ can be introduced. These g 's will be as independent of one another in their contribution to variances as are the various d 's, h 's, i 's, j 's and l 's.

Turning to the case of more than two environments it can be seen that, whatever may be their number, their differences are expressible by a series of orthogonal comparisons equal in number to the degrees of freedom between them. In the case of two environments, there is only one comparison as seen above and represented by e_1 . Three environments yield two comparisons which can be represented by two parameters e_1 and e_2 . Similarly in the case of four environments three comparisons can be represented by three parameters e_1 , e_2 , e_3 . As the number of environments increase so is the case with their comparisons and parameters. The average phenotypes of the different environments can be combined in a variety of ways giving appropriate sets of orthogonal comparisons. We may choose any one set of comparisons whichever is the most convenient for representing environmental differences. As long as the comparisons in a set are orthogonal to one another, the sum of squares will necessarily be equal to the sum of squares of deviations of the environmental means from the general means. The number of e 's, if, increased to more

environments the number of g's will grow too.

Suppose there are two environmental comparisons e_1 and e_2 . Then the interaction terms with these may be represented by $g_{da_1}, g_{ha_1}, g_{db_1}, g_{hb_1}, g_{1ab/1}, g_{ja/b_1}, g_{jb/a_1}, g_{1/ab_1}, g_{da_2}, g_{ha_2}, g_{db_2}, g_{hb_2}, g_{1ab/2}, g_{ja/b_2}, g_{jb/a_2}$

and $g_{1/ab}$. With the same nine genotypes in four environments e_2 there will be thirty-six Phenotypes. Thirty-five parameters are needed for representing differences among the thirty-six phenotypes. The situation is represented in Table No. 2 (vide Appendix II). As mentioned earlier there are number of ways of assigning these parameters, all equally appropriate for genetical purposes. Only one way of assigning them is shown in the table.

Contribution of interaction to Variation:-

When the chances of occurrence of the various genotypes are the same in all environments the overall mean phenotype will be independent of the genotype-environment interaction as represented by g items. Sampling variation, however, will reflect the magnitudes and relations of the g's. The effects of the interaction on the phenotypic variances can be illustrated from the case of two gene differences in two environments as set out in Table No. 1 (vide Appendix II).

The variance of a line pure for AABB genotype over two environments can be seen to be equal to

$$(e_1 + \frac{g_{d_{a_1}}}{2} + \frac{g_{d_{b_1}}}{2} + \frac{g_{i_{ab/1}}}{2} - \frac{1}{2}g_{j_{a/b_1}} - \frac{1}{2}g_{j_{b/a_1}} + \frac{1}{2}g_{l_{ab_1}})^2$$

= (I), say, when taken about its own mean of $\frac{1}{ab_1}$

$$(d_a + d_b + i_{ab/} - \frac{1}{2}j_{a/b} - \frac{1}{2}j_{b/a}) = (I'), \text{ say.}$$

If we take the variance about zero, which is of course not the mid-parental value in presence of epistasis, (I)² is to be added. In this manner, the variance of the various homozygotes ^{and heterozygotes} can be obtained. In terms of notations given in Appendix I these variances are given below.

Genotype	Variance when taken about zero
AABB ...	(I) ² + (II) ²
AABb ...	(III) ² + (IV) ²
AAbb ...	(V) ² + (VI) ²
aABB ...	(VII) ² + (VIII) ²
aABb ...	(IX) ² + (X) ²
aAbb ...	(XI) ² + (XII) ²
aaBB ...	(XIII) ² + (XIV) ²
aaBb ...	(XV) ² + (XVI) ²
aabb ...	(XVII) ² + (XVIII) ²

(1) Mean variance of true breeding parents $\frac{1}{2} (V_{P_1} + V_{P_2}) :-$

With two gene differences, there are four possible homozygotes AABB, AAbb, aaBB and aabb and there can be two types of parental crosses 'Associated' and 'Dispersed'. In the former viz., (AABB x aabb), both the positive alleles are in one parent and both the negative alleles in another, while in the latter viz., (AAbb x aaBB) the

alleles are dispersed.

In the case of 'Associated' cross, the variances of the two true breeding parents are respectively $(I_1)^2$ and $(IX_1)^2$ when taken about its own mean over the two environments. The mean ~~var~~ variance would, therefore, be $[(I_1)^2 + (IX_1)^2] / 2$ which can be expressed in the form

$$(e_1 + g_{1_{ab}/} + \frac{1}{2}g_{1_{/ab}})^2 + [g_{d_a} + g_{d_b} - \frac{1}{2}(g_{j_{a/b}} + g_{j_{b/a}})]^2$$

In a similar manner it can be shown that the mean variance of true breeding parents, with 'Dispersed' type of cross, is

$$(e_1 - g_{1_{ab}/} + \frac{1}{2}g_{1_{/ab}})^2 + [g_{d_a} - g_{d_b} - \frac{1}{2}(g_{j_{a/b}} - g_{j_{b/a}})]^2$$

The two types of situation enumerated above can, however, be described in one way if parameters θ_a and θ_b are introduced to indicate the association of the genes in the parents.

The genotypic value of the homozygotes AAbb or Aabb in the two environments P and Q can be represented by respectively by

$$[d_a \theta_a + d_b \theta_b + i_{ab} \theta_a \theta_b - \frac{1}{2}(j_{a/b} \theta_a + j_{b/a} \theta_b) + \frac{1}{4}l_{ab}] + [g_{d_a} \theta_a + g_{d_b} \theta_b + g_{i_{ab}} \theta_a \theta_b - \frac{1}{2}(g_{j_{a/b}} \theta_a + g_{j_{b/a}} \theta_b) + \frac{1}{4}g_{l_{ab}} + e_1]$$

and

$$[d_a \theta_a + d_b \theta_b + i_{ab} \theta_a \theta_b - \frac{1}{2}(j_{a/b} \theta_a + j_{b/a} \theta_b) + \frac{1}{4}l_{ab}] - [g_{d_a} \theta_a + g_{d_b} \theta_b + g_{i_{ab}} \theta_a \theta_b - \frac{1}{2}(g_{j_{a/b}} \theta_a + g_{j_{b/a}} \theta_b) + \frac{1}{4}g_{l_{ab}} + e_1]$$

Similarly the genotypic value of aabb and aabb in the two environments P and Q can be represented by

$$[-d_a \theta_a - d_b \theta_b + i_{ab} \theta_a \theta_b + \frac{1}{2}(j_{a/b} \theta_a + j_{b/a} \theta_b) + \frac{1}{4} l_{ab}]$$

$$+ [-g_{d_a} \theta_a - g_{d_b} \theta_b + g_{i_{ab}} \theta_a \theta_b + \frac{1}{2}(g_{j_{a/b}} \theta_a + g_{j_{b/a}} \theta_b) + \frac{1}{4} g_{l_{ab}} + e,]$$

and

$$[-d_a \theta_a - d_b \theta_b + i_{ab} \theta_a \theta_b + \frac{1}{2}(j_{a/b} \theta_a + j_{b/a} \theta_b) + \frac{1}{4} M_{ab}]$$

$$- [-g_{d_a} \theta_a - g_{d_b} \theta_b + g_{i_{ab}} \theta_a \theta_b + \frac{1}{2}(g_{j_{a/b}} \theta_a + g_{j_{b/a}} \theta_b) + \frac{1}{4} g_{l_{ab}} + e,]$$

Here θ_a and θ_b are positive unity when the first parent contains the positive homozygote of the corresponding gene and negative unity when the second parent contains the positive homozygote.

The mean variances of the parents in either of the two types of crosses, can, therefore be shown to have the value

$$[e, + g_{i_{ab}} \theta_a \theta_b + \frac{1}{4} g_{l_{ab}}]^2 + [g_{d_a} \theta_a + g_{d_b} \theta_b - \frac{1}{2}(g_{j_{a/b}} \theta_a + g_{j_{b/a}} \theta_b)]^2$$

With more than two gene differences, this expression would take the form $[e, + \sum_{a < b} g_{i_{ab}} \theta_a \theta_b + \frac{1}{4} \sum_{a < b} g_{l_{ab}}]^2$

$$+ [\sum_a g_{d_a} \theta_a - \frac{1}{2} \sum_{a < b} (g_{j_{a/b}} \theta_a + g_{j_{b/a}} \theta_b)]^2 = (e, + g_i + \frac{1}{4} g_l)^2 + (g_d - g_j)^2$$

where g_d, g_i, g_j and g_l are pooled effects of corresponding interactions defined below.

$$g_d = \sum_a g_{d_a} \theta_a \quad ; \quad g_i = \sum_{a < b} g_{i_{ab}} \theta_a \theta_b \quad ; \quad g_l = \sum_{a < b} g_{l_{ab}}$$

$$g_j = \frac{1}{2} \sum_{a < b} (g_{j_{a/b}} \theta_a + g_{j_{b/a}} \theta_b)$$

Bringing in more than two environments, would lead to the general expression $[\frac{1}{2}(V_{p_1} + V_{p_2})]$

$$= \sum (e, + g_i + \frac{1}{4} g_l)^2 + \sum (g_d - g_j)^2 = \sqrt{(e, + g_i + \frac{1}{4} g_l)^2} + \sqrt{(g_d - g_j)^2}$$

and \sum is the summation over environmental comparisons.

The difference between the two parental variances would turn out to be the covariance between $(e, + g_i + \frac{1}{4} g_l)$ and $(g_d - g_j)$

(ii) Variance of F_1 (V_{F_1}) :-

The F_1 -generation from a cross between two true breeding parents, with two gene differences, would contain uniformly $AaBb$ genotypes. The variance would be $(e_1 + g_{h_a} + g_{h_b} + \frac{1}{4} g_{L_{ab}})^2 = (V_1)^2$, when taken about its own mean over the environments. With several gene differences, this variance has the expression $[e_1 + g_h + \frac{1}{4} g_L]^2$

where $g_h = \sum_a g_{h_a}$ and g_L is defined earlier.

With more than two environments, V_{F_1} is given by

$$V_{F_1} = \sum (e_1 + g_h + \frac{1}{4} g_L)^2 = V_{(e_1 + g_h + \frac{1}{4} g_L)}$$

(iii) Variance of F_2 (V_{F_2}) :-

The F_2 -generation descended from a cross between two true breeding parents contain the nine genotypes as listed earlier in the proportions

$$\frac{1}{16} : \frac{1}{8} : \frac{1}{16} : \frac{1}{8} : \frac{1}{4} : \frac{1}{8} : \frac{1}{16} : \frac{1}{8} : \frac{1}{16}$$

V_{F_2} can then be obtained by multiplying the expressions for 'variances of different genotypes when taken about the origin zero' (given earlier) by their respective proportions and subtracting the square of the overall F_2 mean i.e., $(\frac{1}{2}h_a + \frac{1}{2}h_b) = (\bar{X})$, from it.

Thus in terms of notations used, this is equal to

$$\frac{1}{16} [(I)^2 + (I_1)^2 + (IX)^2 + (IX_1)^2 + (III)^2 + (III_1)^2 + (VII)^2 + (VII_1)^2] + \frac{1}{8} [(II)^2 + (II_1)^2 + (VIII)^2 + (VIII_1)^2 + (IV)^2 + (IV_1)^2 + (VI)^2 + (VI_1)^2] + \frac{1}{4} [(V)^2 + (V_1)^2] - (\bar{X})^2$$

After simplifying this becomes

$$\left[\frac{1}{2}d_a^2 + \frac{1}{2}d_b^2 + \frac{1}{4}h_a^2 + \frac{1}{4}h_b^2 + \frac{1}{4}i_{ab}^2 + \frac{1}{8}j_{a/b}^2 + \frac{1}{8}j_{b/a}^2 + \frac{1}{16}l_{/ab}^2 \right]$$

$$+ \left\{ \left[\frac{1}{2}g_{d_a}^2 + \frac{1}{2}g_{d_b}^2 + \frac{1}{4}g_{h_a}^2 + \frac{1}{4}g_{h_b}^2 + \frac{1}{4}g_{i_{ab}}^2 + \frac{1}{8}g_{j_{a/b}}^2 + \frac{1}{8}g_{j_{b/a}}^2 + \frac{1}{16}g_{l_{/ab}}^2 \right] \right.$$

$$\left. + \left[e_1 + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{h_b} \right]^2 \right\}$$

The terms in the first bracket are the same as that of V F in case of two gene differences with no genotype-environment interactions as demonstrated by Hayman and Mather (1955). The terms in the second bracket are the contributions due to interaction terms between genotype and environment.

In the case of more than two environments, the terms in the first bracket remain as they are. The terms in the second bracket can be shown to be equal to

$$\frac{1}{2} \sum g_{d_a}^2 + \frac{1}{2} \sum g_{d_b}^2 + \frac{1}{4} \sum g_{h_a}^2 + \frac{1}{4} \sum g_{h_b}^2 + \frac{1}{4} \sum g_{i_{ab}}^2$$

$$+ \frac{1}{8} \sum g_{j_{a/b}}^2 + \frac{1}{8} \sum g_{j_{b/a}}^2 + \frac{1}{16} \sum g_{l_{/ab}}^2 + \sum (e_1 + \frac{1}{2} g_{h_a} + \frac{1}{2} g_{h_b})^2$$

$$= \frac{1}{2} V_{g_{d_a}} + \frac{1}{2} V_{g_{d_b}} + \frac{1}{4} V_{g_{h_a}} + \frac{1}{4} V_{g_{h_b}} + \frac{1}{4} V_{g_{i_{ab}}}$$

$$+ \frac{1}{8} V_{g_{j_{a/b}}} + \frac{1}{8} V_{g_{j_{b/a}}} + \frac{1}{16} V_{g_{l_{/ab}}} + V_{(e_1 + \frac{1}{2} g_{h_a} + \frac{1}{2} g_{h_b})}$$

where the summation is over different environmental comparisons.

The interaction components (with environment) i.e., g's have means zero overall environments, but the heritable variation measured within environments includes g's as well as other terms. Therefore the terms $\sum g_{d_a}^2$, $\sum g_{d_b}^2$, $\sum g_{h_a}^2$, ... may also be regarded as the variances of d_a , d_b , h_a , ... as measured in each environment, round their overall mean

which is free from g_d 's and g_h 's, being averaged over all environments.

In the case of distinguishable environments, e.g., where each environment is a block in a replicated experiment, the mean phenotype of each environment or block is given by $E(\frac{1}{2}h_a + \frac{1}{2}h_b + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{h_b} + e_1)$.

Then the variance of block means round the grand mean is given by $\sum (e_i + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{h_b})^2 = V_{(e + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{h_b})}$

which can be seen to be one of the terms in V_{F_1} .

Therefore the effect of the heterozygotes' interaction is expressed partly by inflation of the estimate of environmental variation. Then the effects of all other interaction terms and that of the remainder of the heterozygotes' interaction, remain with their true genetical variation after deduction from V_{F_1} of the environmental variation as measured by differences among the environmental means. The genetic and interactive components of variation remaining with them could be separated if the individuals of the different genotypes were regularly identifiable. This is not generally possible in continuous variation. Therefore, generally, the heritable variation as measured by a simple analysis of variance will be inflated by such interactions with environment as may exist.

In the case of more than two gene differences, the V_{F_1} takes the following general form.

$$V_{F_2} = \frac{1}{2}D + \frac{1}{4}H + \frac{1}{4}I + \frac{1}{8}J + \frac{1}{16}L \\ + \frac{1}{2}G_D + \frac{1}{4}G_H + \frac{1}{4}G_I + \frac{1}{8}G_J + \frac{1}{16}G_L + E_{F_2}$$

$$\text{where } D = \sum_a d_a^2 \quad ; \quad H = \sum_a h_a^2 \quad ; \quad I = \sum_{a < b} i_{ab}^2$$

$$J = \sum_{a < b} (j_{a/b}^2 + j_{b/a}^2) \quad ; \quad L = \sum_{a < b} l_{ab}^2$$

$$G_D = \sum_a V_{g_{da}} \quad ; \quad G_H = \sum_a V_{g_{ha}} \quad ; \quad G_I = \sum_{a < b} V_{g_{iab}}$$

$$G_J = \sum_{a < b} (V_{g_{j_{a/b}}} + V_{g_{j_{b/a}}}) \quad ; \quad G_L = \sum_{a < b} V_{g_{lab}} \quad ; \quad E_{F_2} = V_{(e + \frac{1}{2} \sum_a g_{ha})}$$

(iv) Variance of F_3 generation (V_{F_3}):-

An F_3 Population obtained from selfing individual genotypes of F_2 would contain the nine genotypes listed earlier in the proportions

$$\frac{9}{64} : \frac{3}{32} : \frac{9}{64} : \frac{3}{32} : \frac{1}{16} : \frac{3}{32} : \frac{9}{64} : \frac{3}{32} : \frac{9}{64}$$

As before, the total variance of F_3 population is

obtained by multiplying the expressions for variances around zero with the corresponding proportions and subtracting the square of the overall F_3 mean i.e.,

$$(\frac{1}{2}h_a + \frac{1}{2}h_b + \frac{1}{16}g_{1/ab}) = (XV), \text{ from it.}$$

In terms of notations, this is equal to

$$\frac{9}{64} \left[(I)^2 + (I_1)^2 + (III)^2 + (III_1)^2 + (VII)^2 + (VII_1)^2 \right. \\ \left. + (IX)^2 + (IX_1)^2 \right] \\ + \frac{3}{32} \left[(II)^2 + (II_1)^2 + (IV)^2 + (IV_1)^2 + (VI)^2 + (VI_1)^2 \right. \\ \left. + (VIII)^2 + (VIII_1)^2 \right] \\ + \frac{1}{16} \left[(V)^2 + (V_1)^2 \right] = (XV)^2$$

This expression on simplification, reduces in original symbols, to

$$\begin{aligned} & \left[\frac{3}{4} (d_a - \frac{1}{4} j_{a|b})^2 + \frac{3}{4} (d_b - \frac{1}{4} j_{b|a})^2 + \frac{3}{16} (h_a - \frac{1}{4} l_{ab})^2 + \frac{3}{16} (h_b - \frac{1}{4} l_{ab})^2 \right. \\ & \left. + \frac{9}{16} i_{ab}^2 + \frac{9}{64} (j_{a|b}^2 + j_{b|a}^2) + \frac{9}{256} l_{ab}^2 \right] + \left[\frac{3}{4} (g_{d_a} - \frac{1}{4} g_{j_{a|b}})^2 \right. \\ & \left. + \frac{3}{4} (g_{d_b} - \frac{1}{4} g_{j_{b|a}})^2 + \frac{3}{16} (g_{h_a} - \frac{1}{4} g_{l_{ab}})^2 + \frac{3}{16} (g_{h_b} - \frac{1}{4} g_{l_{ab}})^2 + \frac{9}{16} g_{i_{ab}}^2 \right. \\ & \left. + \frac{9}{64} (g_{j_{a|b}}^2 + g_{j_{b|a}}^2) + \frac{9}{256} g_{l_{ab}}^2 + (e + \frac{1}{4} g_{h_a} + \frac{1}{4} g_{h_b} + \frac{1}{16} g_{l_{ab}})^2 \right] \end{aligned}$$

With more than two environments, the second bracket in the above expression takes the following form, whereas the first bracket remains unchanged.

$$\begin{aligned} & \left[\frac{3}{4} \sum' (g_{d_a} - \frac{1}{4} g_{j_{a|b}})^2 + \frac{3}{4} \sum' (g_{d_b} - \frac{1}{4} g_{j_{b|a}})^2 + \frac{3}{16} \sum' (g_{h_a} - \frac{1}{4} g_{l_{ab}})^2 \right. \\ & \left. + \frac{3}{16} \sum' (g_{h_b} - \frac{1}{4} g_{l_{ab}})^2 + \frac{9}{16} \sum' g_{i_{ab}}^2 + \frac{9}{64} \sum' (g_{j_{a|b}}^2 + g_{j_{b|a}}^2) + \frac{9}{256} \sum' g_{l_{ab}}^2 \right. \\ & \left. + \sum' (e + \frac{1}{4} g_{h_a} + \frac{1}{4} g_{h_b} + \frac{1}{16} g_{l_{ab}})^2 \right] \\ & = \frac{3}{4} V'_{d_a} + \frac{3}{4} V'_{d_b} + \frac{3}{16} V'_{h_a} + \frac{3}{16} V'_{h_b} + \frac{9}{16} V'_{i_{ab}} + \frac{9}{64} V'_{j_{a|b}} + \frac{9}{64} V'_{j_{b|a}} + \frac{9}{256} V'_{l_{ab}} \\ & \quad + V' (e + \frac{1}{4} g_{h_a} + \frac{1}{4} g_{h_b} + \frac{1}{16} g_{l_{ab}}) \end{aligned}$$

Generalising the total variance of F_3 Population to more than two gene differences, we get

$$\begin{aligned} V_{F_3} = & \frac{3}{4} D' + \frac{3}{16} H' + \frac{9}{16} I + \frac{9}{64} J + \frac{9}{256} L \\ & + \frac{3}{4} G_{D'} + \frac{3}{16} G_{H'} + \frac{9}{16} G_I + \frac{9}{64} G_J + \frac{9}{256} G_L + E_{F_3} \end{aligned}$$

$$\text{where } D' = \sum_{a \neq b} (d_a - \frac{1}{4} j_{a|b})^2 ; \quad H' = \sum_{a < b} (h_a - \frac{1}{4} l_{ab})^2$$

I, J and L are as defined earlier.

$$G_{D'} = \sum_a V'_{g_{d_a}} ; \quad G_{H'} = \sum_a V'_{g_{h_a}}$$

G_I, G_J and G_L are as defined earlier.

$$\text{and } E_{F_3} = V' (e + \frac{1}{4} \sum_a g_{h_a} + \frac{1}{16} \sum_{a < b} g_{l_{ab}})$$

This total variance is composed of two parts viz., variance of F_3 means (V_{1F_3}) and the mean variance of F_3 families (V_{2F_3}) i.e.,

$$V_{F_3} = V_{1F_3} + V_{2F_3}$$

If each F_3 family is consisting of a large number of individuals and the families are distributed equally over the environments, the variances of F_3 families would be the variance of families averaged over environments. The families would have means as shown in Table No. 3 (vide Appendix I) the various families occurring in the proportions

$$\frac{1}{16} : \frac{1}{8} : \frac{1}{16} : \frac{1}{8} : \frac{1}{4} : \frac{1}{8} : \frac{1}{16} : \frac{1}{8} : \frac{1}{16}$$

The contribution of two gene differences to V_{1F_3} with

such a design of experiment would be

$$\begin{aligned} & \frac{1}{16} \left[(I)^2 + (III)^2 + (VII)^2 + (IX)^2 \right] \\ & + \frac{1}{8} \left[(XI)^2 + (XII)^2 + (XIII)^2 + (XIV)^2 \right] \\ & + \frac{1}{4} \left[(X)^2 \right] = \left[(XV)^2 \right] \end{aligned}$$

This, on simplification, leads to

$$\begin{aligned} & \frac{1}{2} \left(d_a - \frac{1}{4} j_{a|b} \right)^2 + \frac{1}{2} \left(d_b - \frac{1}{4} j_{b|a} \right)^2 + \frac{1}{16} \left(h_a - \frac{1}{4} h_{ab} \right)^2 \\ & + \frac{1}{16} \left(h_b - \frac{1}{4} h_{ab} \right)^2 + \frac{1}{4} (a_b)^2 + \frac{1}{32} (j_{a|b}^2 + j_{b|a}^2) + \frac{1}{156} h_{ab}^2 \end{aligned}$$

With more than two gene differences, this can be expressed in the form

$$V_{1F_3} = \frac{1}{2} D' + \frac{1}{16} H' + \frac{1}{4} I + \frac{1}{32} J + \frac{1}{256} L$$

The mean variance of F_3 families is then obtained by subtraction.

$$\text{i.e., } V_{2F_3} = V_{F_3} - V_{1F_3}$$

$$V_{2F_3} = \frac{1}{4}D^2 + \frac{1}{8}H^2 + \frac{5}{16}I^2 + \frac{7}{64}J^2 + \frac{1}{32}L^2 \\ + \frac{3}{4}GD^2 + \frac{3}{16}GH^2 + \frac{9}{16}GI^2 + \frac{9}{64}GJ^2 + \frac{9}{256}GL^2 + E_{F_3}.$$

When the families are small in size or the member individuals of each family are kept together within the experimental design and not distributed randomly over the environments, V_{1F_3} would be inflated partly by sampling variation and partly by the environmental and associated interactive differences between their different sites or plots. The same situation was noticed by Mather and Jones (1958).

The heritable portion viz., $\frac{3}{4}D^2 + \frac{3}{16}H^2 + \frac{9}{16}I^2 + \frac{9}{64}J^2 + \frac{9}{256}L^2$ would always be capable of separation into $\frac{1}{4}D^2 + \frac{1}{8}H^2 + \frac{5}{16}I^2 + \frac{7}{64}J^2 + \frac{1}{32}L^2$ (for V_{2F_3}) and $\frac{1}{2}D^2 + \frac{1}{16}H^2 + \frac{1}{4}I^2 + \frac{1}{32}J^2 + \frac{1}{256}L^2$ (for V_{1F_3})

whatever may be the size of the families and howsoever the families are distributed over the environments, but the separation of the associated interactive variation into between families and within families would depend on the structure of the population and the ^{design} of the experiment in which the variation is measured. This would be dealt with in the next chapter in detail.

(v) Variance of Bi-parental generation (V_{S_3}):-

A bi-parental generation raised from an F_2 population would contain the nine (9) genotypes in the same overall proportions

$$\frac{1}{16} : \frac{1}{8} : \frac{1}{16} : \frac{1}{8} : \frac{1}{4} : \frac{1}{8} : \frac{1}{16} : \frac{1}{8} : \frac{1}{16}$$

as in case of F_2 .

As such the total variance of a bi-parental generation would be same as that of F_2 . i.e.,

$$V_{S_3} = \frac{1}{2}D + \frac{1}{4}H + \frac{1}{4}I + \frac{1}{8}J + \frac{1}{16}L \\ + \frac{1}{2}G_D + \frac{1}{4}G_H + \frac{1}{4}G_I + \frac{1}{8}G_J + \frac{1}{16}G_L + V(e + \frac{1}{2}I g_h)$$

This total variance is, however, composed of two parts; one is the variance of means of bi-parental progenies denoted by V_{1S_3} and the other is the mean

of variances of bi-parental progenies denoted by V_{2S_3} .

As already indicated while dealing variances in F_3 generation, the exact partitioning of total variance into its two components would depend on whether the families of bi-parental progenies are quite large in size to make sampling variation negligible and whether these families are distributed randomly over the environment. If these conditions are satisfied, as expected otherwise, the whole of the interactive variation would tend to appear in the mean variance of families.

With two gene differences, there would be eighty one bi-parental families as shown in Table No. 4 (vide Appendix II). Within each of these families the genotypic values are shown for two environments P and Q. With random distribution, the mean of families would contain no environmental and associated interaction effects, these being averaged out. The variances of each of these eighty one families can be worked out.

To simplify the working, the eighty-one squares are numbered (1), (2), (3), (81). It is seen that all these eighty-one squares can be divided into sixteen groups depending upon their similarity. The sixteen groups are as follows:

1. (1), (21), (61) and (81)
2. (2), (12), (62) and (72) each occurring twice.
3. (4), (24), (34) and (54) each occurring twice.
4. (6), (36) each occurring ~~six times~~ four times.
5. (8), (18) each occurring four times.
6. (3), (63) each occurring twice.
7. (7), (27) each occurring twice.
8. (14), (44) each occurring twice.
9. (32), (42) each occurring twice.
10. (9) occurring four times.
11. (17) occurring ^{two} ~~four~~ times.
12. (33) occurring two times.
13. (11) and (71)
14. (31) and (51)
15. (41)
16. (5), (15), (35), and (45) each occurring four times.

The variances of the squares in each group are calculated and then all the variances in a group are combined. The contribution of various groups to the mean variances are as follows:

Group	Contribution to the mean variance
1.	$\dots \frac{1}{256} \left[(I_1)^2 + (III_1)^2 + (VII_1)^2 + (IX_1)^2 \right]$
2.	$\dots \frac{2}{128} \left[\left\{ (I)^2 + (I_1)^2 + (II)^2 + (II_1)^2 \right\} - (XXVI)^2 \right.$ $\quad + \frac{1}{2} \left\{ (III)^2 + (III_1)^2 + (VII)^2 + (VII_1)^2 \right\} - (XXI)^2$ $\quad + \frac{1}{2} \left\{ (VIII)^2 + (VIII_1)^2 + (XII)^2 + (XII_1)^2 \right\} - (XXXVI)^2$ $\quad \left. + \frac{1}{2} \left\{ (XIII)^2 + (XIII_1)^2 + (IX)^2 + (IX_1)^2 \right\} - (XXXVII)^2 \right]$
3.	$\dots \frac{2}{128} \left[\frac{1}{2} \left\{ (I)^2 + (I_1)^2 + (IV)^2 + (IV_1)^2 \right\} - (XVII)^2 \right.$ $\quad + \frac{1}{2} \left\{ (III)^2 + (III_1)^2 + (VI)^2 + (VI_1)^2 \right\} - (XXVI)^2$ $\quad + \frac{1}{2} \left\{ (IV)^2 + (IV_1)^2 + (VIII)^2 + (VIII_1)^2 \right\} - (XXIX)^2$ $\quad \left. + \frac{1}{2} \left\{ (V)^2 + (V_1)^2 + (IX)^2 + (IX_1)^2 \right\} - (XXXV)^2 \right]$
4.	$\dots \frac{4}{128} \left[\frac{1}{2} \left\{ (II)^2 + (II_1)^2 + (V)^2 + (V_1)^2 \right\} - (XIX)^2 \right.$ $\quad \left. + \frac{1}{2} \left\{ (VII)^2 + (VII_1)^2 + (X)^2 + (X_1)^2 \right\} - (XXXI)^2 \right]$
5.	$\dots \frac{4}{128} \left[\frac{1}{2} \left\{ (IV)^2 + (IV_1)^2 + (V)^2 + (V_1)^2 \right\} - (XX)^2 \right.$ $\quad \left. + \frac{1}{2} \left\{ (VI)^2 + (VI_1)^2 + (VII)^2 + (VII_1)^2 \right\} - (XXV)^2 \right]$
6.	$\dots \frac{2}{256} \left[(II_1)^2 + (VIII_1)^2 \right]$
7.	$\dots \frac{2}{256} \left[(IV_1)^2 + (VI_1)^2 \right]$
8.	$\dots \frac{2}{32} \left[\frac{1}{8} \left\{ (I)^2 + (I_1)^2 + (III)^2 + (III_1)^2 + (IV)^2 + (IV_1)^2 \right\} \right.$ $\quad + (VI)^2 + (VI_1)^2 + \frac{1}{4} \left\{ (II)^2 + (II_1)^2 + (V)^2 + (V_1)^2 \right\}$ $\quad - (XXII)^2 + \frac{1}{8} \left\{ (IV)^2 + (IV_1)^2 + (VI)^2 + (VI_1)^2 \right.$ $\quad + (VII)^2 + (VII_1)^2 + (IX)^2 + (IX_1)^2 + \frac{1}{4} \left\{ (V)^2 + (V_1)^2 \right.$ $\quad \left. + (VIII)^2 + (VIII_1)^2 \right\} - (XXXIII)^2 \left. \right]$
9.	$\dots \frac{2}{32} \left[\frac{1}{8} \left\{ (I)^2 + (I_1)^2 + (II)^2 + (II_1)^2 + (VIII)^2 + (VIII_1)^2 \right\} \right.$ $\quad + (XIII)^2 + (XIII_1)^2 + \frac{1}{4} \left\{ (IV)^2 + (IV_1)^2 + (V)^2 + (V_1)^2 \right\}$ $\quad - (XXVII)^2 + \frac{1}{8} \left\{ (II)^2 + (II_1)^2 + (III)^2 + (III_1)^2 \right.$ $\quad + (VIII)^2 + (VIII_1)^2 + (IX)^2 + (IX_1)^2 \left. \right\} - (XXXII)^2$ $\quad \left. + \frac{1}{4} \left\{ (VI)^2 + (VI_1)^2 + (VII)^2 + (VII_1)^2 \right\} \right]$

(Contd.)

Group	Contribution to the mean variance
10.	$\frac{4}{256} [(V_1)^2]$
11.	$\frac{2}{64} \left[\frac{1}{4} \{ (IV)^2 + (IV_1)^2 + (VI)^2 + (VI_1)^2 \} + \frac{1}{2} \{ (V)^2 + (V_1)^2 \} - (XXIV)^2 \right]$
12.	$\frac{2}{64} \left[\frac{1}{4} \{ (II)^2 + (II_1)^2 + (VIII)^2 + (VIII_1)^2 \} + \frac{1}{2} \{ (V)^2 + (V_1)^2 \} - (XXVIII)^2 \right]$
13.	$\frac{1}{64} \left[\frac{1}{4} \{ (I)^2 + (I_1)^2 + (III)^2 + (III_1)^2 \} + \frac{1}{2} \{ (II)^2 + (II_1)^2 \} - (XI)^2 + \frac{1}{4} \{ (VII)^2 + (VII_1)^2 + (IX)^2 + (IX_1)^2 \} + \frac{1}{2} \{ (VIII)^2 + (VIII_1)^2 \} - (XIV)^2 \right]$
14.	$\frac{1}{64} \left[\frac{1}{4} \{ (I)^2 + (I_1)^2 + (VII)^2 + (VII_1)^2 \} + \frac{1}{2} \{ (IV)^2 + (IV_1)^2 \} - (XII)^2 + \frac{1}{4} \{ (III)^2 + (III_1)^2 + (IX)^2 + (IX_1)^2 \} + \frac{1}{2} \{ (VI)^2 + (VI_1)^2 \} - (XIII)^2 \right]$
15.	$\frac{1}{16} \left[\frac{1}{16} \{ (I)^2 + (I_1)^2 + (III)^2 + (III_1)^2 + (VII)^2 + (VII_1)^2 + (IX)^2 + (IX_1)^2 \} + \frac{1}{8} \{ (II)^2 + (II_1)^2 + (IV)^2 + (IV_1)^2 + (VI)^2 + (VI_1)^2 + (VIII)^2 + (VIII_1)^2 \} + \frac{1}{4} \{ (V)^2 + (V_1)^2 \} - (X)^2 \right]$
16.	$\frac{4}{64} \left[\frac{1}{4} \{ (I)^2 + (I_1)^2 + (II)^2 + (II_1)^2 + (IV)^2 + (IV_1)^2 + (V)^2 + (V_1)^2 \} - (XVII)^2 + \frac{1}{4} \{ (II)^2 + (II_1)^2 + (III)^2 + (III_1)^2 + (V)^2 + (V_1)^2 + (VI)^2 + (VI_1)^2 \} - (XXIII)^2 + \frac{1}{4} \{ (IV)^2 + (IV_1)^2 + (V)^2 + (V_1)^2 + (VII)^2 + (VII_1)^2 + (VIII)^2 + (VIII_1)^2 \} - (XXX)^2 + \frac{1}{4} \{ (V)^2 + (V_1)^2 + (VI)^2 + (VI_1)^2 + (VIII)^2 + (VIII_1)^2 + (IX)^2 + (IX_1)^2 \} - (XXXIV)^2 \right]$

Combining the contribution of sixteen groups we

get

$$\begin{aligned} & \frac{15}{256} \left[(I)^2 + (III)^2 + (VII)^2 + (IX)^2 \right] + \frac{15}{128} \left[(IV)^2 + (VI)^2 \right. \\ & \left. + (VIII)^2 \right] + \frac{15}{64} \left[(V)^2 \right] + \frac{1}{16} \left[(I_1)^2 + (III_1)^2 + (VII_1)^2 + (IX_1)^2 \right] \\ & + \frac{1}{8} \left[(IV_1)^2 + (VI_1)^2 + (VIII_1)^2 \right] + \frac{1}{4} (V_1)^2 \\ & - \frac{1}{64} \left[(XVI)^2 + (XXI)^2 + (XXXVI)^2 + (XXXVII)^2 + (XVII)^2 + (XXVI)^2 \right. \\ & \left. + (XXIX)^2 + (XXXV)^2 + (XI)^2 + (XIV)^2 + (XII)^2 + (XIII)^2 \right] \\ & - \frac{1}{32} \left[(XIX)^2 + (XXXI)^2 + (XX)^2 + (XXV)^2 + (XXIV)^2 + (XXVIII)^2 \right] \\ & + \frac{1}{16} \left[(XXII)^2 + (XXXIII)^2 + (XXVII)^2 + (XXXII)^2 + (X)^2 + (XVIII)^2 \right. \\ & \left. + (XXIII)^2 + (XXX)^2 + (XXXIV)^2 \right] \end{aligned}$$

Simplifying the above expression, we get in the original symbols

$$\begin{aligned} & \frac{1}{4} d_a^2 + \frac{1}{4} d_b^2 + \frac{3}{16} h_a^2 + \frac{3}{16} h_b^2 + \frac{3}{16} i_{ab}^2 + \frac{1}{64} (j_{a|b}^2 + j_{b|a}^2) + \frac{15}{256} l_{ab}^2 \\ & + \frac{1}{8} g_a^2 + \frac{1}{8} g_b^2 + \frac{1}{4} g_{h_a}^2 + \frac{1}{4} g_{h_b}^2 + \frac{1}{4} g_{i_{ab}}^2 + \frac{1}{8} (g_{j_{a|b}}^2 + g_{j_{b|a}}^2) + \frac{1}{16} g_{l_{ab}}^2 \\ & + (e_1 + \frac{1}{8} g_{h_a} + \frac{1}{8} g_{h_b})^2 \end{aligned}$$

With more than two environmental comparisons and more than two gene differences, the expression takes the form:

$$\begin{aligned} V_{2S_3} = & \frac{1}{4} D + \frac{3}{16} H + \frac{3}{16} I + \frac{1}{64} J + \frac{15}{256} L + \frac{1}{8} G_D + \frac{1}{4} G_H \\ & + \frac{1}{4} G_I + \frac{1}{8} G_J + \frac{1}{16} G_L + E_{F_2} \end{aligned}$$

Where D, H, ... are the same as defined earlier in the case of F₂ generation.

V_{1S₃} is, then, easily obtained by subtracting

V_{2S₃} from V_{S₃}. The result is given below.

$$V_{1S_3} = \frac{1}{4} D + \frac{1}{16} H + \frac{1}{16} I + \frac{1}{64} J + \frac{1}{256} L$$

This can also be obtained independently by simplifying the expression given below (in terms of notations) and generalising over gene differences.

$$\begin{aligned} & \frac{1}{2s^2} [(1)^2 + (111)^2 + (VII)^2 + (IX)^2] + \frac{1}{64} [(XVI)^2 + (XXI)^2 \\ & + (XXXVI)^2 + (XXXVII)^2 + (XVII)^2 + (XXVI)^2 + (XXIX)^2 \\ & + (XXXV)^2 + (V)^2 + (XI)^2 + (XIV)^2 + (XII)^2 + (XIII)^2] \\ & + \frac{1}{32} [(XIX)^2 + (XXXI)^2 + (XX)^2 + (XXV)^2 + (XXIV)^2 + (XXVIII)^2] \\ & + \frac{1}{128} [(II)^2 + (VIII)^2 + (IV)^2 + (VI)^2] + \frac{1}{16} [(XXII)^2 + (XXXII)^2 \\ & + (XXVII)^2 + (XXXII)^2 + (X)^2 + (XVIII)^2 + (XXIII)^2 + (XXX)^2 \\ & + (XXXIV)^2] - [(X)^2] \end{aligned}$$

It may be noted that the expression for V_{1S_3} is free from environmental and associated interactive components because the families are assumed to be equally distributed over the environments. With non-random distribution of families over environments, the above partitioning is not perfect and either of the two components into which V_{S_3} is divided, receive environmental and associated interactive components depending upon the design of the experiment used. This case would be discussed in detail in the next chapter.

(vi) Variances in Maternal Progenies :-

The maternal progenies, in case of two gene differences and two environmental comparisons are shown in Table No. 5 (vide Appendix II)

As before, the total variance of maternal progenies would be the same as that of an F₂ population i.e.,

$$V_{M_3} = \frac{1}{8}D + \frac{1}{4}H + \frac{1}{4}I + \frac{1}{8}J + \frac{1}{16}L + \frac{1}{8}GD + \frac{1}{4}GH + \frac{1}{4}GI + \frac{1}{8}GJ + \frac{1}{16}GL + V(e + \frac{1}{2}Lg_h)$$

This total variance is composed of two parts. viz., Variance of means of maternal progenies (V_{1M_3}) and mean variances of maternal progenies (V_{2M_3}).

As in the case of bi-parental progenies, V_{2M_3} and V_{1M_3} are calculated with the assumption that families are large enough to make sampling variation negligible and that they are distributed at random over the environments. The case of non-random distribution of families over environments is discussed in detail in the next chapter.

For calculation of V_{2M_3} , variances of different maternal progeny families are obtained as given below for two gene differences and two environmental comparisons:

Frequency	Genotype	Variance of family
$\frac{1}{16}$	AABB	$\frac{1}{4} [(I)^2 + (I_1)^2 + (II)^2 + (II_1)^2 + (IV)^2 + (IV_1)^2 + (V)^2 + (V_1)^2] - (XVII)^2$
$\frac{1}{8}$	AABb	$\frac{1}{8} [(I)^2 + (I_1)^2 + (III)^2 + (III_1)^2 + (IV)^2 + (IV_1)^2 + (VI)^2 + (VI_1)^2] + \frac{1}{4} [(II)^2 + (II_1)^2 + (V)^2 + (V_1)^2] - (XXII)^2$

(Contd.)

Frequency	Genotype	Variance of Family
$\frac{1}{16}$	AAbb	$\frac{1}{4} [(II)^2 + (II_1)^2 + (III)^2 + (III_1)^2 + (V)^2 + (V_1)^2 + (VI)^2 + (VI_1)^2] - (XXIII)^2$
$\frac{1}{8}$	AABB	$\frac{1}{8} [(I)^2 + (I_1)^2 + (II)^2 + (II_1)^2 + (VII)^2 + (VII_1)^2 + (VIII)^2 + (VIII_1)^2] + \frac{1}{4} [(IV)^2 + (IV_1)^2 + (V)^2 + (V_1)^2] - (XXVII)^2$
$\frac{1}{4}$	AaBb	$\frac{1}{16} [(I)^2 + (I_1)^2 + (III)^2 + (III_1)^2 + (VII)^2 + (VII_1)^2 + (IX)^2 + (IX_1)^2] + \frac{1}{8} [(II)^2 + (II_1)^2 + (IV)^2 + (IV_1)^2 + (VI)^2 + (VI_1)^2 + (VIII)^2 + (VIII_1)^2] + \frac{1}{4} [(V)^2 + (V_1)^2] - (X)^2$
$\frac{1}{8}$	Aabb	$\frac{1}{8} [(II)^2 + (II_1)^2 + (III)^2 + (III_1)^2 + (VII)^2 + (VII_1)^2 + (VIII)^2 + (VIII_1)^2 + (IX)^2 + (IX_1)^2] + \frac{1}{4} [(V)^2 + (V_1)^2] - (XXXI)^2 + \frac{1}{4} [(X)^2 + (X_1)^2]$
$\frac{1}{16}$	aaBB	$\frac{1}{4} [(IV)^2 + (IV_1)^2 + (V)^2 + (V_1)^2 + (VII)^2 + (VII_1)^2 + (VIII)^2 + (VIII_1)^2] - (XXX)^2$
$\frac{1}{8}$	aaBb	$\frac{1}{8} [(IV)^2 + (IV_1)^2 + (VI)^2 + (VI_1)^2 + (VII)^2 + (VII_1)^2 + (VIII)^2 + (VIII_1)^2 + (IX)^2 + (IX_1)^2] + \frac{1}{4} [(V)^2 + (V_1)^2 + (X)^2 + (X_1)^2] - (XXXIII)^2$
$\frac{1}{16}$	aabb	$\frac{1}{4} [(V)^2 + (V_1)^2 + (VI)^2 + (VI_1)^2 + (VII)^2 + (VII_1)^2 + (VIII)^2 + (VIII_1)^2 + (IX)^2 + (IX_1)^2] - (XXXIV)^2$

Then the contribution to V_{M_3} would be equal to

$$\begin{aligned} & \frac{1}{16} [(I)^2 + (I_1)^2 + (III)^2 + (III_1)^2 + (VII)^2 + (VII_1)^2 + (IX)^2 + (IX_1)^2] \\ & + \frac{1}{8} [(II)^2 + (II_1)^2 + (IV)^2 + (IV_1)^2 + (VI)^2 + (VI_1)^2 + (VIII)^2 + (VIII_1)^2] \\ & + \frac{1}{4} [(V)^2 + (V_1)^2] - \frac{1}{16} [(XVII)^2 + (XXIII)^2 + (XXX)^2 + (XXXIV)^2] \\ & - \frac{1}{8} [(XXI)^2 + (XXVII)^2 + (XXXI)^2 + (XXXIII)^2] - \frac{1}{4} (X)^2 \end{aligned}$$

This simplifies, in original symbols, to

$$\begin{aligned} & \frac{3}{8} d_a^2 + \frac{3}{8} d_b^2 + \frac{1}{4} h_a^2 + \frac{1}{4} h_b^2 + \frac{15}{64} i_{ab}^2 + \frac{1}{8} j_{a|b}^2 + \frac{1}{8} j_{b|a}^2 + \frac{1}{16} l_{ab}^2 \\ & + \frac{1}{2} g_{d_a}^2 + \frac{1}{2} g_{d_b}^2 + \frac{1}{4} g_{h_a}^2 + \frac{1}{4} g_{h_b}^2 + \frac{1}{4} g_{i_{ab}}^2 + \frac{1}{8} g_{j_{a|b}}^2 + \frac{1}{8} g_{j_{b|a}}^2 + \frac{1}{16} g_{l_{ab}}^2 + (\theta_1 + \frac{1}{2} g_{h_a} + \frac{1}{2} g_{h_b})^2 \end{aligned}$$

With more than two gene differences and more than two environmental comparisons the above expression takes the following form

$$V_{2M_3} = \frac{3}{8} D + \frac{1}{4} H + \frac{15}{64} I + \frac{1}{8} J + \frac{1}{16} L$$

$$+ \frac{1}{2} G_D + \frac{1}{4} G_H + \frac{1}{4} G_I + \frac{1}{8} G_J + \frac{1}{16} G_L + E_{F_2}$$

where D, H, are the same as defined earlier.

V_{1M_3} is, then, easily obtained by subtracting

V_{2M_3} from V_{M_3} and is given by

$$V_{1M_3} = \frac{1}{8} D + \frac{1}{64} I$$

This variance can also be obtained independently by simplifying the expression given below (in terms of notations) and generalizing for more than two gene differences.

$$\frac{1}{16} [(XVIII)^2 + (XXIII)^2 + (XXX)^2 + (XXXIV)^2]$$

$$+ \frac{1}{8} [(XXII)^2 + (XXVII)^2 + (XXXII)^2 + (XXXIII)^2]$$

$$+ \frac{1}{4} [(X)^2] - (X)^2$$

(vii) Covariance of Parents and offspring :-

Generally, in a well designed experiment, Parents and offspring are distributed independently of one another among the environments so that their environmental conditions are uncorrelated. In description of genotypic

values, it means that the environmental as well as associated interactive effects are to be taken different for parents and offsprings. For instance, if we consider an F₂ as parental generation and a bi-parental or maternal Progenies derived from it as offspring generation, the situation for the calculation of covariance, can be described, for two gene differences, ^{and intra environmental comparisons} as shown in ~~table No.~~ ~~Table No.~~

~~Table No.~~ The covariance of F₂ and BIP/MAT means is then calculated after taking averages over environments for each parent and corresponding Progeny means. The contribution to covariance is equal to

$$\frac{1}{16}[(I)(XVII) + (II)(XXII) + (III)(XXX) + (IV)(XXXIV)] + \frac{1}{8}[(I)(XXI) + (II)(XXVII) + (III)(XXXI) + (IV)(XXXIII)] + \frac{1}{4}[(V)(X)] - (X)^2$$

which simplifies to $\frac{1}{4}d_a^2 + \frac{1}{4}d_b^2 + \frac{1}{16}i_{ab}^2$

Thus, summing over several gene differences,

$$W_{P/O} = \frac{1}{4}D + \frac{1}{16}I$$

When, however, the environmental conditions of Parents and offspring are perfectly correlated, i.e., the offsprings fall into the same environment as the parent, ~~the corresponding situation can be set out as shown in table No.~~ ~~(see Appendix)~~, the contribution to the covariance would then, be equal to

$$\frac{1}{16}[(I)(XVII) + (I_1)(XVII_1) + (II)(XXII) + (II_1)(XXII_1) + (III)(XXX) + (III_1)(XXX_1) + (IV)(XXXIV) + (IV_1)(XXXIV_1)] + \frac{1}{8}[(I)(XXI) + (I_1)(XXI_1) + (II)(XXVII) + (II_1)(XXVII_1) + (III)(XXXI) + (III_1)(XXXI_1) + (IV)(XXXIII) + (IV_1)(XXXIII_1)] + \frac{1}{4}[(V)(X) + (V_1)(X_1)] - (X)^2$$

which simplifies to $\frac{1}{4}d_a^2 + \frac{1}{4}d_b^2 + \frac{1}{16}i_{ab}^2 + \frac{1}{4}e_a^2 + \frac{1}{4}e_b^2 + \frac{1}{16}e_{ab}^2 + (e_1 + \frac{1}{2}e_2 + \frac{1}{2}e_3)^2$

Then, summing over environmental comparisons and gene

differences, we get

$$\begin{aligned} \frac{W}{p/o} &= \frac{1}{4} D + \frac{1}{16} I \\ &+ \frac{1}{4} G_D + \frac{1}{16} G_I + E_{F2} \end{aligned}$$

∴ 0 ∴

Chapter 4.

Biometrical Analysis.

In the earlier chapter, it has been shown how the total phenotypic variation can be expressed in terms of quantities denoted by $D, H, D', H', I, J, L, G_D, G_H, G_D', G_H', G_I, G_J, G_L$ AND E . It is apparent that in presence of gene-environmental interactions, additional components of variance like G_D, G_H, G_I, G_J and G_L come into picture and in such a case, the genetic components of variation viz., D, H, I, J and L are to be separated from these and the environmental ^{Component} to enable a proper assessment of the genetic situation in the character under study. Further, the environmental component of variance is not, in such circumstances free from g 's, the parameters, measuring interaction effects. A certain confounding of g 's with environmental effects (e 's) appears in the expression for E . The expressions for various statistics in terms of these components are set out in Table No. 1 (a) (Vide Appendix III).

The biometrical analysis for the separation of the interaction components of variance from the other components of variance, as well as the estimation of all the components would depend on the design of the experiment and the multiplicity of the statistics available for estimation. There is, however a complication that in the most general case (i.e., when digenic interactions are taken into account), the definitions of D, H, G_D and G_H , AS in F_2 do not remain the same in the subsequently selfed generation i.e., F_3, F_4 , etc.. As such, where D, H, G_D, G_H are estimated from selfed

generations F_3 and onwards, they do not strictly measure the variance components due to additive effects of genes, dominance deviations, and associated interaction effects. The additive effects get confounded with additive x dominance type epistatic interactions and the dominance deviation effects, with dominance x dominance type epistatic interactions. Similar corresponding confounding appears for interaction effects. But, if F_2 generation and their subsequent bi-parental and maternal generations (S_3, M_3) are utilised for estimation purposes, we get measures of D, H, G_D, G_H clear of any confounding and strictly giving additive genetic variance (D), dominance variance (H), Variance due to interaction of additive effects with environment (G_D), and variance due to interaction of dominance effects with environment (G_H). A successful estimation, in such a case, would, however, require at least as many statistics as the number of components i.e., $D, H, I, J, L, G_{D1}, G_{D2}, G_{D3}, G_{D4}, G_{D5}, G_{D6}, G_{D7}, G_{D8}, G_{D9}, G_{D10}, G_{D11}$ and E i.e., eleven in all. If more than eleven statistics are available for use method of least squares is required to be used for estimation as outlined by Mather (1949).

Handwritten notes:
 1. 11 statistics
 2. 11 statistics
 3. 11 statistics

The use of biparental or maternal generations derived from F_2 obtained from a cross between two true breeding strains, is, however, dependent on the design of experiment used. The total variance of either of them is the same as

that of F_2 but variances within and between families are dependent on the design of the experiment as pointed out in Chapter 3. The design chiefly depends on how the families are distributed over environments. The two cases of random and non-random distribution are discussed serially below.

Random distribution over environments:

In case of families grown over a comparable range of environments which are large enough to make the sampling variation negligible in respect of genotype (if segregation is occurring), and of environments (whether segregation is occurring or not), the differences in average genetical constitution; the associated interactive effects, having been cancelled in taking the means. Thus if we compare the means of a set of large S_3 families grown over comparable environments the expected variance of these means i.e., V_{1S_3} will be $\frac{1}{2} D + \frac{1}{16} H + \frac{1}{16} I + \frac{1}{64} J + \frac{1}{256} L$ as proved in the previous ~~chapter~~ chapter.

Variation between individuals within families will reflect the differences amongst the environments of the individuals and also the interactions which arise from these differences. Variances of genetically uniform families, parents and F_1 , will include no genetic components. They will contain only the main effects of environmental differences together with the interactions of these differences with the particular genotype of each family. The mean

variance of the two true breeding parents is given by

$$\sum' (e_1 + \sum \epsilon_{1_{ab/}} + \frac{1}{4} \sum \epsilon_{1_{/ab}})^2 + \sum' (\sum \epsilon_{d_a} - \frac{1}{2} \sum \epsilon_{j_{a/b}})^2 = \delta, \text{ say}$$

and variance of F₁ family is given by

$$\sum' (e_1 + \sum \epsilon_{h_a} + \frac{1}{2} \sum \epsilon_{1_{/ab}})^2 = \epsilon, \text{ say}$$

as shown in the previous chapter. \sum' is summation over environmental comparisons and \sum over the gene differences.

Now if all the families are distributed at random over the environments, we can use δ and ϵ to correct the variance of F₂ for environmental and interactive variations. we then find

$$V_{F_2} = \frac{1}{2}D + \frac{1}{4}H + \frac{1}{2}I + \frac{1}{8}J + \frac{1}{16}L + \frac{1}{2}\alpha + \frac{1}{4}\beta + \frac{1}{2}\gamma + \frac{1}{8}\delta + \frac{1}{8}\epsilon$$

$$\text{where } \alpha = G_D + \frac{1}{4}G_J - \sum' (\sum \epsilon_{d_a} - \frac{1}{2} \sum \epsilon_{j_{a/b}})^2$$

$$\beta = G_H + \frac{1}{4}G_L - \sum' (\sum \epsilon_{h_a} + \frac{1}{2} \sum \epsilon_{1_{/ab}})^2$$

$$\gamma = G_I + 2 \sum' (e - \frac{1}{4} \sum \epsilon_{1_{/ab}})^2 - 2 \sum' (e + \sum \epsilon_{1_{ab/}} + \frac{1}{4} \sum \epsilon_{1_{/ab}})^2$$

The variances of segregating generations except F₃ generation can be written in terms of D, H, α , β , γ , δ and ϵ as shown in Table No. 1 (b) (Vide Appendix III)

In case of F_3 generation we have to use different quantities α' , β' , and γ' where

$$\begin{aligned}\alpha' &= G_D + \frac{3}{16} G_J - \sum' \left(\sum \varepsilon_{1a} - \frac{1}{2} \sum \varepsilon_{j_{a/b}} \right)^2 \\ \beta' &= G_H + \frac{3}{16} G_L - \sum' \left(\sum \varepsilon_{h_a} + \frac{1}{2} \sum \varepsilon_{l_{ab}} \right)^2 \\ \gamma' &= 2\gamma + G_I + \frac{5}{64} G_L + \sum' \left(e_1 + \frac{1}{4} \sum \varepsilon_{h_a} \right) \\ &\quad - \sum' \left(e_1 + \frac{1}{4} \sum \varepsilon_{h_a} - \frac{1}{4} \sum \varepsilon_{l_{ab}} \right)^2\end{aligned}$$

to correct for environmental and interactive components. Ofcourse, in case of, F_3 , biparentals and maternals, the correction is only required for within family variances.

The coefficients of δ and ϵ , in all cases are the proportions of homozygotes and heterozygotes expected in the family under consideration.

The variances of family means shown in Table No. 1(b) assume that the families are large enough for sampling variation to be negligible. If the assumption is not valid, they will be inflated by an appropriate item for sampling variation; and to this extent will depend on the non-heritable and non-interactive components as well as D, H, I, J and L.

The variances, such as $W_{1F_{23}}$ and $W_{1S_{23}}$ will not, in general, be capable of use in analysing variation where gene-environment interactions are present, for the

parents may be raised at a different time or in different environments from their progeny. If, however, parents and progeny are raised and measured in the same range of environments, without ofcourse, introducing cofrelation between environmental effects, the covariances can be included in the group of data for analysis.

As far as E component is concerned, it is of the form given by

$$V_{(e + xZg_h)} = V_e + 2xW_{(e, Zg_h)} + x^2 V_{Zg_h}$$

It involves three constants. It appears, therefore, that if enough different types of segregating generations are available these constants can also be estimated together with D, H, I, J, L, G_D , G_H , G_I , G_J , G_L and V_e , the variance due to environment gets separated from $V_{(e + xZg_h)}$. This may not however, always be possible since the estimation of G_D , G_H , G_I , G_J and G_L is not direct. These components are estimated in the form of α , β and γ so always get entangled with other quantities.

Non-Random Distribution Over Environments:

In most experiments it may not be possible to have families distributed at random over a common range of environments. Hence it is desirable to extend consideration to the case where each family is raised in one or more relatively compact groups, which are themselves distributed

over a wider range of environments. In experiments involving F_3 , S_3 or M_3 families each of them is commonly grown in its own individual plot the various plots being distributed at random over the block of ground which also includes all other families. The environmental differences affecting the variation of individuals within the plot are then different from those affecting the variation in plot and family means.

Let the contribution made by environment to the phenotype of an individual be broken down into two parts, the one being the deviation from the plot means (${}_1e$) caused by environmental differences within the plot, and the other being the deviation from the gross mean (${}_2e$) caused by environmental differences between plots, with the assumption that the variance of ${}_2e$ is the same for all values of ${}_1e$ apart from sampling variation. It is also assumed that the same is true of the interaction with genotype to which the different environments give rise.

Consider two gene differences, then the nine genotypes will give rise to phenotypes (the phenotypic values are expressed in terms of notations already introduced with modification that the inferior suffixes 1 and 2 on the left correspond to ${}_1e$ and ${}_2e$).

AABB:	I	+	1 ^I ₁	+	2 ^I ₁
AABb:	II	+	1 ^{II} ₁	+	2 ^{II} ₁
AAbb:	III	+	1 ^{III} ₁	+	2 ^{III} ₁
AaBB:	IV	+	1 ^{IV} ₁	+	2 ^{IV} ₁
AaBb:	V	+	1 ^V ₁	+	2 ^V ₁
Aabb:	VI	+	1 ^{VI} ₁	+	2 ^{VI} ₁
aaBB:	VII	+	1 ^{VII} ₁	+	2 ^{VII} ₁
aaBb:	VIII	+	1 ^{VIII} ₁	+	2 ^{VIII} ₁
aabb:	IX	+	1 ^{IX} ₁	+	2 ^{IX} ₁

The means of F₃ families, each grown in a separate plot are given below, which are derived from different F₂ plants.

Genotype of F ₂ parent <u>plant.</u>	Mean of F ₃ <u>family.</u>
AABB:	I + 2 ^I ₁
AABb:	XI + 2 ^{XI} ₁
AAbb:	III + 2 ^{III} ₁
AaBB:	XII + 2 ^{XII} ₁
AaBb:	X + 2 ^X ₁
Aabb:	XIII + 2 ^{XIII} ₁
aaBB:	VII + 2 ^{VII} ₁
aaBb:	XIV + 2 ^{XIV} ₁
aabb:	IX + 2 ^{IX} ₁

Then the variance of F_3 means is (neglecting sampling variation) given by, for two gene differences,

$$\begin{aligned}
 V_{1F_3} &= \frac{1}{2}(d_a - \frac{1}{2}j_{a/b})^2 + \frac{1}{2}(d_b - \frac{1}{2}j_{b/a})^2 \\
 &+ \frac{1}{16}(h_a - \frac{1}{4}l_{ab})^2 + \frac{1}{16}(h_b - \frac{1}{4}l_{ab})^2 \\
 &+ \frac{1}{4}i_{ab}^2 + \frac{1}{32}j_{a/b}^2 + \frac{1}{32}j_{b/a}^2 + \frac{1}{256}l_{ab}^2 + \frac{1}{2}V_{2^8 d_a} \\
 &+ \frac{1}{2}V_{2^8 d_b} + \frac{1}{16}V_{2^8 h_a} + \frac{1}{16}V_{2^8 h_b} + \frac{1}{4}V_{2^8 l_{ab}} \\
 &+ \frac{1}{32}V_{2^8 j_{a/b}} + \frac{1}{32}V_{2^8 j_{b/a}} + \frac{1}{256}V_{2^8 l_{ab}} \\
 &+ V_{2^0} \left(2^0 + \frac{1}{4}2^8 h_a + \frac{1}{4}2^8 h_b + \frac{1}{16}2^8 l_{ab} \right)
 \end{aligned}$$

In case of V_{2F_3} the mean variance within families, it is apparent that for wholly AABB families this is $\sum (I_1 I_1)^2$, for aabb families it is $\sum (IX_1)^2$, for aaBB families it is $\sum (VII_1)^2$, for AAbb families it is $\sum (III_1)^2$. For segregating families from parents AABB, AaBB, AaBb, Aabb and ~~A~~ aaBb, we can ~~expect~~ split the phenotypic family variance into components within and between genotypes. Consider segregating families from AABB parents. Within $\frac{1}{4}$ of the families comprising plants of genotype AABB and AAbb, the within component will be $\sum (I_1 I_1)^2$ and $\sum (III_1 I_1)^2$ respectively, where as within $\frac{1}{2}$ of the families consisting of plants of genotype AABb, it will be $\sum (II_1 I_1)^2$. The variance between genotypes will, however, be equal to

$$\begin{aligned}
 &\sum \left[\frac{1}{4} \left\{ (I + 2I_1)^2 + (III + 2III_1)^2 \right\} \right. \\
 &\quad \left. + \frac{1}{2} (II + 2II_1)^2 - (XI + 2XI_1)^2 \right]
 \end{aligned}$$

The total variance within segregating families from AABB

parents is then given by

$$\sum \left[\frac{1}{4} \{ (1I_1)^2 + (1III_1)^2 \} + \frac{1}{4} \{ (II_1)^2 \} + \frac{1}{4} \{ (I) + (2I_1) \}^2 + \frac{1}{4} \{ (III) + (2III_1) \}^2 + \frac{1}{4} \{ (II) + (2II_1) \}^2 - \{ (XI) + (2XI_1) \}^2 \right]$$

similarly for the segregating families from parents AaBb, aaBb, Aabb. For the segregating family from parents AaBb the varinace is given by

$$\begin{aligned} & \sum \left[\frac{1}{16} \{ (I) + (2I_1) \}^2 + \frac{1}{16} \{ (III) + (2III_1) \}^2 + \frac{1}{16} \{ (VII) + (2VII_1) \}^2 \right. \\ & + \frac{1}{16} \{ (IX) + (2IX_1) \}^2 + \frac{1}{8} \{ (II) + (2II_1) \}^2 + \frac{1}{8} \{ (IV) + (2IV_1) \}^2 \\ & + \frac{1}{8} \{ (VI) + (2VI_1) \}^2 + \frac{1}{8} \{ (VIII) + (2VIII_1) \}^2 + \frac{1}{4} \{ (V) + (2V_1) \}^2 \\ & - \{ (X) + (2X_1) \}^2 + \frac{1}{16} \{ (1I_1)^2 + (1III_1)^2 + (1VII_1)^2 + (1IX_1)^2 \} \\ & \left. + \frac{1}{8} \{ (1II_1)^2 + (1IV_1)^2 + (1VI_1)^2 + (1VIII_1)^2 \} + \frac{1}{4} (1V_1)^2 \right] \end{aligned}$$

In original terms, the above, simplifies to

$$\begin{aligned} & \frac{1}{4} (d_a^2 + \sum 1g_a^2 + \sum 2g_a^2) + \frac{1}{4} (d_b^2 + \sum 1g_b^2 + \sum 2g_b^2) \\ & + \frac{1}{4} (h_a^2 + \sum 1g_{h_a}^2 + \sum 2g_{h_a}^2) + \frac{1}{4} (h_b^2 + \sum 1g_{h_b}^2 + \sum 2g_{h_b}^2) \\ & + \frac{1}{4} (i_{ab/}^2 + \sum 1g_{i_{ab/}}^2 + \sum 2g_{i_{ab/}}^2) + \frac{1}{4} (j_{a/b}^2 + \sum 1g_{j_{a/b}}^2 + \sum 2g_{j_{a/b}}^2) \\ & + \frac{1}{4} (j_{b/a}^2 + \sum 1g_{j_{b/a}}^2 + \sum 2g_{j_{b/a}}^2) + \frac{1}{16} (l_{ab}^2 + \sum 1g_{l_{ab}}^2 + \sum 2g_{l_{ab}}^2) \\ & + \frac{1}{2} \left(e + \frac{1}{2} 1g_{h_a} + \frac{1}{2} 1g_{h_b} \right)^2 \end{aligned}$$

Then combining the variances of all these nine types of segregating and non-segregating families in their expected proportions we find that

$$\begin{aligned} V_{2F_3} = & \frac{1}{4} (d_a - \frac{1}{2} j_{a/b})^2 + \frac{1}{4} (d_b - \frac{1}{2} j_{b/a})^2 + \frac{1}{4} (h_a - \frac{1}{2} l_{ab})^2 \\ & + \frac{1}{4} (h_b - \frac{1}{2} l_{ab})^2 + \frac{5}{16} i_{ab/}^2 + \frac{7}{64} j_{a/b}^2 + \frac{7}{64} j_{b/a}^2 + \frac{1}{32} l_{ab}^2 \\ & + \frac{1}{4} V_{2g_a} + \frac{1}{4} V_{2g_b} + \frac{1}{4} V_{2g_{h_a}} + \frac{1}{4} V_{2g_{h_b}} + \frac{5}{16} V_{2g_{i_{ab/}}} \\ & + \frac{7}{64} V_{2g_{j_{a/b}}} + \frac{7}{64} V_{2g_{j_{b/a}}} + \frac{1}{32} V_{2g_{l_{ab}}} + \end{aligned}$$

(Contd.)

$$\begin{aligned}
 & +\frac{1}{2}V'_{1g_a} + \frac{1}{2}V'_{1g_b} + \frac{3}{16}V'_{1g_{ha}} + \frac{3}{16}V'_{1g_{hb}} + \frac{9}{16}V'_{1g_{ab}} + \frac{9}{64}V'_{1g_{j_a/b}} \\
 & + \frac{9}{64}V'_{1g_{j_b/a}} + \frac{9}{256}V'_{1g_{1/ab}} + V'_{(1+\frac{1}{4}1g_{ha} + \frac{1}{4}1g_{hb} + \frac{1}{16}1g_{1/ab})}
 \end{aligned}$$

With more than two gene differences the above expression

for V_{1F_3} and V_{2F_3} takes the form

$$\begin{aligned}
 V_{1F_3} = & \frac{1}{2}D' + \frac{1}{16}H' + \frac{1}{4}I + \frac{1}{32}J + \frac{1}{256}L + \frac{1}{2}2G' + \frac{1}{16}2G'' + \frac{1}{4}2G_I \\
 & + \frac{1}{32}2G_J + \frac{1}{256}2G_L + 2E_{F_3}
 \end{aligned}$$

$$\begin{aligned}
 V_{2F_3} = & \frac{1}{4}(D' + 2G') + \frac{1}{8}(H' + 2G'') + \frac{5}{16}(I + 2G_I) + \frac{7}{64}(J + 2G_J) \\
 & + \frac{1}{32}(L + 2G_L) + \frac{1}{2}1G' + \frac{1}{16}1G'' + \frac{1}{16}1G_I + \frac{1}{64}(1G_J) + \frac{1}{256}1G_L + 1E_{F_3}
 \end{aligned}$$

where $1G' = \int V'_{1g_a}$ and $2G' = \int V'_{2g_a}$ etc.

Combining these two we get,

$$\begin{aligned}
 V_{1F_3} + V_{2F_3} = & \frac{3}{4}(D' + 1G' + 2G') + \frac{3}{16}(H' + 1G'' + 2G'') \\
 & + \frac{9}{16}(I + 1G_I + 2G_I) + \frac{9}{64}(J + 1G_J + 2G_J) \\
 & + \frac{9}{256}(L + 1G_L + 2G_L) + (E_{F_3} + 2E_{F_3})
 \end{aligned}$$

In a similar manner, the variances within and between families for S_3 and M_3 generation can be worked out.

These are given in Table No. 2 (vide Appendix III).

Apart from the designs of the experiment which have been considered above in form of random and non-random distribution over environments, there is also the familiar type of design used by Mather and Vines (1952) where a

pair of true breeding lines, their F_1 , F_2 and the two backcrosses to the two parents were raised over three years. The different years can be regarded as providing a common range of environments distinguished from each other in providing large effects between them.

Though it is not possible to undertake the analysis of the data cited in this study according to the theoretical frame work discussed above because of limited number of statistics available, yet it may be of interest to separate out the composite effects due to additive action of genes, dominance deviations, digenic interaction deviations, effects of environments and corresponding associated interactions. This can be done by studying the generation means.

Let the two components of one environmental comparison may be denoted by Q and R. Then the expectations of various \bar{x} family and generation means derived from a cross of between two inbred lines can be expressed in terms of overall effects $d, h, i, j, l, g_d, g_h, g_i, g_j, g_l$, as defined in chapter 3 and the environmental effect e_1 .

These expectations are given by:

$$P_Q = (m + d - \frac{1}{2}h + i + j + l) + (g_d - \frac{1}{2}g_h + g_i - g_j + l g_l + e_1)$$

$$P_R = (\quad \quad \quad) - (\quad \quad \quad)$$

$$P'_Q = (m - d - \frac{1}{2}h + i + j + \frac{1}{2}l) + (-\frac{1}{2}g_d - \frac{1}{2}g_h + g_i + g_j + \frac{1}{2}g_l + e_1)$$

$$P'_R = (\quad " \quad) - (\quad " \quad)$$

$$F_{1Q} = (m + \frac{1}{2}h + \frac{1}{2}l) + (\frac{1}{2}g_h + \frac{1}{2}g_l + e_1)$$

$$F_{1R} = (\quad " \quad) - (\quad " \quad)$$

$$F_{2Q} = (m + e_1) \bar{E} \bar{E}$$

$$F_{2R} = (m - e_1)$$

$$B_Q = (m + \frac{1}{2}d + \frac{1}{2}i) + (\frac{1}{2}g_d + \frac{1}{2}g_i + e_1)$$

$$B_R = (\quad " \quad) - (\quad " \quad)$$

$$B'_Q = (m - \frac{1}{2}d + \frac{1}{2}i) + (-\frac{1}{2}g_d + \frac{1}{2}g_i + e_1)$$

$$B'_R = (\quad " \quad) - (\quad " \quad)$$

where P'_Q and P'_R are the two means of two parental families, F_{1Q} the mean of their progeny, F_{2Q} , the mean of selfed progenies from F_{1Q} , B_Q and B'_Q , the means of the first backcrosses to the parents, all generations raised in one macro-environment Q (a season or year can be regarded as such an environment). Similarly for the other macro-environment R . It may be noted that these expectations are around m , the F_2 mean taken over both the macro-environments. The above twelve equations can be solved for twelve parameters. The variances of the parameters can however be obtained only if the error variances of various generations means are available, If, however, more generation means are available, the parameters can be fitted to them by the least squares technique.

Chapter 5.

Summary.

The description of genetic components of variation in presence of gene-environment interactions has been dealt with in its most general form. An attempt has been made to indicate the methods of biometrical analysis for the separation of various components in two cases viz., random and non-random distribution of individuals over environments. A review of the already existing literature on the relevant topic has also been presented.

given by nine genotypes

The differences among the eighteen phenotypes with two gene differences A-a and B-b in each of the two environments can be described in terms of seventeen parameters. Eight of these parameters are $d_a, d_b, h_a, h_b, i_{ab}/j_{a/b}, j_{b/a}, l_{ab}$ measuring the average effects of the genic differences, the allelic interactions and the non-allelic digenic type of interactions as introduced by Mather (1949), and Hayman and Mather (1955). One is e_1 , measuring the average effect of difference in environments and the rest eight parameters are $g_{d_a}, g_{d_b}, g_{h_a}, g_{h_b}, g_{i_{ab}/j_{a/b}}, g_{j_{b/a}}, g_{l_{ab}}$ and $g_{l_{ab}}$ measuring the interaction of $d_a, d_b, h_a, h_b, i_{ab}/j_{a/b}, j_{b/a}$ and l_{ab} with e_1 . More than two environments can be accommodated by partitioning the environmental differences into orthogonal e components. Then the interaction terms can be described in terms of corresponding sets of orthogonal g components.

The variance of F_2 derived from a cross between two true breeding strains and of segregating families S_3 (biparental progenies) and M_3 (maternal progenies) derived from F_2 are shown to be expressible in terms of $D, H, I, J, L, G_D, G_H, G_I, G_J, G_L$ and E_{F_2} . It is shown that comparisons occur with g_h terms so that measuring the variation due to environments gets inflated by part of g_h interaction. It is also interesting to note that the same is true also when digenic interactions are not taken into account as shown by Mather and Jones (1958). In case of variances for F_3 , derived from F_2 the terms D, H, G_D, G_H and E_{F_2} change to $D', H', G_{D'}, G_{H'}$ and E_{F_3} respectively. The first four quantities change their definitions in the sense that j 's, and g_j 's get confounded with d 's and g_d 's, l 's and g_l 's get confounded with h 's and g_h 's respectively. In E_{F_3} , apart from the confounding of g_h with e as in E_{F_2} we also get confounding of $g_{1/ab}$ the proportion of g_h confounded being $\frac{1}{4}$ and that of $g_{1/ab}$ being $\frac{1}{16}$.

So far as covariances of parents and offspring is concerned it is found to be $\frac{1}{4}D + \frac{1}{16}I$ when the environments of parents and offsprings are uncorrelated whereas it becomes $\frac{1}{4}D + \frac{1}{16}I + \frac{1}{4}G_D + \frac{1}{16}G_I + E_{F_2}$ when the environments of parents and offsprings gets correlated.

With all individuals of all generations distributed at random over ^{the same range of} environments, G_D, G_H, G_I, G_J, G_L and E_{F_2} , appear in the forms of certain transforms viz., $\alpha, \beta, \gamma, \delta,$ and ϵ . These transforms are consistent in case of F_2, S_3 and M_3 generations. But in case of F_3 generation because of G_D, G_H and E_{F_2} having changed to $G_{D'}, G_{H'}$ and E_{F_3} respectively, different transforms viz., $\alpha', \beta',$ and γ' are used in place of α, β, γ . δ and ϵ remain unchanged but their coefficients change from $\frac{1}{2}$ and $\frac{1}{2}$ to $\frac{2}{3}$ and $\frac{1}{3}$. When in a generations such as F_3, S_3 or M_3 the different families are each raised in a separate plot or group the effects of environmental differences may be separated into those within plots and those between plot means. The expressions of variances between and within family, in such circumstances change characteristically.

-: 0 :-

REFERENCES

1. Falconer D.S. (1960) Introduction to Quantitative Genetics.
2. Falconer D.S. (1952) The problem of environment and Selection. Amer. Nat. Vol. 86, 293-298.
3. Falconer D.S. and Latyszewski M. (1952) The environment in relation to Selection for size in mice. J.Genet. Vol.51, 67-80.
4. Fisher R.A., Immer F.R. and Tedin O. (1932) The genetical interpretation of Statistics of the third degree in the study of quantitative inheritance. Genetics. Vol.17, 107-124.
5. Haldane J.B.S. (1946) The interaction of nature and nurture. Ann.Eugen. (Lond) Vol.13, 197-205.
6. Hammond J. (1947) Animal Breeding in relation to nutrition and environmental conditions. Biol. Rev. Vol.22, 195-213.
- ✓ 7. Hayman B.I. and Mather K. (1955) The description of genic interactions in continuous variation I. ~~Description~~ Biometrics Vol.11. 69-82.
8. Huston T.M. and Joiner W.P. (1957) Breed differences in egg production of domestic fowl held at high environmental temperatures. Poult.Sci. Vol.36, 1128-1129.
- ✓ 9. Jones R.Morley and Mather K. (1958) Interaction of Genotype and environment in continuous variation II. Analysis. Biometrics Vol.14. 489-498.
- ✓ 10. Mather K. and Jones M. (1958) Interaction of Genotype and environment in continuous variation I. Description Biometrics Vol.14. 343-359.
11. Mather K. and Vines A. (1952) The inheritance of height and flowering time in a cross of *Nicotiana rustica*. Quantitative inheritance. ed. E.C.Reeve and Waddington C.H. 49-79. H.M.S.O.
12. Mather K. Biometrical Genetics. (1949).
- ✓ 13. McBride G. (1958) The environment and animal breeding ~~plans~~ problems. Animal Breeding Abstracts Vol.26. 349-358.

14. Robertson, Alan, and Mason, I.L. (1956) The progeny testing of dairy bulls, a comparison of special station and field results. J. Agri. Sci. Vol. 47. (376-381).
15. Robertson, F.W, and Reeve E.C.R. (1952) Heterozygosity, environmental variation and heterosis. Nature Vol. 170. 286.
16. Wright (1939) Genetic principles governing the rate of progress of livestock breeding. Proc. Amer. Soc. Anim. Prod.

-: 0 :-

(i)

APPENDIX I.NOTATIONS USED.

Expression	Notation
$d_a + d_b + i_{ab} / -\frac{1}{2}j_{a/b} \quad -\frac{1}{2}j_{b/a} \quad +\frac{1}{4}l_{/ab} \quad \dots$	I
$g_{d_a} + g_{d_b} + g_{i_{ab}} / -\frac{1}{2}g_{j_{a/b}} \quad -\frac{1}{2}g_{j_{b/a}} \quad +\frac{1}{4}g_{l_{/ab}} + e_1 \dots$	I_1
$d_a + h_b + \frac{1}{2}j_{a/b} \quad -\frac{1}{4}l_{/ab} \quad \dots$	II
$g_{d_a} + g_{h_b} + \frac{1}{2}g_{j_{a/b}} \quad -\frac{1}{4}g_{l_{/ab}} + e_1 \quad \dots$	II_1
$d_a - d_b - i_{ab} / -\frac{1}{2}j_{a/b} \quad +\frac{1}{2}j_{b/a} \quad +\frac{1}{4}l_{/ab} \quad \dots$	III
$g_{d_a} - g_{d_b} - g_{i_{ab}} / -\frac{1}{2}g_{j_{a/b}} \quad +\frac{1}{2}g_{j_{b/a}} \quad +\frac{1}{4}g_{l_{/ab}} + e_1$	III_1
$h_a + d_b + \frac{1}{2}j_{a/b} \quad -\frac{1}{4}l_{/ab} \quad \dots$	IV
$g_{h_a} + g_{d_b} + \frac{1}{2}g_{j_{a/b}} \quad -\frac{1}{4}g_{l_{/ab}} + e_1 \quad \dots$	IV_1
$h_a + h_b + \frac{1}{4}l_{/ab} \quad \dots$	V
$g_{h_a} + g_{h_b} + \frac{1}{4}g_{l_{/ab}} + e_1 \quad \dots$	V_1
$h_a - d_b - \frac{1}{2}j_{b/a} \quad -\frac{1}{4}l_{/ab} \quad \dots$	VI
$g_{h_a} - g_{d_b} - \frac{1}{2}g_{j_{b/a}} \quad -\frac{1}{4}g_{l_{/ab}} + e_1 \quad \dots$	VI_1
$-d_a + d_b - i_{ab} / +\frac{1}{2}j_{a/b} \quad -\frac{1}{2}j_{b/a} \quad +\frac{1}{4}l_{/ab} \quad \dots$	VII
$-g_{d_a} + g_{d_b} - g_{i_{ab}} / +\frac{1}{2}g_{j_{a/b}} \quad -\frac{1}{2}g_{j_{b/a}} \quad +\frac{1}{4}g_{l_{/ab}} + e_1$	VII_1
$-d_a + h_b - \frac{1}{2}j_{a/b} \quad -\frac{1}{4}l_{/ab} \quad \dots$	VIII
$-g_{d_a} + g_{h_b} - \frac{1}{2}g_{j_{a/b}} \quad +\frac{1}{4}g_{l_{/ab}} + e_1 \quad \dots$	$VIII_1$

(ii)

Express on	Notation
$-d_a -d_b +i_{ab}/ +\frac{1}{2}j_{a/b} +\frac{1}{2}j_{b/a} +\frac{1}{4}l_{/ab} \dots$	IX
$-g_{d_a} -g_{d_b} +g_{i_{ab}/} +\frac{1}{2}g_{j_{a/b}} +\frac{1}{2}g_{j_{b/a}} +\frac{1}{4}g_{l_{/ab}} +e_1$	IX ₁
$\frac{1}{2}h_a +\frac{1}{2}h_b \dots$	X
$\frac{1}{2}g_{h_a} +\frac{1}{2}g_{h_b} +e_1 \dots$	X ₁
$d_a +\frac{1}{2}h_b \dots$	XI
$g_{d_a} +\frac{1}{2}g_{h_b} +e_1 \dots$	XI ₁
$\frac{1}{2}h_a +d_b \dots$	XI'
$\frac{1}{2}g_{h_a} +g_{d_b} +e_1 \dots$	XI' ₁
$\frac{1}{2}h_a -d_b \dots$	XI''
$\frac{1}{2}g_{h_a} -g_{d_b} +e_1 \dots$	XI'' ₁
$-d_a +\frac{1}{2}h_b \dots$	XIV
$-g_{d_a} +\frac{1}{2}g_{h_b} +e_1 \dots$	XIV ₁
$\frac{1}{4}h_a +\frac{1}{4}h_b +\frac{1}{16}l_{/ab} \dots$	XV
$\frac{1}{4}g_{h_a} +\frac{1}{4}g_{h_b} +\frac{1}{16}g_{l_{/ab}} +e_1 \dots$	XV ₁
$d_a +\frac{1}{2}d_b +\frac{1}{2}h_b +\frac{1}{2}i_{ab}/ -\frac{1}{2}j_{b/a} \dots$	XVI
$g_{d_a} +\frac{1}{2}g_{d_b} +\frac{1}{2}g_{h_b} +\frac{1}{2}g_{i_{ab}/} +e_1 -\frac{1}{2}g_{j_{b/a}} \dots$	XVI ₁

(ii)

Expression	Notation
$\frac{1}{2}d_a + d_b + \frac{1}{2}h_a + \frac{1}{2}i_{ab} / -\frac{1}{4}j_{a/b}$.. XVII
$\frac{1}{2}g_d + \frac{1}{2}g_{d_a} + g_{d_b} + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{i_{ab}} / -\frac{1}{4}g_{j_{a/b}} + e_1$	XVII ₁
$\frac{1}{2}d_a + \frac{1}{2}d_b + \frac{1}{2}h_a + \frac{1}{2}h_b + \frac{1}{4}i_{ab} /$.. XVIII
$\frac{1}{2}g_d + \frac{1}{2}g_{d_a} + \frac{1}{2}g_{d_b} + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{h_b} + \frac{1}{4}g_{i_{ab}} + e_1$.. XVIII ₁
$\frac{1}{2}d_a + \frac{1}{2}h_a + h_b + \frac{1}{4}j_{a/b}$.. XIX
$\frac{1}{2}g_d + \frac{1}{2}g_{h_a} + g_{h_b} + \frac{1}{4}g_{j_{a/b}} + e_1$.. XIX ₁
$h_a + \frac{1}{2}h_b + \frac{1}{2}d_b + \frac{1}{4}i_{b/a}$.. XX
$g_{h_a} + \frac{1}{2}g_{h_b} + \frac{1}{2}g_{d_b} + \frac{1}{4}g_{j_{b/a}} + e_1$.. XX ₁
$d_a - \frac{1}{2}d_b + \frac{1}{2}h_b + \frac{1}{2}i_{ab} / +\frac{1}{4}j_{b/a}$.. XXI
$g_d - \frac{1}{2}g_{d_b} + \frac{1}{2}g_{h_b} - \frac{1}{2}g_{i_{ab}} + \frac{1}{4}g_{j_{b/a}} + e_1$.. XXI ₁
$\frac{1}{2}d_a + \frac{1}{2}h_a + \frac{1}{2}h_b$.. XXII
$\frac{1}{2}g_d + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{h_b} + e_1$.. XXII ₁
$\frac{1}{2}d_a - \frac{1}{2}d_b + \frac{1}{2}h_a + \frac{1}{2}h_b - \frac{1}{4}i_{ab} /$.. XXIII
$\frac{1}{2}g_d - \frac{1}{2}g_{d_b} + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{h_b} - \frac{1}{4}g_{i_{ab}} + \frac{1}{4} + e_1$.. XXIII ₁
$h_a + \frac{1}{2}h_b$.. XXIV
$g_{h_a} + \frac{1}{2}g_{h_b} + e_1$.. XXIV ₁

Expression		Notation
$h_a + \frac{1}{2}h_b - \frac{1}{2}d_b - \frac{1}{4}j_{b/a}$..	XXV
$g_{h_a} + \frac{1}{2}g_{h_b} - \frac{1}{2}g_{d_b} - \frac{1}{4}g_{j_{b/a}} + e_1$..	XXV ₁
$\frac{1}{2}d_a - \frac{1}{2}d_b + \frac{1}{2}h_a - \frac{1}{4}ab/ - \frac{1}{4}j_{a/b}$..	XXVI _±
$\frac{1}{2}g_{d_a} - g_{d_b} + \frac{1}{2}g_{h_a} - \frac{1}{2}g_{i_{ab/}} - \frac{1}{4}g_{j_{a/b}} + e_1$..	XXVI ₁
$\frac{1}{2}d_b + \frac{1}{2}h_a + \frac{1}{2}h_b$..	XXVII
$\frac{1}{2}g_{d_b} + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{h_b} + e_1$..	XXVII ₁
$h_b + \frac{1}{2}h_a$..	XXVIII
$g_{h_b} + \frac{1}{2}g_{h_a} + e_1$..	XXVIII ₁
h $-\frac{1}{2}d_a + d_b + \frac{1}{2}h_a - \frac{1}{2}i_{ab/} + \frac{1}{4}j_{a/b}$..	XXIX
$-\frac{1}{2}g_{d_a} + g_{d_b} + \frac{1}{2}g_{h_a} - \frac{1}{2}g_{i_{ab/}} + \frac{1}{4}g_{j_{a/b}} + e_1$..	XXIX ₁
$-\frac{1}{2}d_a + \frac{1}{2}d_b + \frac{1}{2}h_a + \frac{1}{2}h_b - \frac{1}{4}ab/$..	XXX
$-\frac{1}{2}g_{d_a} + \frac{1}{2}g_{d_b} + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{h_b} - \frac{1}{2}g_{i_{ab/}} + e_1$..	XXX ₁
$-\frac{1}{2}d_a + \frac{1}{2}h_a + h_b - \frac{1}{4}j_{a/b}$..	XXXI
$-\frac{1}{2}g_{d_a} + \frac{1}{2}g_{h_a} + g_{h_b} - \frac{1}{4}g_{j_{a/b}} + e_1$..	XXXI ₁
$-\frac{1}{2}d_b + \frac{1}{2}h_a + \frac{1}{2}h_b$..	XXXII
$-\frac{1}{2}g_{d_b} + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{h_b} + e_1$..	XXXII ₁

Expression		Notation
$-\frac{1}{2}d_a + \frac{1}{2}h_a + \frac{1}{2}h_b$..	XXXIII
$-\frac{1}{2}g_{d_a} + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{h_b} + e_1$..	XXXIII ₁
$-\frac{1}{2}d_a - \frac{1}{2}d_b + \frac{1}{2}h_a + \frac{1}{2}h_b + \frac{1}{2}i_{ab}/$..	XXXIV
$-\frac{1}{2}g_{d_a} - \frac{1}{2}g_{d_b} + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{h_b} + \frac{1}{2}g_{i_{ab}} + e_1$..	XXXIV ₁
$-\frac{1}{2}d_a - d_b + \frac{1}{2}h_a + \frac{1}{2}i_{ab}/ + \frac{1}{2}j_{a/b}$..	XXXV
$-\frac{1}{2}g_{d_a} - g_{d_b} + \frac{1}{2}g_{h_a} + \frac{1}{2}g_{i_{ab}} + \frac{1}{2}g_{j_{a/b}} + e_1$..	XXXV ₁
$-d_a + \frac{1}{2}d_b + \frac{1}{2}h_b - \frac{1}{2}i_{ab}/ + \frac{1}{2}j_{b/a}$..	XXXVI
$-g_{d_a} + \frac{1}{2}g_{d_b} + \frac{1}{2}g_{h_b} - \frac{1}{2}g_{i_{ab}} + \frac{1}{2}g_{j_{b/a}} + e_1$..	XXXVI ₁
$-d_a - \frac{1}{2}d_b + \frac{1}{2}h_b + \frac{1}{2}i_{ab}/ + \frac{1}{2}j_{b/a}$..	XXXVII
$-g_{d_a} - \frac{1}{2}g_{d_b} + \frac{1}{2}g_{h_b} + \frac{1}{2}g_{i_{ab}} + \frac{1}{2}g_{j_{b/a}} + e_1$..	XXXVII ₁

APPENDIX II

TABLE 1.

Eighteen Phenotypes from nine Genotypes in two environments:-

GENOTYPE ENVIRONMENT	AABB	AABB	AABB	AaBb	AaBb	AaBb	Aabb	aaBB	aaBb	aabb	F ₂ Mean
P	I+I ₁	II+ II ₁	III +III ₁	IV+ IV ₁	V+ V ₁	VI+ VI ₁	VII+ VII ₁	VIII+ VIII ₁	IX+ IX ₁	X+X ₁	
Q	I-I ₁	II- II ₁	III- III ₁	IV- IV ₁	V- V ₁	VI- VI ₁	VII- VII ₁	VIII- VIII ₁	IX- IX ₁	X-X ₁	
Mean	I	II	III	IV	V	VI	VII	VIII	IX	X	

Thirty-six Phenotypes from δ APPENDIX II δ nine genotypes in four environments.
TABLE 2.

GENOTYPE ENVIRONMENT	Phenotypes									F ₂ Mean
	AABB	AABb	AAbb	AaBB	AaBb	Aabb	aaBB	aaBb	aabb	
P	I + I ₁ + I ₂ + I ₃	II + II ₁ + II ₂ + II ₃	III + III ₁ + III ₂ + III ₃	IV + IV ₁ + IV ₂ + IV ₃	V + V ₁ + V ₂ + V ₃	VI + VI ₁ + VI ₂ + VI ₃	VII + VII ₁ + VII ₂ + VII ₃	VIII + VIII ₁ + VIII ₂ + VIII ₃	IX + IX ₁ + IX ₂ + IX ₃	X + X ₁ + X ₂ + X ₃
Q	I + I ₁ - I ₂ - I ₃	II + II ₁ - II ₂ - II ₃	III + III ₁ - III ₂ - III ₃	IV + IV ₁ - IV ₂ - IV ₃	V + V ₁ - V ₂ - V ₃	VI + VI ₁ - VI ₂ - VI ₃	VII + VII ₁ - VII ₂ - VII ₃	VIII + VIII ₁ - VIII ₂ - VIII ₃	IX + IX ₁ - IX ₂ - IX ₃	X + X ₁ - X ₂ - X ₃
R	I - I ₁ + I ₂ - I ₃	II - II ₁ + II ₂ - II ₃	III - III ₁ + III ₂ - III ₃	IV - IV ₁ + IV ₂ - IV ₃	V - V ₁ + V ₂ - V ₃	VI - VI ₁ + VI ₂ - VI ₃	VII - VII ₁ + VII ₂ - VII ₃	VIII - VIII ₁ + VIII ₂ - VIII ₃	IX - IX ₁ + IX ₂ - IX ₃	X - X ₁ + X ₂ - X ₃
S	I - I ₁ - I ₂ + I ₃	II - II ₁ - II ₂ + II ₃	III - III ₁ - III ₂ + III ₃	IV - IV ₁ - IV ₂ + IV ₃	V - V ₁ - V ₂ + V ₃	VI - VI ₁ - VI ₂ + VI ₃	VII - VII ₁ - VII ₂ + VII ₃	VIII - VIII ₁ - VIII ₂ + VIII ₃	IX - IX ₁ - IX ₂ + IX ₃	X - X ₁ - X ₂ + X ₃
Mean	I	II	III	IV	V	VI	VII	VIII	IX	X

NOTE: The inferior suffixes 1, 2, 3 to the right of each notation correspond to the three environmental comparisons involved.

TABLE 3

Phenotypic F₃ family means in two environments:-

GENOTYPE ENVIRONMENT	AABB	AABb	AAbb	AaBB	AaBb	Aabb	aaBB	aaBb	aabb	Mean of F ₃ Means.
P	I + I, XI + XI,	II + II,	III + III,	XII + XII,	X + X,	XIII + XIII,	VII + VII,	XIV + XIV,	IX + IX,	XV + XV,
Q	I - I,	II - II,	III - III,	XII - XII,	X - X,	XII - XII,	VII - VII,	XIV - XIV,	IX - IX,	XV - XV,
Mean	I	II	III	XII	X	XIII	VII	XIV	IX	XV

TABLE 4Biparental progenies in two environments:-

The eighty-one possible squares are numbered as below.

	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>
1	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
2	(10)	(11)	--	--	--	--	--	--	(18)
3	--	--							--
4	--	--							--
5	--	--							--
6	--	--							--
7	--	--							--
8	--	--							--
9	(73)	(74)							(81)

The progenies in different squares are exhibited below, and in the following pages.

1.	<u>AABB</u>	Square No.
	P : I. +I,	
	AABB:	(1)
	Q : I - I,	

2.

	AABB	
AABb	P	I+I ₁ II+II ₁
	Q	I-I ₁ II-II ₁

Square Nos.
(2) and (10)

3.

	AABb	
AABB	P	I+I ₁
	Q	I-I ₁

Square Nos.
(3) and (19)

4.

		<u>AaBB</u>	
AABB	P	I+I ₁	IV+IV ₁
	Q	I-I ₁	IV-IV ₁

Square Nos.,
(4) and (28)

5.

		<u>AaBb</u>			
AABB:	P	I+I ₁	II+II ₁	IV+IV ₁	V+V ₁
	Q	I-I ₁	II-II ₁	IV-IV ₁	V-V ₁

Square Nos.
(5) & (37)

6.

Square Nos. ~~(5)~~ (13) and (29) will be having the progeny as above but they are obtained from a cross between (AABb x AaBB).

7. AABB: P II+II_1 $\frac{\text{Aabb}}{1}$ V+V_1 Square Nos.
 Q II-II_1 V-V_1 (6) & (46)

8. The cross (AAbb x AaBB) yields the same progeny as the above one and the squares having this type of cross are (22) & (30).

9. AABB: P $\frac{\text{aaBB}}{\text{IV+IV}_1}$ Square Nos.
 Q IV-IV_1 (70) & (55)

10. AABB: P IV+IV_1 $\frac{\text{aaBB}}{1}$ V+V_1 Square Nos.
 Q IV-IV_1 V-V_1 (8) & (64)

11. The cross (AABb x aaBB) gives the same progeny as the above one and the squares having this type of cross are (16) & (56)

12. AABB: P $\frac{\text{aabb}}{\text{V+V}_1}$ Square Nos.
 Q V-V_1 (9) & (73)

13. The cross (AAbb x aaBB) gives the same progeny as the above one and the squares having this type of cross are (25) & (57).

14. AABb: P I+I_1 $\frac{\text{AABb}}{\text{II+II}_1}$ III+III_1 Square Nos.
 Q I-I_1 II-II_1 III-III_1 (11)

15. AABb: P I+I_1 $\frac{\text{AAbb}}{\text{III+III}_1}$ Square Nos.
 Q I-I_1 III-III_1 (12) & (20)

16. AaBb Square Nos.
 AABb: P $I+I_1 II+II_1 III+III_1 IV+IV_1 V+V_1 VI+VI_1$ (14) & (38)
 Q $I-I_1 II-II_1 III-III_1 IV-IV_1 V-V_1 VI-VI_1$
17. Aabb Square Nos.
 AABb: P $II+II_1 III+III_1 V+V_1 VI+VI_1$ (15) & (47)
 Q $II-II_1 III-III_1 V-V_1 VI-VI_1$
18. The cross (AAbb x AaBb) gives the progeny same as the above one and the squares having this type of cross are (23) & (48)
19. aaBb Square Nos.
 AABb: P $IV+IV_1 V+V_1 VI+VI_1$ (17) & (65)
 Q $IV-IV_1 V-V_1 VI-VI_1$
20. aabb Square Nos.
 AABb: P $V+V_1 VI+VI_1$ (18) & (74)
 Q $V-V_1 VI-VI_1$
21. The cross (AAbb x aaBb) gives the progeny same as the above one and the squares having this type of cross are (26) & (66)
22. AAbb Square No.
 AAbb: P $III+III_1$ (21)
 Q $III-III_1$
23. Aabb Square Nos.
 AAbb: P $III+III_1 VI+VI_1$ (24) & (48)
 Q $III-III_1 VI-VI_1$
24. aabb Square Nos.
 AAbb: P $VI+VI_1$ (27) & (75)
 Q $VI-VI_1$

25. AaBB
 P I+I₁ IV+IV₁ VII+VII₁ Square No.
 AaBB: Q I-I₁ IV-IV₁ VII-VII₁ (31)

26. AaBb
 P I+I₁ III+III₁ IV+IV₁ V+V₁ VII+VII₁ IX+IX₁
 AaBB: Q I-I₁ III-III₁ IV-IV₁ V-V₁ VII-VII₁ IX-IX₁
 Square Nos. (32) & (40)

27. Aabb
 P II+II₁ V+V₁ VIII+VIII₁ Square Nos.
 AaBB: Q II-II₁ V-V₁ VIII-VIII₁ (33) & (49)

28. aaBB
 P IV+IV₁ VII+VII₁ Square Nos,
 AaBB: Q IV-IV₁ VII-VII₁ (34)&(48)

29. aaBb
 P IV+IV₁ V+V₁ VII+VII₁ VIII+VIII₁ Square Nos.
 AaBB: Q IV-IV₁ V-V₁ VII-VII₁ VIII-VIII₁ (35) & (67)

30. The cross (AaBb x aaBB) gives the progeny as the above one and the squares having this type of cross are (43) & (59).

31. aabb
 P V+V₁ VIII+VIII₁ Square Nos.
 AaBB: Q V-V₁ VIII-VIII₁ (36) & (76)

32. The cross (Aabb x ~~A~~ aaBB) gives the progeny as the above one and the squares having this type of cross are (52) & (60).

33. AaBb
 P I+I₁ II+II₁ III+III₁ IV+IV₁ V+V₁ VII+VII₁ VI+VI₁
 AaBb: Q I-I₁ II-II₁ III-III₁ IV-IV₁ V-V₁ VII-VII₁ VI-VI₁
 P VIII+VIII₁ IX+IX₁ Square Nos.
 Q VIII-VIII₁ IX-IX₁ (41)

34.

Aabb

$$\begin{array}{l} \text{AaBb: P } II+II_1 III+III_1 V+V_1 VI+VI_1 VIII+VIII_1 IX+IX_1 \\ \text{Q } II-II_1 III-III_1 V-V_1 VI-VI_1 VIII-VIII_1 IX-IX_1 \end{array}$$

Square Nos. (42) & (50)

35.

aaBb

$$\begin{array}{l} \text{AaBb: P } IV+IV_1 V+V_1 VI+VI_1 VII+VII_1 VIII+VIII_1 IX+IX_1 \\ \text{Q } IV-IV_1 V-V_1 VI-VI_1 VII-VII_1 VIII-VIII_1 IX-IX_1 \end{array}$$

Square Nos. (44) & (68)

36.

aabb

$$\begin{array}{l} \text{AaBb: P } V+V_1 VI+VI_1 VIII+VIII_1 IX+IX_1 \\ \text{Q } V-V_1 VI-VI_1 VIII-VIII_1 IX-IX_1 \end{array}$$

Square Nos,
(45) & (77)

37. The cross (Aabb x aaBb) gives the progeny same as the above one and the squares having this type of cross are (53) & (69).

38.

Aabb

$$\begin{array}{l} \text{Aabb: P } III+III_1 VI+VI_1 IX+IX_1 \\ \text{Q } III-III_1 VI-VI_1 IX-IX_1 \end{array}$$

Square No,
(51)

39.

aabb

$$\begin{array}{l} \text{Aabb:P } VI+VI_1 IX+IX_1 \\ \text{Q } VI-VI_1 IX-IX_1 \end{array}$$

Square Nos.
(54) & (78)

40.

aaBB

$$\begin{array}{l} \text{aaBB: P } VII+VII_1 \\ \text{Q } VII-VII_1 \end{array}$$

Square No,
(61)

41. aaBb Square Nos.
 P VII+VII₁ VIII+VIII₁ (62) & (70)
 aaBB: Q VII-VIII₁ VIII-VIII₁
42. aabb Square Nos.
 P VIII+VIII₁ (63) & (79)
 aaBB: Q VIII-VIII₁
43. aaBb Square No.
 P VII+VII₁ VIII+VIII₁ IX+IX₁ (71)
 aaBb: Q VII-VII₁ VIII-VIII₁ IX-IX₁
44. aabb Square Nos.
 P VIII+VIII₁ IX+IX₁ (72) & (80)
 aaBB: Q VIII -VIII₁ IX-IX₁
45. aabb Square No.
 P IX+IX₁ (81)
 aabb: Q IX-IX₁

TABLE 5
Maternal Progenies with two environments:-

GENOTYPE	AABB		AaBb		AaBB		AaBb		aaBB		aaBb		aabb		MEANS.
	P	Q	P	Q	P	Q	P	Q	P	Q	P	Q	P	Q	
AABB	I + I, II + II,	I - I, II - II,	I + I, II + II,	I - I, II - II,	I + I, II + II,	I - I, II - II,	I + I, II + II,	I - I, II - II,	I + I, II + II,	I - I, II - II,	I + I, II + II,	I - I, II - II,	I + I, II + II,	I - I, II - II,	XXXX
AaBb	III + III, IV + IV,	III - III, IV - IV,	III + III, IV + IV,	III - III, IV - IV,	III + III, IV + IV,	III - III, IV - IV,	III + III, IV + IV,	III - III, IV - IV,	III + III, IV + IV,	III - III, IV - IV,	III + III, IV + IV,	III - III, IV - IV,	III + III, IV + IV,	III - III, IV - IV,	XXXX
AaBB	V + V, VI + VI,	V - V, VI - VI,	V + V, VI + VI,	V - V, VI - VI,	V + V, VI + VI,	V - V, VI - VI,	V + V, VI + VI,	V - V, VI - VI,	V + V, VI + VI,	V - V, VI - VI,	V + V, VI + VI,	V - V, VI - VI,	V + V, VI + VI,	V - V, VI - VI,	XXXX
Aabb	VII + VII, VIII + VIII,	VII - VII, VIII - VIII,	VII + VII, VIII + VIII,	VII - VII, VIII - VIII,	VII + VII, VIII + VIII,	VII - VII, VIII - VIII,	VII + VII, VIII + VIII,	VII - VII, VIII - VIII,	VII + VII, VIII + VIII,	VII - VII, VIII - VIII,	VII + VII, VIII + VIII,	VII - VII, VIII - VIII,	VII + VII, VIII + VIII,	VII - VII, VIII - VIII,	XXXX
aaBB	IX + IX, X + X,	IX - IX, X - X,	IX + IX, X + X,	IX - IX, X - X,	IX + IX, X + X,	IX - IX, X - X,	IX + IX, X + X,	IX - IX, X - X,	IX + IX, X + X,	IX - IX, X - X,	IX + IX, X + X,	IX - IX, X - X,	IX + IX, X + X,	IX - IX, X - X,	XXXX
aaBb	XI + XI, XII + XII,	XI - XI, XII - XII,	XI + XI, XII + XII,	XI - XI, XII - XII,	XI + XI, XII + XII,	XI - XI, XII - XII,	XI + XI, XII + XII,	XI - XI, XII - XII,	XI + XI, XII + XII,	XI - XI, XII - XII,	XI + XI, XII + XII,	XI - XI, XII - XII,	XI + XI, XII + XII,	XI - XI, XII - XII,	XXXX
aabb	XIII + XIII, XIV + XIV,	XIII - XIII, XIV - XIV,	XIII + XIII, XIV + XIV,	XIII - XIII, XIV - XIV,	XIII + XIII, XIV + XIV,	XIII - XIII, XIV - XIV,	XIII + XIII, XIV + XIV,	XIII - XIII, XIV - XIV,	XIII + XIII, XIV + XIV,	XIII - XIII, XIV - XIV,	XIII + XIII, XIV + XIV,	XIII - XIII, XIV - XIV,	XIII + XIII, XIV + XIV,	XIII - XIII, XIV - XIV,	XXXX
Means.	XVII	XVII	XXII	XXII	XXIII	XXIII	XXVII	XXVII	X	XXXII	XXXII	XXXIII	XXXIII	XXXIV	XXXIV

H P > I O Z H G

APPENDIX III

Table 1 (a)

Variances in terms of P, H, I, J, L, G_D ?
G_H, G_I, G_J, G_L and E.

$$\frac{1}{2}(V_{P1} + \frac{1}{2}V_{P2})$$

$$V_{F1}$$

$$V_{1F2}$$

$$V_{1F3}$$

$$V_{2F3}$$

$$V_{1S3}$$

$$V_{2S3}$$

$$V_{1M3}$$

$$V_{2M3}$$

$$\Sigma'(e_1 + \Sigma g_{a/b} + \frac{1}{4} \Sigma g_{a/b})^2 + \Sigma'(\Sigma g_{a/b} - \frac{1}{2} \Sigma g_{a/b})^2$$

$$\Sigma'(e_1 + \Sigma g_{h_a} + \frac{1}{4} \Sigma g_{a/b})^2$$

$$\frac{1}{2}D + \frac{1}{4}H + \frac{1}{8}I + \frac{1}{16}J + \frac{1}{32}L + \frac{1}{4}G_D + \frac{1}{4}G_I + \frac{1}{8}G_J + \frac{1}{16}G_L + E_{F2}$$

$$\frac{1}{2}D' + \frac{1}{16}H' + \frac{1}{4}I + \frac{1}{32}J + \frac{1}{256}L$$

$$\frac{1}{4}D' + \frac{1}{8}H' + \frac{5}{16}I + \frac{1}{64}J + \frac{1}{32}L + \frac{3}{4}G_D' + \frac{3}{16}G_H' + \frac{9}{16}G_I + \frac{9}{64}G_J + \frac{9}{256}G_L + E_{F3}$$

$$\frac{1}{4}D + \frac{1}{16}H + \frac{1}{16}I + \frac{1}{64}J + \frac{1}{256}L$$

$$\frac{1}{4}D + \frac{3}{16}H + \frac{3}{16}I + \frac{7}{64}J + \frac{15}{256}L + \frac{1}{2}G_D + \frac{1}{4}G_H + \frac{1}{4}G_I + \frac{1}{8}G_J + \frac{1}{16}G_L + E_{F2}$$

$$\frac{1}{8}D + \frac{1}{64}I$$

$$\frac{3}{4}D + \frac{1}{4}H + \frac{15}{64}I + \frac{1}{8}J + \frac{1}{16}L + \frac{1}{2}G_D + \frac{1}{4}G_H + \frac{1}{4}G_I + \frac{1}{8}G_J + \frac{1}{16}G_L + E_{F2}$$

Table 1 (b)

Variances in terms of D, H, I, J, L, α, β, γ, δ, and ε.

δ

ε

$$\frac{1}{2}D + \frac{1}{4}H + \frac{1}{4}I + \frac{1}{8}J + \frac{1}{16}L + \frac{1}{2}\alpha + \frac{1}{4}\beta + \frac{1}{4}\gamma + \frac{1}{2}\delta + \frac{1}{2}\epsilon$$

$$\frac{1}{2}D' + \frac{1}{16}H' + \frac{1}{4}I + \frac{1}{32}J + \frac{1}{256}L$$

$$\frac{1}{4}D' + \frac{1}{8}H' + \frac{5}{16}I + \frac{7}{64}J + \frac{1}{32}L + \frac{3}{4}\alpha' + \frac{3}{16}\beta' + \frac{3}{16}\gamma' + \frac{3}{4}\delta + \frac{1}{4}\epsilon$$

$$\frac{1}{4}D + \frac{1}{16}H + \frac{1}{16}I + \frac{1}{64}J + \frac{1}{256}L$$

$$\frac{1}{4}D + \frac{3}{16}H + \frac{3}{16}I + \frac{7}{64}J + \frac{15}{256}L + \frac{1}{2}\alpha + \frac{1}{4}\beta + \frac{1}{4}\gamma + \frac{1}{2}\delta + \frac{1}{2}\epsilon$$

$$\frac{1}{8}D + \frac{1}{64}I$$

$$\frac{3}{8}D + \frac{1}{4}H + \frac{15}{64}I + \frac{1}{8}J + \frac{1}{16}L + \frac{1}{2}\alpha + \frac{1}{4}\beta + \frac{1}{4}\gamma + \frac{1}{2}\delta + \frac{1}{2}\epsilon$$

TABLE 2.

Between Plots.

Within Plots.

V_{1^F3}	--	--	$\frac{1}{2}(D'+2G_D') + \frac{1}{16}(H'+2G_H') + \frac{1}{4}(I+2G_I) + \frac{1}{32}(J+2G_J) + \frac{1}{256}(L+2G_L) + 2EF_3$
V_{2^F3}	$\frac{1}{4}(D'+2G_D') + \frac{1}{8}(H'+2G_H') + \frac{5}{16}(I+2G_I) + \frac{7}{64}(J+2G_J) + \frac{2}{64}(L+2G_L) + \frac{3}{4}G_D' + \frac{3}{16}G_H' + \frac{9}{16}G_I + \frac{9}{64}G_J + \frac{9}{256}G_L + 1EF_3$	--	--
V_{1^S3}	--	--	$\frac{1}{2}(D+2G_D) + \frac{1}{16}(H+2G_H) + \frac{1}{16}(I+2G_I) + \frac{1}{64}(J+2G_J) + \frac{1}{256}(L+2G_L) + 2EF_2$
V_{2^S3}	$\frac{1}{4}(D+2G_D) + \frac{3}{16}(H+2G_H) + \frac{3}{16}(I+2G_I) + \frac{7}{64}(J+2G_J) + \frac{15}{256}(L+2G_L) + \frac{1}{2}G_D + \frac{1}{4}G_H + \frac{1}{4}G_I + \frac{1}{8}G_J + \frac{1}{16}G_L + 1EF_2$	--	--
V_{1^M3}	--	--	$\frac{1}{8}(D+2G_D) + \frac{1}{64}(I+2G_I) + 2EF_2$
V_{2^M3}	$\frac{3}{8}(D+2G_D) + \frac{1}{4}(H+2G_H) + \frac{15}{64}(I+2G_I) + \frac{1}{8}(J+2G_J) + \frac{1}{16}(L+2G_L) + \frac{1}{2}G_D + \frac{1}{4}G_H + \frac{1}{4}G_I + \frac{1}{8}G_J + \frac{1}{16}G_L + 1EF_2$	--	--

TABLE 2: Variance components with non-random distribution over environments.