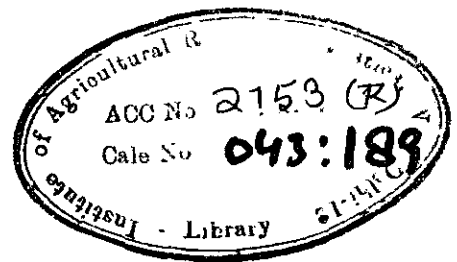


GENETIC VARIANCE AND COVARIANCE UNDER
POSITIVE ASSORTATIVE MATING

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By

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(A. V. Rao)

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I N T R O D U C T I O N

The basic tools for plant and animal breeders to improve upon characters of economic importance are (1) selection and (2) proper breeding system. Causing or permitting some kinds of individuals to produce more offspring than other kinds do is known as "Selection". Selection modifies the relative frequencies of the genetic factors and effects a permanent change in the average genetic composition of the population. The control on the way in which the parents are mated defines a breeding system. The systems of breeding can be broadly grouped into (a) inbreeding (b) outbreeding and (c) mating on the basis of phenotypic appearance. Inbreeding is the mating of individuals which are more related than the individuals of the population on an average whereas outbreeding is mating of unrelated individuals. In inbreeding the relative frequencies of different genetic factors in the original population remain constant. It breaks the population into lines such that the individuals within a line are as genotypically alike as possible and those between lines are genotypically as different as possible. On the other hand, outbreeding creates genetic variation by bringing together the genetic potentialities of different individuals involved in the mating. Mating two individuals on the basis of phenotypic appearance may be either (i) like to like, or (ii) like to unlike.

Mating like to like means mating big with big, little with little, medium with medium, compact with compact, rangy with rangy, sluggish with sluggish etc. This is known as 'Positive Assortative Mating'. Mating like to unlike means big with small, high with low etc. and is known as "Negative Assortative Mating" or simply "Disassortative Mating".

The positive assortative mating has been studied theoretically by Jennings (1916), Fisher (1918) and Wright (1921). In the wild animals it has been studied in Blue-Snow Goose (Cooch and Beardmore, 1959) and the Arctic Skua (O'Donald, 1959). In man, Pearson and Lee (1903) demonstrated this type of breeding for various characters such as stature and fore-arm length. Fisher (1930) argued that this mating system is potentially an important agent promoting evolutionary change. Rendel (1944) found in Drosophila subobscura that yellow males tended to mate with yellow females far more readily than with females of other genotypes. Breese (1956) studied the genetic consequences of such a system with quantitative characters using Mather's biometrical method (1949) in the analysis of some specially designed experiments with Nicotiana rustica.

Wright (1921) showed that, provided the number of genes involved is large, positive assortative mating is not likely to achieve a greater genetic correlation than is obtained under random mating. In particular he showed that with two factors the percentage of heterozygosis for a given pair of allelomorphs in successive generations form the series

$1/2$, $3/8$, $10/32$, $17/84$, $29/128$ etc. The assumptions involved in obtaining this result are (i) the two pairs of alleles are equally numerous, (ii) the population is in equilibrium before the starting of assortative mating and (iii) there is no dominance in either of the factors. It is held by Wright that assortative mating leads to the greatest diversification of the population as a whole. It is always accompanied by selection either in nature or in livestock breeding. If there is no selection, the assortative mating leads to increased variability in the population as a whole.

Breese (1956), probably for the first time, studied the possible consequences of a system of assortative mating with quantitative characters considering situations involving different conditions of dominance. Experiments were devised to investigate within a common parental population changes in heritable variation ^{affected} by assortative mating as compared with selfing and random mating. The experiments demonstrated a significant increase in the genetic variability of family means under assortative mating compared with that found under random mating. Breese, however, did not take into account the complex genetical situations like genic interaction and linkage, but he anticipated that these disturbing factors would retard the process of fixation of the extreme expression of ^{the} characters involved. The demonstration of the significant changes in the distribution of heritable variation, though considered for a single generation of mating, suggested that assortative mating may profitably have wider use as a

technique in plant or animal breeding, especially where inbreeding methods are impracticable or undesirable. Further assortative mating can ^a affect divergence within a population and if sufficiently strong can, by itself, form a basis for speciation. From evolutionary point of view it is, therefore, a force which provides impetus for divergence and speciation.

In the studies made by Breese (1956), it assumed that the two allelomorphs of a pair of genes have equal frequencies in the population and that the genes are equal in effect. Only few conditions of dominance are studied. The complex genetic phenomenon of linkage and genic interaction are avoided. Various results on first and second rank statistics though given for any finite number of genes, relate to the case if the assortative mating is resorted to for one generation only. Further the effects of assortative mating combined with selection have not been studied. The object of the present investigation is, therefore, to discuss some of these untouched aspects of assortative mating with quantitative characters.

The present study is divided into four chapters. In the first chapter only one locus with two alleles with given gene frequency is considered. In the second chapter, the consequences of any number of genetic factors, all independent in action and distribution are worked out; whereas in chapter three, the effects of linkage are considered. In the last chapter, the effects of positive assortative mating combined with selection are investigated.

CHAPTER - 1Genotypic composition and variation with
one locus segregating

The effects of assortative mating depends upon how similar are the parents to be mated in regard to the character under study phenotypically. As Wright (1921) suggested it depends on the "degree of determination by heridity" and the phenotypic correlation between the parents. It may be assumed at the very outset that the environmental effects are negligible so that by resorting to assortative mating, almost perfect genetic correlation is achieved. This would allow studies on assortative mating to be made from first principles. With such an assumption one can find out the composition of genotypic intra-mating groups by considering the genotypes of a population and the particular action of genes like dominance or epistasis and the particular distribution of genes like independent distribution or linkage.

Consider a random mating population with one locus segregating. Let the three genotypes AA, Aa and aa be in the proportions p^2 , $2pq$ and q^2 respectively where p is the frequency of gene 'A' and $q = (1-p)$ is that of gene 'a'. With regard to dominance we can consider the following three cases:

- (i) There is no dominance so that all the three genotypes are phenotypically different.
- (ii) Gene 'A' is completely dominant over gene 'a' so that AA and Aa are phenotypically alike.

(iii) Gene 'a' is completely dominant over gene 'A' so that Aa and aa are phenotypically alike, i.e. dominance in the negative direction.

1.1. No dominance

1.11. Genotypic Composition

When there is no dominance, all the three genotypes are phenotypically recognisably distinct. Therefore, the tendency to assortative mating will yield the mating types with the corresponding frequencies given below:

<u>Mating type</u>	<u>Frequency</u>
AA x AA	p^2
Aa x Aa	$2pq$
aa x aa	q^2

The proportion of genotype in the next generation would be

AA	$\frac{p(p+1)}{2}$
Aa	pq
aa	$\frac{q(q+1)}{2}$

This shows that the heterozygosity has decreased by 50%.

1.12 Calculation of means, variances and covariance

Let d_a and $-d_a$ measure the departure of AA and aa respectively from the mid-parent. The frequencies, mean values and within family variances for various mating types would be

as given in the table below:

Table 1

Mating type	Frequency	Parental mean value	Family mean	Within family variance
AA x AA	p^2	d_a	d_a	0
Aa x Aa	$2pq$	0	0	pd_a^2
aa x aa	q^2	$-d_a$	$-d_a$	0

$$\begin{aligned}
 & \text{Therefore, mean of parental mean values } (M_{A_0}) \\
 & = \text{Mean of family means } (M_{A_1}) \\
 & = (p - q) d_a,
 \end{aligned}$$

so that there is no change in the mean as a result of assortative mating.

The variance of family means termed as first rank variance is given by

$${}^1V_{A_1} = 2pq d_a^2$$

The mean variance within families termed as second rank variance is given by

$${}^2V_{A_1} = pq d_a^2$$

The total variance is, therefore, given by

$$\begin{aligned}
 V_{A_1} & = {}^1V_{A_1} + {}^2V_{A_1} \\
 & = 2pq d_a^2 + pq d_a^2 \\
 & = 3pq d_a^2.
 \end{aligned}$$

The variance in the parental generation (V_{A_0}) is, however, $2pq d_a^2$, so that the effect of assortative mating, in this case, is to increase the total genetic variations in such a way that the within family variance is halved.

The covariance between family means and parental mean values is given by

$$W_{A_0i} = 2pq d_a^2$$

1.2 'A' is completely dominant over 'a'

1.21 Genotypic composition:

If 'A' is completely dominant over 'a', AA and Aa are not phenotypically recognisably distinct. There will be two intra-mating groups, one comprising of the genotypes AA and Aa, and another comprising of aa only. The tendency to assortative mating will yield the following mating types with frequencies given below :-

<u>Mating type</u>	<u>Frequency</u>
AA x AA	$p^3 / (1+q)$
AA x Aa	$4p^2q / (1+q)$
Aa x Aa	$4pq^2 / (1+q)$
aa x aa	q^2

The distribution of genotypes in the next generation would be

AA	$p / (1+q)$
Aa	$2pq / (1+q)$
aa	$2q^2 / (1+q)$

This shows that the proportion of heterozygotes has decreased by $2pq^2 / (1+q)$. In this case, therefore, the decrease in the heterozygosis depends on the gene frequency.

1.22 Calculation of Means, Variances and Covariances

Let d_a , h_a and $-d_a$ measure the departures of AA, Aa and aa respectively from the mid-parent. The frequencies, mean values and within family variances for various mating types would be as given in Table below:

Table 2

Mating type	Frequency	Parental mean value	Family mean	Within family variance
AA x AA	$p^3/(1+q)$	d_a	d_a	0
AA x Aa	$4p^2q/(1+q)$	$\frac{1}{2}(d_a+h_a)$	$\frac{1}{2}(d_a+h_a)$	$\frac{1}{4}(d_a - h_a)^2$
Aa x Aa	$4pq^2/(1+q)$	h_a	$\frac{1}{2}h_a$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$
aa x aa	q^2	$-d_a$	$-d_a$	0

Therefore, mean of family means is given by

$$M_{A_1} = (p-q) d_a + \frac{2pq}{1+q} h_a$$

The mean of parental mean values is given by

$$M_{A_0} = (p-q) d_a + 2pq h_a.$$

Thus the mean value has decreased by $\frac{2pq^2}{1+q} h_a$

= (decrease in the proportion of heterozygotes) x (effect of heterozygote).

The variance of family means is given by

$$1V_{A_1} = \frac{pq(3q+1)}{(1+q)} d_a^2 + \frac{pq(1+q-4pq)}{(1+q)^2} h_a^2 + \frac{2pq(3q-1)}{(1+q)} d_a h_a$$

The mean variance within families is given by

$$2V_{A_1} = pq d_a^2 + \frac{pq}{1+q} h_a^2 - \frac{2p^2q}{1+q} d_a h_a$$

The total variance is, therefore, given by

$$\begin{aligned} V_{A_1} &= 1V_{A_1} + 2V_{A_1} \\ &= \left(2pq + \frac{2pq^2}{1+q}\right) d_a^2 + \left[2pq(1-2pq) - \frac{2pq^2}{(1+q)^2} (2q^3 + 2q^2 - 3q + 1)\right] h_a^2 \\ &\quad + \frac{4pq(q-p)}{1+q} d_a h_a \end{aligned}$$

The parental variance is, however, obtained as

$$V_{A_0} = 2pq d_a^2 + 2pq(1-2pq) h_a^2 + 4pq(q-p) d_a h_a$$

Comparing V_{A_1} and V_{A_0} , it is found that while the coefficient of d_a^2 has increased, the coefficients of h_a^2 and $d_a h_a$ have decreased. The decrease in the coefficient of h_a^2 is apparent since $(2q^3 + 2q^2 - 3q + 1)$ is a positively increasing function of q for admissible values of q between 0 and 1. The increase in the coefficient of d_a^2 is such that the coefficient of d_a^2 in the within family variance is halved whereas the decrease in the coefficient of h_a^2 is such that the coefficient of h_a^2 in the within family variance viz.,

$$\frac{pq}{1+q} = \frac{2pq(1-2pq)}{2(1+q)(p^2+q^2)} \quad \text{is also decreased in the proportion } 1 / 2(1+q)(p^2+q^2).$$

The covariance between family means and parental mean values is given by

$$w_{A01} = \frac{pq(3q + 1)}{1+q} d_a^2 + \frac{pq(1+q-4pq)}{1+q} h_a^2 + \frac{2pq\sqrt{2q(1+q)-1}}{1+q} d_a h_a$$

1.3 'a' is completely dominant over 'A'

1.31 Genotypic Compositions:

If 'a' is completely dominant over 'A', aa and Aa are not phenotypically recognisably distinct. So there will be two intra-mating groups, one comprising of the genotypes Aa and aa, and another comprising of AA only. The tendency to assortative mating will yield the mating types with the corresponding frequencies given below :-

<u>Mating type</u>	<u>Frequency</u>
AA x AA	p^2
Aa x Aa	$4p^2q / (1 + p)$
Aa x aa	$4pq^2 / (1 + p)$
aa x aa	$q^3 / (1 + p)$

The distribution of the genotypes in the next generation would be

AA	$2p^2 / (1+p)$
Aa	$2pq / (1+p)$
aa	$q / (1+p),$

so that the decrease in the proportion of heterozygotes is obtained as $2p^2q / (1+p)$, and consequently it depends on the gene frequency.

1.32 Calculation of Means, Variances and Covariance

Let d_a , h_a and $-d_a$ measure the departures of AA, Aa and aa respectively from the mid-parent. The frequencies, mean values and within family variances for various mating types are given in the following table.

Table 3

Mating type	Frequency	Parental mean value	Family mean	Within family variance
AA x AA	p^2	d_a	d_a	0
Aa x Aa	$4p^2q/(1+p)$	h_a	$\frac{1}{2} h_a$	$\frac{1}{2} d_a^2 + \frac{1}{2} h_a^2$
Aa x aa	$4pq^2/(1+p)$	$\frac{1}{2}(h_a - d_a)$	$\frac{1}{2}(h_a - d_a)$	$\frac{1}{2} (d_a + h_a)^2$
aa x aa	$q^3/(1+p)$	$-d_a$	$-d_a$	0

Therefore mean of family means is given by

$$M_{A1} = (p - q) d_a + \frac{2pq}{1+p} h_a$$

Mean of parental mean values is given by

$$M_{A0} = (p - q) d_a + 2pq h_a$$

Thus the mean value has decreased by $\frac{2p^2q}{1+p} h_a$

= (decrease in the proportion of heterozygotes) x (effect of heterozygote)

The variance of family means is given by

$$1V_{A1} = \frac{pq(3p+1)}{1+p} d_a^2 + \frac{pq(1+p-4pq)}{(1+p)^2} h_a^2 - \frac{2pq(3p-1)}{1+p} d_a h_a$$

It may be noted that this expression can simply be obtained

by replacing 'q' by 'p' in the expression of first rank variance given under 1.22 and changing the sign of d_a .

The mean variance within families is given by

$$2V_{A_1} = (pq) d_a^2 + \frac{pq}{1+p} h_a^2 + \frac{2pq^2}{1+p} d_a h_a$$

The total variance is, therefore, given by

$$\begin{aligned} V_{A_1} &= 1V_{A_1} + 2V_{A_1} \\ &= \left(2pq + \frac{2p^2q}{1+p}\right) d_a^2 + \left[2pq(1-2pq) - \frac{2p^2q}{(1+p)^2}(2p^3+2p^2-3p+1)\right] h_a^2 \\ &\quad + \frac{4pq(q-p)}{1+p} d_a h_a \end{aligned}$$

Comparing V_{A_1} with V_{A_0} already given under 1.22, it is found that while the coefficient of d_a^2 has increased, the coefficients of h_a^2 and $d_a h_a$ have decreased. The decrease in the coefficient of h_a^2 is apparent since $(2p^3 + 2p^2 - 3p + 1)$ is a positively increasing function of p for admissible values of p between 0 and 1. The increase in the coefficient of d_a^2 is such that the coefficient of d_a^2 in the within family variance is halved whereas the decrease in the coefficient of h_a^2 is such that the coefficient of h_a^2 in the within family variance viz.,

$$\frac{pq}{1+p} = \frac{2pq(1-2pq)}{2(1+p)(p^2+q^2)} \text{ is also decreased in the}$$

proportion $1/2(1+p)(p^2+q^2)$.

The covariance between family means and parental mean values is given by

$$w_{A01} = \frac{pq(3p+1)}{1+p} d_a^2 + \frac{pq(1+p-4pq)}{1+p} h_a^2 - \frac{2pq[2p(1+p)-1]}{1+p} d_a h_a$$

It may be noted that this expression can simply be obtained by replacing 'q' by 'p' in the expression of the covariance between family means and parental mean values given under section 1.22 and changing the sign of d_a .

1.4 Genotypic Composition and Variation after another round of positive assortative mating

When positive assortative mating is again adopted in the progenies of the earlier generation, the following results under various cases of dominance are obtained:

1.41. No dominance

1.411 Genotypic Composition

As we have seen under 1.11 the proportions of genotypes in the earlier generation are

$$\begin{array}{ll} AA & p(p+1)/2 \\ Aa & pq \\ aa & q(q+1)/2 \end{array}$$

The tendency to assortative mating in this generation will yield the mating types with the frequencies as given below:

<u>Mating type</u>			<u>Frequency</u>
AA	x	AA	$p(p+1)/2$
Aa	x	Aa	pq
aa	x	aa	$q(q+1)/2$

The distribution of genotypes in the next generation would be

$$AA \quad p(p + 3) / 4$$

$$Aa \quad pq / 2$$

$$aa \quad q(q + 3) / 4$$

This shows that the heterozygosity has again decreased by 50%.

1.412 Calculation of means, variances and covariance

Let d_a and $-d_a$ measure the departure of AA and aa from the mid-parent. The frequencies, mean values and within family variances for various mating types are given in the table below:

Table 4

Mating type	Frequency	Parental mean value in A_1	Family mean in A_2	Within family variance
AA x AA	$p(p+1)/2$	d_a	d_a	0
Aa x Aa	pq	0	0	$\frac{1}{2} d_a^2$
aa x aa	$q(q+1)/2$	$-d_a$	$-d_a$	0

Therefore,

$$\begin{aligned} M_{A_1} &= M_{A_2} \\ &= (p - q) d_a \\ 1V_{A_2} &= 3pq d_a^2 \end{aligned}$$

It is thus seen that the first rank variance has increased from $2pq d_a^2$ to $3pq d_a^2$.

$$2V_{A_2} = \frac{1}{2} pq d_a^2$$

The second rank variance is, therefore, halved after another round of assortative mating.

Therefore, the total variance is given by

$$\begin{aligned} V_{A_2} &= 1V_{A_2} + 2V_{A_2} \\ &= 3pq d_a^2 + \frac{1}{2} pq d_a^2 \\ &= \frac{7}{2} pq d_a^2 \end{aligned}$$

as against

$$\begin{aligned} V_{A_1} &= 1V_{A_1} + 2V_{A_1} \\ &= 2pq d_a^2 + pq d_a^2 \\ &= 3pq d_a^2 \end{aligned}$$

This shows that again the total genetic variation is increased in such a way that the second rank variance is halved whereas the first rank variance is increased to 3/2 of its value in the previous generations.

$$W_{A_{12}} = 3pq d_a^2$$

This is found to be more than $W_{A_{01}}$.

1.42 'A' is completely dominant over 'a'

1.421 Genotypic Composition:

As we have seen under section 1.21, the proportions of genotypes in the resulting population would be

$$\begin{array}{ll} AA & p / (1 + q) \\ Aa & 2pq / (1 + q) \\ aa & 2q^2 / (1 + q) \end{array}$$

The tendency to assortative mating in this generation will yield the mating types with the corresponding frequencies

as given below:-

<u>Mating type</u>	<u>Frequency</u>
AA x AA	$p / (1 + q) (1+ 2q)$
AA x Aa	$4 pq / (1+q)(1+2q)$
Aa x Aa	$4 pq^2 / (1+q) (1+ 2q)$
aa x aa	$2 q^2 / (1 + q)$

The distribution of genotypes in the next generation would be

AA	$p(1+q) / (1+2q)$
Aa	$2pq / (1+2q)$
aa	$3q^2 / (1+2q)$

This shows that the proportion of heterozygotes has decreased by $2pq^2 / (1+q) (1+2q)$. Relative to the initial proportion of heterozygotes the decrease is, however, $4 pq^2 / (1 + 2q)$.

$$\text{Writing } H_0 = 2pq; \text{ we have } H_1 = \frac{H_0}{1+q} \text{ and}$$

$$H_2 = \frac{H_0}{1+2q}$$

$$\text{Also } H_2 = \left(\frac{1 + q}{1+ 2q} \right) H_1,$$

where H_r measures the heterozygosity in the r^{th} generation.

1.422 Calculation of Means, Variances and Covariance

Let d_a , h_a and $-d_a$ measure as usual the departures of AA, Aa and aa respectively from the mid-parent. The frequencies, mean values and the within family variances for various mating types are given in the table below:

Table 5

Mating type	Frequency	Parental mean value in A_1	Family mean in A_2	Within family variance
AA x AA	$\frac{p}{(1+q)(1+2q)}$	d_a	d_a	0
AA x Aa	$\frac{4pq}{(1+q)(1+2q)}$	$\frac{1}{2}(d_a+h_a)$	$\frac{1}{2}(d_a+h_a)$	$\frac{1}{4}(d_a-h_a)^2$
Aa x Aa	$\frac{4pq^2}{(1+q)(1+2q)}$	h_a	$\frac{1}{2}(h_a)$	$\frac{1}{4}(d_a^2)+\frac{1}{4}(h_a^2)$
aa x aa	$\frac{2q^2}{(1+q)}$	$-d_a$	$-d_a$	0

From the above table the following results are obtained:

$$M_{A_2} = (p - q) d_a + \frac{2pq}{1+2q} h_a, \text{ whereas}$$

$M_{A_1} = (p - q) d_a + \frac{2pq}{1+q} h_a$ so that the mean value has again decreased.

$$1V_{A_2} = \frac{pq(1+16q - 8pq)}{(1+q)(1+2q)} d_a^2 + \frac{pq(1+2q - 4pq)}{(1+2q)^2} h_a^2 +$$

$$\frac{2pq(6q - 4pq - 1)}{(1+q)(1+2q)} d_a h_a$$

$$2V_{A_2} = \frac{pq}{1+q} d_a^2 + \frac{pq}{1+2q} h_a^2 + \frac{2pq}{(1+q)(1+2q)} d_a h_a$$

The total variance is then given by

$$\begin{aligned} V_{A_2} &= 1V_{A_2} + 2V_{A_2} \\ &= \frac{2pq(1+4q)}{(1+2q)} d_a^2 + \frac{2pq(1+2q^2)}{(1+2q)^2} h_a^2 + \frac{4pq(2q-1)}{(1+2q)} d_a h_a \end{aligned}$$

The comparisons of these variances with the variances in the previous generation are made graphically later under section 1.6.

$$W_{A12} = \frac{pq(1+16q-8pq)}{(1+q)(1+2q)} d_a^2 + \frac{pq(1+2q-4pq)}{(1+q)(1+2q)} h_a^2 + \frac{2pq(3q-1)}{(1+q)} d_a h_a$$

1.43 'a' is completely dominant over 'A'

1.431 Genotypic composition:

As we have seen earlier under section 1.31 the proportions of genotypes in this generation would be

$$\begin{array}{ll} AA & 2p^2 / (1 + p) \\ Aa & 2pq / (1 + p) \\ aa & q / (1 + p) \end{array}$$

The tendency to assortative mating in this generation will yield the matings with the corresponding frequencies as given below:

<u>Mating type</u>	<u>Frequency</u>
AA x AA	$\frac{2p^2}{1+p}$
Aa x Aa	$\frac{4p^2q}{(1+p)(1+2p)}$
Aa x aa	$\frac{4pq}{(1+p)(1+2p)}$
aa x aa	$\frac{q}{(1+p)(1+2p)}$

The distribution of genotypes in the next generation would be given by

$$\begin{array}{ll} AA & 3p^2 / 1+2p \\ Aa & 2pq / 1+2p \\ aa & q(1+p) / 1+2p \end{array}$$

This shows that the proportion of heterozygotes has decreased by $2p^2q / (1+p)(1+2p)$. Relative to the initial proportion of heterozygotes of $2pq$, the decrease is $4p^2q / (1+2p)$.

The recurrence relation for the heterozygosity in this case, would be given by

$$H_2 = \frac{1+p}{1+2p} H_1$$

1.432 Calculation of Means, Variances and Covariance

Let $-d_a$, h_a and $-d_a$ measure, as usual, the departures of AA, Aa and aa respectively from the mid-parent. The frequencies, mean values and within family variances for various mating types are given in the table below :-

Table 6

Mating Type	Frequency	Parental Mean value in A_1	Family Mean in A_2	Within family variance
AA x AA	$\frac{2p^2}{1+p}$	d_a	d_a	0
Aa x Aa	$\frac{4p^2q}{(1+p)(1+2p)}$	h_a	$\frac{1}{2} h_a$	$\frac{1}{2} d_a^2 + \frac{1}{2} h_a^2$
Aa x aa	$\frac{4pq}{(1+p)(1+2p)}$	$\frac{1}{2}(h_a - d_a)$	$\frac{1}{2}(h_a - d_a)$	$\frac{1}{2}(d_a + h_a)^2$
aa x aa	$\frac{q}{(1+p)(1+2p)}$	$-d_a$	$-d_a$	0

From the above table the following results are obtained:

$$M_{A_2} = (p-q) d_a + \frac{2pq}{1+2p} h_a,$$

whereas

$$M_{A_1} = (p-q) d_a + \frac{2pq}{1+p} h_a.$$

This shows that the mean has decreased as expected.

$$\begin{aligned}
 {}_1V_{A_2} &= \frac{pq(1+16p-8pq)}{(1+p)(1+2p)} d_a^2 + \frac{pq(1+2p-4pq)}{(1+2p)^2} h_a^2 - \\
 &\quad \frac{2pq(6p-4pq-1)}{(1+p)(1+2p)} d_a h_a
 \end{aligned}$$

It may be noted that this expression can simply be obtained by replacing 'q' by 'p' in the expression for variance of family means under section 1.422 and changing the sign of d_a .

$${}_2V_{A_2} = \frac{pq}{1+p} d_a^2 + \frac{pq}{1+2p} h_a^2 + \frac{2pq}{(1+p)(1+2p)} d_a h_a$$

Again this expression can simply be obtained by replacing 'q' by 'p' in the expression for mean variance within families given under section 1.422 and changing the sign of d_a .

The total variance is then given by

$$V_{A_2} = \frac{2pq(1+4p)}{1+2p} d_a^2 + \frac{2pq(1+2p^2)}{(1+2p)^2} h_a^2 + \frac{4pq(1-2p)}{(1+2p)} d_a h_a$$

The covariance between family means in A_2 and parental mean values in A_1 is given by

$$\begin{aligned}
 W_{A_{12}} &= \frac{pq(1+16p-8pq)}{(1+p)(1+2p)} d_a^2 + \frac{pq(1+2p-4pq)}{(1+p)(1+2p)} h_a^2 - \\
 &\quad \frac{2pq(3p-1)}{(1+p)} d_a h_a
 \end{aligned}$$

Again this expression can simply be obtained by replacing 'q' by 'p' in the expression for covariance obtained under section 1.422 and changing the sign of d_a .

1.5 General results for a population assortatively mated for n generations

If positive assortative mating is again resorted to in the population already subjected to this type of mating for n generations, the following results are obtained under various cases of dominance.

1.51 No dominance

1.511 Genotypic Composition

It can be easily seen by induction that the proportions of genotypes after n generations of positive assortative mating would be

$$AA \quad p(p + 2^n - 1) / 2^n$$

$$Aa \quad pq / 2^{n-1}$$

$$aa \quad q(q + 2^n - 1) / 2^n$$

If the positive assortative mating is again adopted in this generation, the mating types and the corresponding frequencies would be

<u>Mating type</u>	<u>Frequency</u>
AA x AA	$p(p + 2^n - 1) / 2^n$
Aa x Aa	$pq / 2^{n-1}$
aa x aa	$q(q + 2^n - 1) / 2^n$

The distribution of genotypes in the (n + 1)th generation would be as follows:

$$AA \quad p(p + 2^{n+1} - 1) / 2^{n+1}$$

$$Aa \quad pq / 2^n$$

$$aa \quad q(q + 2^{n+1} - 1) / 2^{n+1}$$

Q

This shows that the heterozygosity has again decreased by 50%. Relative to the initial random mating population, the heterozygosity has, however, decreased by

$(1 - \frac{1}{2^{n+1}})$ per cent. In this case, therefore, the

recurrence relation for the heterozygosity H is the same as that found under selfing viz.

$$H_{n+1} = \frac{1}{2} H_n$$

The positive assortative mating with no dominance involved, hence, leads to the same results as those found under selfing.

1.512 Calculation of Means, Variances and Covariance

Let d_a and $-d_a$ measure the departures of AA and aa respectively from the mid-parent. The frequencies, mean values and the within family variances for various mating types are given in the following table:

Table 7

Mating type	Frequency	Parental Mean value in A_n	Family Mean in A_{n+1}	Within family variance
AA x AA	$\frac{p(p + 2^{n-1})}{2^n}$	d_a	d_a	0
Aa x Aa	$\frac{2pq}{2^n}$	0	0	$\frac{1}{2} d_a^2$
aa x aa	$\frac{q(q + 2^{n-1})}{2^n}$	$-d_a$	$-d_a$	0

Therefore, mean of family means ($M_{A_{n+1}}$)
 = Mean of parental mean values (M_{A_n})
 = $(p - q)d_a$

Variance of family means is given by

$$1V_{A_{n+1}} = \left[\frac{2^{n+1} - 1}{2^{n-1}} pq \right] d_a^2 \text{ whereas,}$$

$$1V_{A_n} = \left[\frac{2^n - 1}{2^{n-2}} pq \right] d_a^2$$

The increase in the 1st rank variance over the previous generation therefore,

$$= \frac{pq}{2^{n-1}} d_a^2$$

Mean variance within families is given by

$$2V_{A_{n+1}} = \frac{pq}{2^n} d_a^2$$

so that it is decreased by $\frac{pq}{2^n} d_a^2$

Therefore, the total variance is given by

$$\begin{aligned} V_{A_{n+1}} &= 1V_{A_{n+1}} + 2V_{A_{n+1}} \\ &= \frac{2^{n+1}-1}{2^{n-1}} pq d_a^2 + \frac{1}{2^n} pq d_a^2 \\ &= \left(2^2 - \frac{1}{2^n} \right) pq d_a^2 \end{aligned}$$

Covariance between family means in A_{n+1} and parental mean values in A_n is given by

$$W_{A_n, n+1} = \frac{2^{n+1}-1}{2^{n-1}} pq d_a^2$$

1.52 'A' is completely dominant over 'a'

1.521 Genotypic Composition:

Continuing positive assortative mating in each generation, the proportions of genotypes after n generations would be given by

$$\begin{array}{l} \text{AA} \quad \frac{p \left(1 + (n-1) q \right)}{1 + nq} \\ \text{Aa} \quad \frac{2pq}{1 + nq} \\ \text{aa} \quad \frac{q^2(n + 1)}{1 + nq} \end{array}$$

If the assortative mating is adopted in this generation also, the mating types and the corresponding frequencies would be

<u>Mating type</u>	<u>Frequency</u>
AA x AA	$\frac{p [1+(n-1)q]^2}{(1+nq) [1+(n+1)q]}$
AA x Aa	$\frac{4pq [1+(n-1)q]}{(1+nq) [1+(n+1)q]}$
Aa x Aa	$\frac{4pq^2}{(1+nq) [1+(n+1)q]}$
aa x aa	$\frac{(n+1) q^2}{1 + nq}$

The proportions of genotypes in the next generation would be

$$AA \quad p(1+nq) / [1+(n+1)q]$$

$$Aa \quad 2pq / [1+(n+1)q]$$

$$aa \quad q^2(n+2) / [1+(n+1)q]$$

Therefore, $H_{n+1} = 2pq / [1+(n+1)q]$ and

$$H_n = 2pq / (1 + nq)$$

This leads to the following recurrence relation for the heterozygosity H .

$$H_{n+1} = \frac{2p H_n}{2p + H_n}$$

Since the initial heterozygosity $H_0 = 2pq$, we also have

$$H_{n+1} = \frac{H_0}{1 + (n+1)q}$$

Unlike the recurrence relation for inbreeding based on relationship, this recurrence relation is not independent of gene frequency.

1.522 Calculation of Means, Variances and Covariance

Let d_a , h_a and $-d_a$ measure as usual, the departures of AA, Aa and aa respectively from the mid-parent. The frequencies, mean values and within family variances for various mating types are given in the following table :

Table 8

Mating type	Frequency	Parental Mean value in A_n	Family mean in A_{n+1}	Within family variance
AA x AA	$\frac{p^2 [1+(n-1)q]}{(1+nq) [1+(n+1)q]}$	d_a	d_a	0
AA x Aa	$\frac{4pq [1+(n-1)q]}{(1+nq) [1+(n+1)q]}$	$\frac{1}{2}(d_a+h_a)$	$\frac{1}{2}(d_a+h_a)$	$\frac{1}{4}(d_a-h_a)^2$
Aa x Aa	$\frac{4pq^2}{(1+nq) [1+(n+1)q]}$	h_a	$\frac{1}{2}h_a$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$
aa x aa	$\frac{q^2(n+1)}{(1+nq)}$	$-d_a$	$-d_a$	0

Therefore, mean of family means is given by

$$M_{A_{n+1}} = (p-q)d_a + \frac{2pq}{1+(n+1)q} h_a$$

Mean of parental mean values is given by

$$M_{An} = (p-q)d_a + \frac{2pq}{1+nq} h_a,$$

so that the mean value is decreased by $\frac{2pq^2}{(1+nq) [1+(n+1)q]} h_a$

Compared to the initial population it is decreased by

$$\left[2pq - \frac{2pq}{1+(n+1)q} \right] h_a = \frac{2(n+1) pq^2}{1+(n+1)q}$$

Variance of family means is given by

$$\begin{aligned} 1V_{An+1} &= \frac{pq \left[\left\{ 1+(n-1)q \right\} \left\{ 1+2(n+1)q \right\} + 2(n+1)q \left\{ 1+(n+1)q \right\} \right] d_a^2}{(1+nq) [1+(n+1)q]} \\ &+ \frac{pq [1+(n+1)q - 4pq]}{[1+(n+1)q]^2} h_a^2 \\ &+ \frac{2pq [1+(n-1)q - 2(p-q)(1+nq)]}{(1+nq) [1+(n+1)q]} d_a h_a \end{aligned}$$

Mean variance within families is given by

$$\begin{aligned} 2V_{An+1} &= \frac{pq}{(1+nq)} d_a^2 + \frac{pq}{\{1+(n+1)q\}} h_a^2 \\ &- \frac{2pq [1+(n-1)q]}{(1+nq) [1+(n+1)q]} d_a h_a \end{aligned}$$

The total variance is then given by

$$\begin{aligned}
 V_{A_{n+1}} &= 1V_{A_{n+1}} + 2V_{A_{n+1}} \\
 &= \frac{2pq \left[1+(n+1)2q \right] d_a^2}{1+(n+1)q} + \frac{2pq \left[1+(n+1)q - 2pq \right] h_a^2}{\left[1+(n+1)q \right]^2} \\
 &\quad + \frac{4pq(q-p)}{1+(n+1)q} d_a h_a
 \end{aligned}$$

The covariance between family means in A_{n+1} and parental mean values in A_n is given by

$$\begin{aligned}
 W_{A_n, n+1} &= \frac{pq \left[\left\{ 1+(n-1)q \right\} \left\{ 1+2(n+1)q \right\} + 2q(n+1) \left\{ 1+(n+1)q \right\} \right] d_a^2}{(1+nq) \left\{ 1+(n+1)q \right\}} \\
 &\quad + \frac{pq \left[1+(n+1)q - 4pq \right] h_a^2}{(1+nq) \left[1+(n+1)q \right]} \\
 &\quad + \frac{2pq \left[1+(n-1)q - (p-q) \left\{ 2+(2n+1)q \right\} \right] d_a h_a}{(1+nq) \left[1+(n+1)q \right]}
 \end{aligned}$$

1.53 'a' is completely dominant over 'A'

1.531 Genotypic Composition:

Continuing assortative mating in each generation, the proportions of genotypes in A_n would be

$$\begin{array}{ll}
 AA & (n+1)p^2 / (1+np) \\
 Aa & 2pq / (1+np) \\
 aa & \left[1+(n-1)p \right] q / (1+np)
 \end{array}$$

If the positive assortative mating is adopted in this generation also, the mating types with the corresponding frequencies would be

<u>Mating type</u>	<u>Frequency</u>
AA x AA	$\frac{(n+1) p^2}{(1+np)}$
Aa x Aa	$\frac{4p^2q}{(1+np) [1+(n+1)p]}$
Aa x aa	$\frac{4pq [1 + (n-1) p]}{(1+np) [1+(n+1)p]}$
aa x aa	$\frac{q [1+(n-1)p]^2}{(1+np) [1+(n+1)p]}$

The proportions of genotypes in A_{n+1} would be

AA	$\frac{(n+2) p^2}{1+(n+1) p}$
Aa	$\frac{2pq}{1+ (n+1) p}$
aa	$\frac{(1 + np)q}{1+(n+1) p}$

In this case the recurrence relation for H is obtained as

$$H_{n+1} = \frac{2qH_n}{2q + H_n}$$

As usual, this also can be obtained by replacing 'p' by 'q' in the recurrence relation obtained under 1.521.

$$\text{Also, now } H_{n+1} = \frac{H_0}{1+(n+1)p}$$

1.532 Calculation of Means, variances and covariance

Let d_a , h_a and $-d_a$ measure the departures of AA, Aa and aa respectively from the mid-parent. The frequencies, mean values and within family variances for various mating types are given in the following table:

Table 9

Mating type	Frequency	Parental mean value in A_n	Family mean in A_{n+1}	Within family variance
AA x AA	$\frac{(n+1)p^2}{1+np}$	d_a	d_a	0
Aa x Aa	$\frac{4p^2q}{(1+np)[1+(n+1)p]}$	h_a	$\frac{1}{2}h_a$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$
Aa x aa	$\frac{4pq[1+(n-1)p]}{(1+np)[1+(n+1)p]}$	$\frac{1}{2}h_a - \frac{1}{2}d_a$	$\frac{1}{2}h_a - \frac{1}{2}d_a$	$\frac{1}{4}(d_a+h_a)^2$
aa x aa	$\frac{q[1+(n-1)p]^2}{(1+np)[1+(n+1)p]}$	$-d_a$	$-d_a$	0

Therefore, mean of family means is given by

$$M_{A_{n+1}} = (p - q)d_a + \frac{2pq}{1+(n+1)p} h_a$$

Mean of parental mean values is given by

$$M_{A_n} = (p - q)d_a + \frac{2pq}{1 + np} h_a ,$$

so that the mean value is decreased by

$$\frac{2p^2q}{(1+np) [1 + (n + 1) p]} h_a$$

Compared to the initial population it is decreased

by

$$\frac{2(n+1)p^2q}{1 + (n + 1) p}$$

The variance of family means is given by

$$\begin{aligned} 1V_{A_{n+1}} &= \frac{pq \left[\{1+(n-1)p\} \{1+2(n+1)p\} + 2(n+1)p \{1+(n+1)p\} \right] d_a^2}{(1+np) [1+(n+1)p]} \\ &+ \frac{pq [1 + (n+1)p - 4pq]}{[1 + (n + 1) p]^2} h_a^2 \\ &- \frac{2pq [1+(n-1)p - 2(q-p)(1+np)]}{(1 + np) [1 + (n+1) p]} d_a h_a \end{aligned}$$

Mean variance within families is given by

$$2V_{A_{n+1}} = \frac{pq}{1+np} d_a^2 + \frac{pq}{1+(n+1)p} h_a^2 + \frac{2pq \sqrt{1+(n-1)p}}{(1+np) \sqrt{1+(n+1)p}} d_a h_a$$

Therefore, the total variance is given by

$$\begin{aligned} V_{A_{n+1}} &= 1V_{A_{n+1}} + 2V_{A_{n+1}} \\ &= \frac{2pq \sqrt{1+2(n+1)p}}{1+(n+1)p} d_a^2 + \frac{2pq \sqrt{1+(n+1)p} - 2pq}{\sqrt{1+(n+1)p}^2} h_a^2 - \\ &\quad \frac{4pq(p-q)}{1+(n+1)p} d_a h_a \end{aligned}$$

The covariance between family means in A_{n+1} and parental mean values in A_n is given by

$$\begin{aligned} W_{A_n, n+1} &= \frac{pq \sqrt{\left\{ \frac{1+(n-1)p}{1+np} \right\} \left\{ \frac{1+2(n+1)p}{1+(n+1)p} \right\} + 2(n+1)p \left\{ \frac{1+(n+1)p}{1+(n+1)p} \right\}}}{(1+np) \sqrt{1+(n+1)p}} d_a^2 \\ &+ \frac{pq \sqrt{1+(n+1)p} - 4pq}{(1+np) \sqrt{1+(n+1)p}} h_a^2 \\ &- \frac{2pq \sqrt{1+(n-1)p} - (q-p) \sqrt{2+(2n+1)p}}{(1+np) \sqrt{1+(n+1)p}} d_a h_a \end{aligned}$$

1.6 Graphical Studies

It may be observed from the results obtained in the previous sections, that the variances and covariances in

a particular generation depend not only on d , measuring the difference of effect between homozygotes and h measuring the effect of heterozygote, but also on the gene frequency. This dependence on the gene frequency is such that the coefficients of d^2 , h^2 and dh all change characteristically from one statistic to another, excepting that the coefficient of d^2 in the first rank variance is the same as that in the covariance, this being true in each of the dominance situations studied. Further, the variances and covariances change from one generation to another in a significant manner. To study these changes over the admissible range of values of the gene frequency a set of graphs are shown in Figs. 1.61 to 1.67. Since the case of no dominance is similar to that of selfing and the case of 'a' dominant over 'A' is just the complementary to that of 'A' dominant over 'a', graphs for the case 'A' dominant over 'a' have only been drawn.

Fig. 1.61

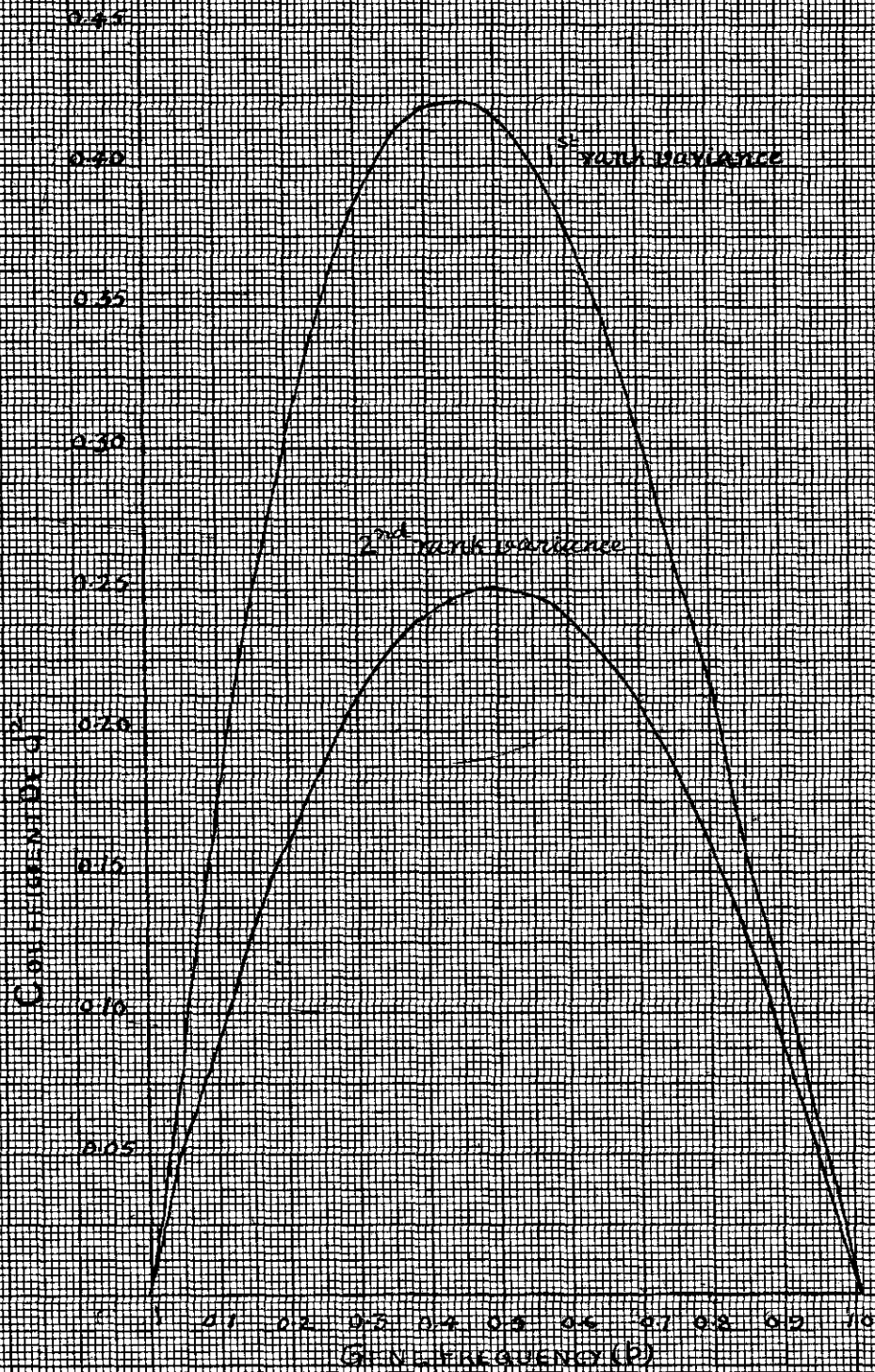


Fig. 162

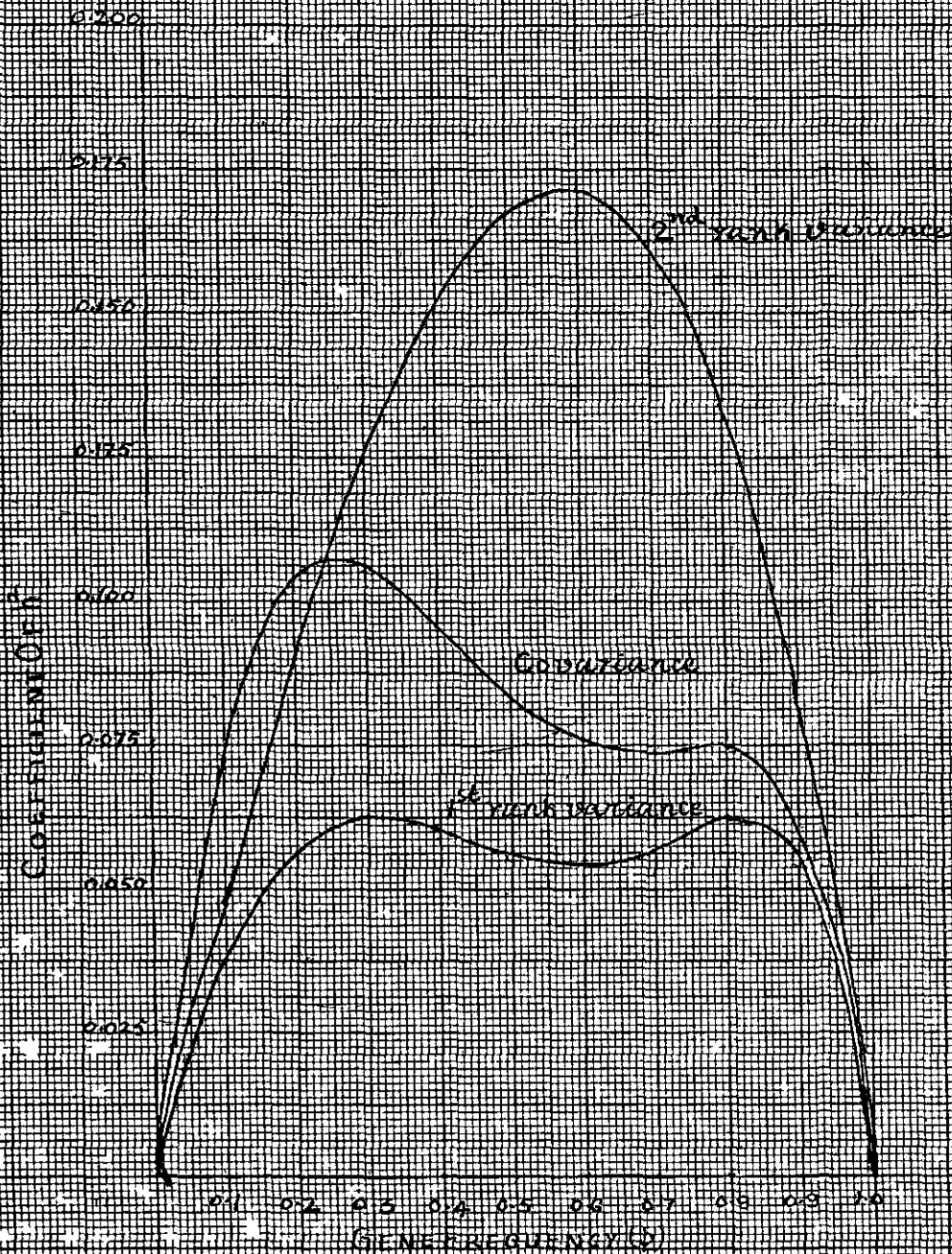


FIG. 1-63

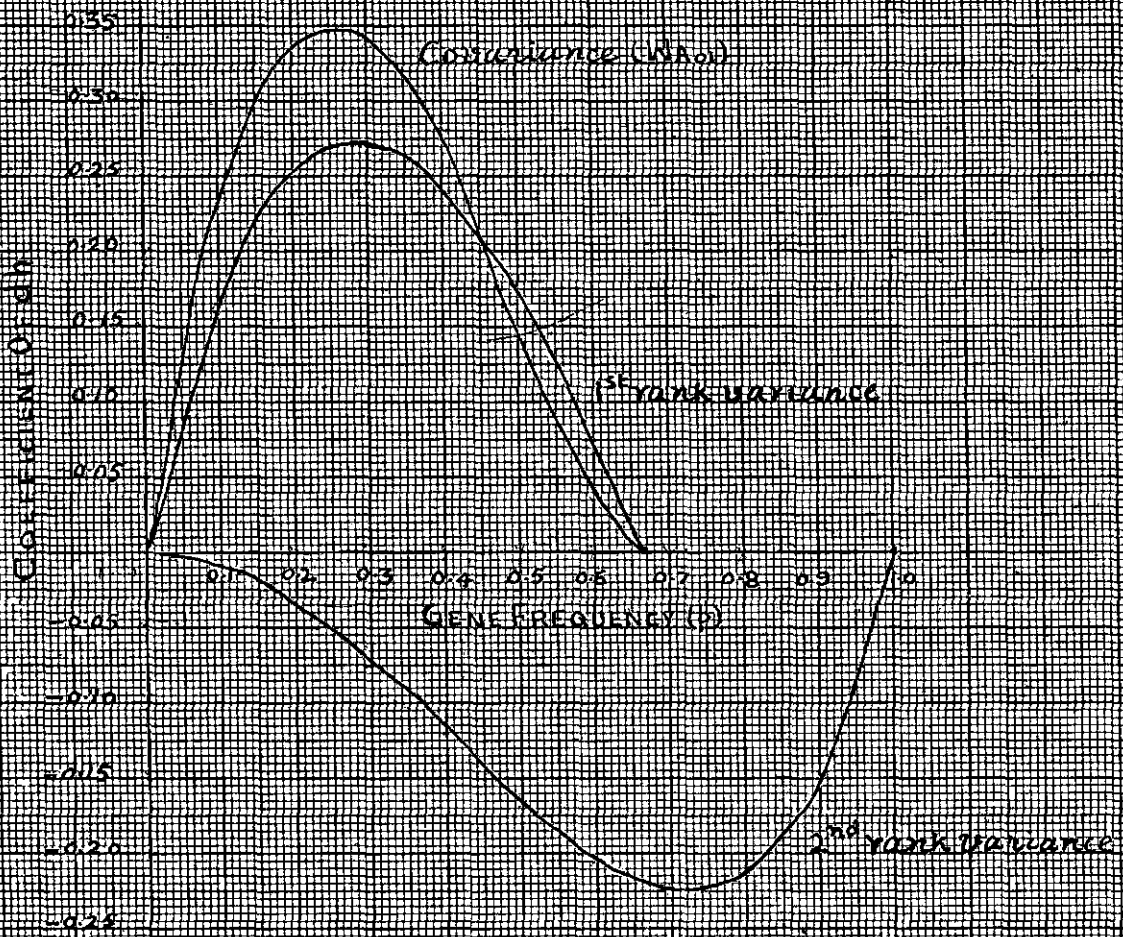
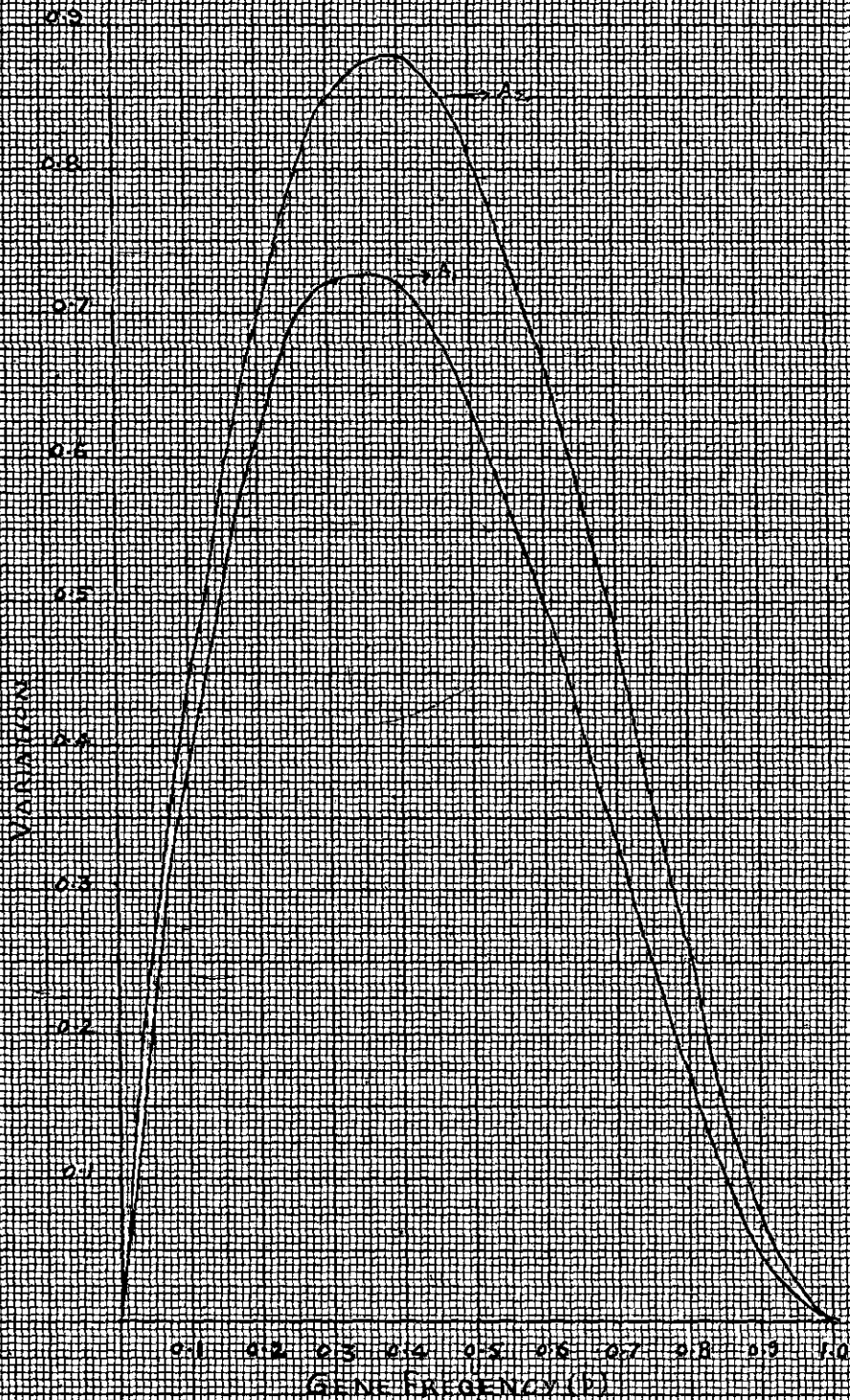
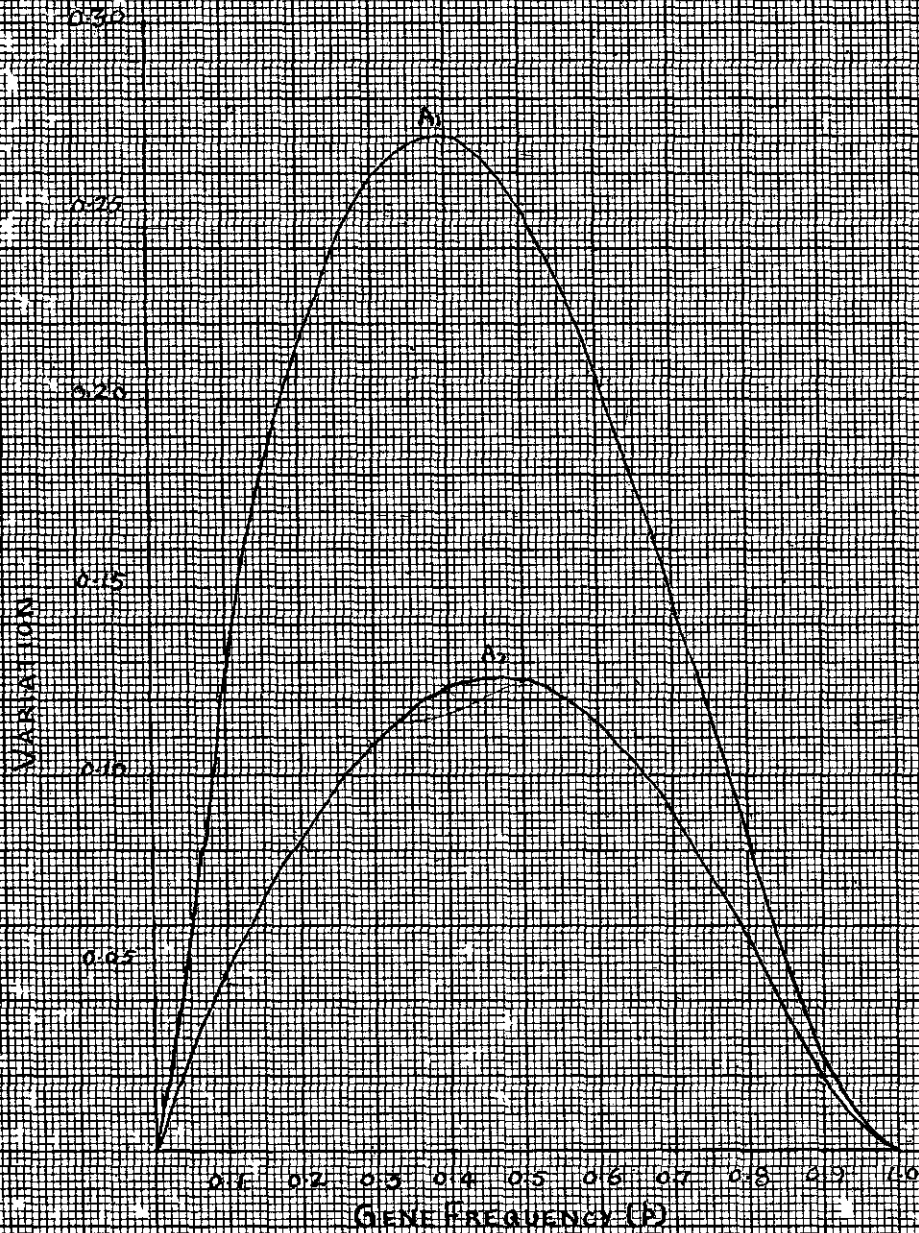


Fig: 64



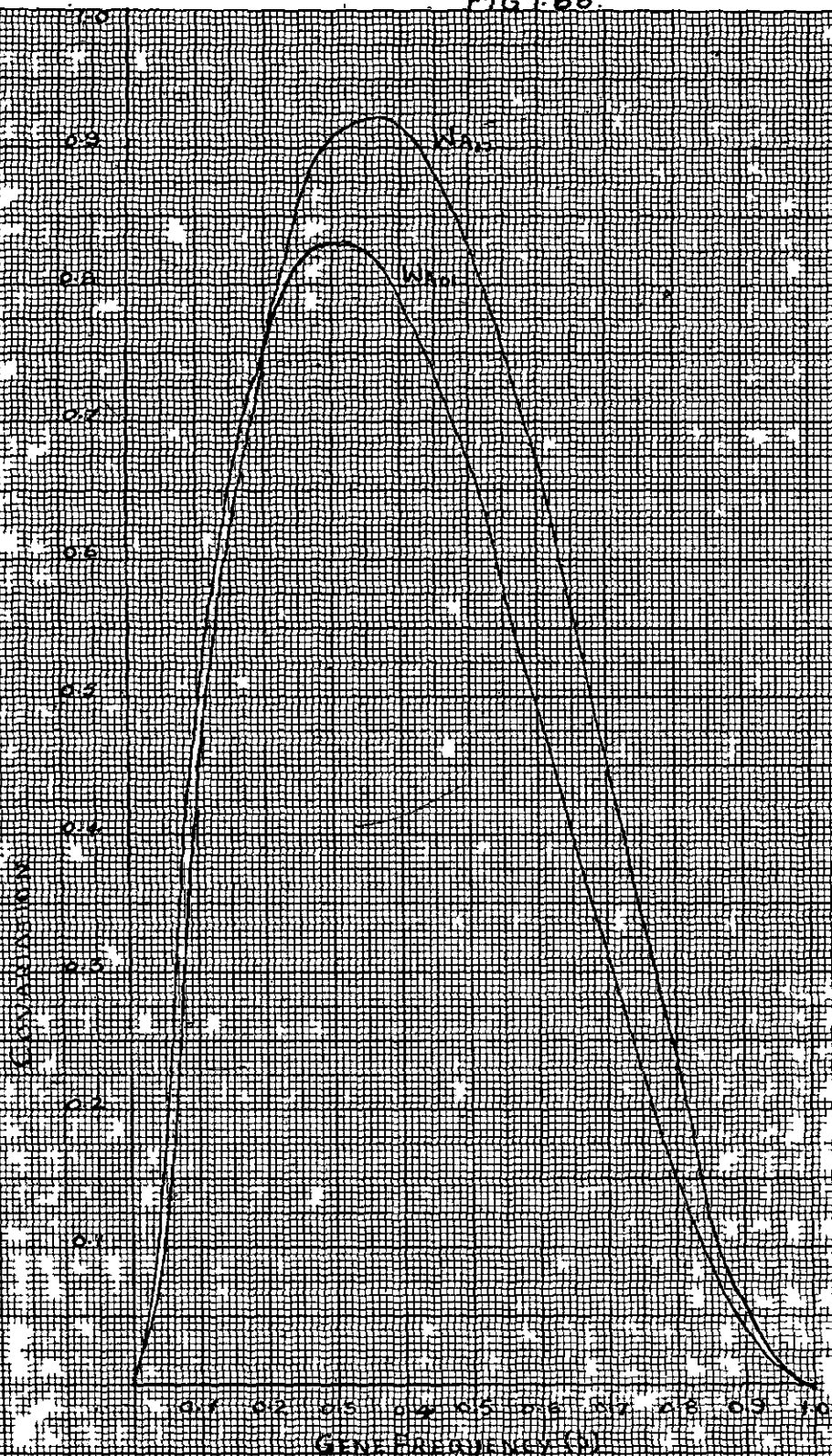
Changes in the contributions made by a gene frequency to the F_2 rank variance σ_{D_1} and σ_{D_2} according to the frequency of its dominant allele mark. Calculations are based on $h=1$.

FIG. 1.65



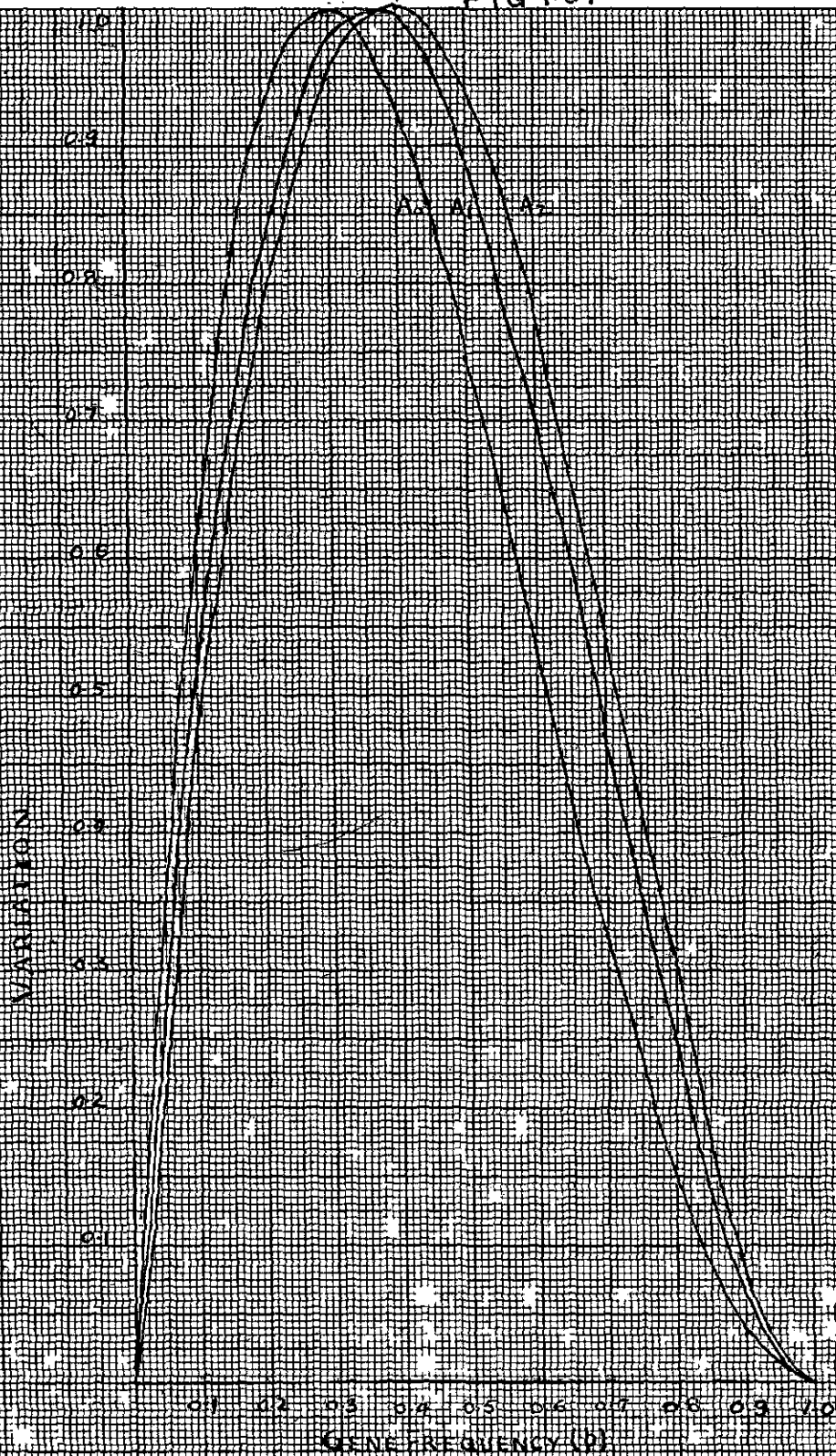
Change in the contributions made by a gene to the 2nd rank variance in A₁ and A₂, according to the frequency of its dominant allelomorph. Calculations are made with $d=h=1$.

FIG. 66.



Changes in the contributions made by a gene to the covariance W_{aa} and W_{aa}' according to the frequency of the dominant allele. Calculations are based on $h=0.1$.

FIG 1.67



Changes in the contributions made by a gene to the total genetic variation in A_1 , A_2 and A_3 according to the frequency of its dominant allelomorph. Calculations are based on $1-h-k$.

From the graphs presented before (Figs. 1.61 to 1.67) the following observations are made.

The coefficient of d^2 is more in the first rank variance and covariance than in the second rank variance (Fig. 1.61) for $0 < p < 1$. The difference in the two coefficients is more for intermediate values of p , being maximum at $p = 0.4$ approximately and less at extreme values of gene frequency. The coefficient of h^2 is, however, less in the first rank variance than in the second rank variance and covariance (Fig. 1.62). The difference is quite substantial between the two rank variances. The coefficient of h^2 in the covariance is more than that in the second rank variance for $0 < p < 0.25$, but is less than that in the second rank variance for $p > 0.25$. The coefficient of dh is positive in the first rank variance and covariance but negative in the second rank variance (Fig. 1.63). The coefficient is more in the covariance than in the first rank variance for $0 < p < 0.5$, whereas the order is reversed for $p > 0.5$. At $p = 0.67$ approximately, the dh term vanishes in the first rank variance and also in the covariance. In the second rank variance, the coefficient, negative in value, is maximum for $p = 0.7$.

The first rank variance increases due to positive assortative mating, variance in A_1 being less than that in A_2 (Fig. 1.64). The increase is very small for values of p less than 0.2 and greater than 0.7. It is substantial for values of p between 0.35 and 0.6. In the second rank variance the

situation is, however, reversed, variance in A_1 being more than that in A_2 (Fig. 1.65). The difference increases rapidly upto $p = 0.4$ and then slowly decreases. The covariance $W_{A_{12}}$ is more than the covariance $W_{A_{01}}$ (Fig. 1.66). The difference is almost negligible for values of p less than 0.25. The total genetic variance is, however, decreasing from generation to generation for values of p less than 0.3, but it is increasing from generation to generation for values of p greater than 0.3 (Fig. 1.67). The decrease or increase from A_0 to A_1 is found to be more than that from A_1 to A_2 .

C H A P T E R - II

Genetic variation with any number of loci segregating

Consider a random mating population with two loci, A-a and B-b, segregating. The nine possible genotypes are in the proportions as given below:-

AABB	-	$p_a^2 p_b^2$
AABb	-	$2 p_a^2 p_b q_b$
AAbb	-	$p_a^2 q_b^2$
AaBB	-	$2 p_a q_a p_b^2$
AaBb	-	$4 p_a q_a p_b q_b$
Aabb	-	$2 p_a q_a q_b^2$
aaBB	-	$q_a^2 p_b^2$
aaBb	-	$2 q_a^2 p_b q_b$
aabb	-	$q_a^2 q_b^2$

where p_a and p_b are respectively the gene frequencies of A and B and $q_a = 1 - p_a$; $q_b = 1 - p_b$ are respectively those of a and b. We will assume that the two pairs of genes are independent in action and distribution i.e., there is no epistasis and linkage. The following four types of dominance situations can be considered:

- (i) No dominance
- (ii) 'A' is completely dominant over 'a' and there is no dominance in B-b,
- (iii) 'A' is completely dominant over 'a' and 'B' is completely dominant over 'b', and

- (iv) 'a' is completely dominant over 'A' and 'B'
is completely dominant over 'b'.

2.1 No dominance

In this case, all the nine possible genotypes will be phenotypically recognisably distinct leading to nine intra-mating groups, each group consisting of identical genotypes. It may be remarked that there will be five intra-mating groups if we also assume the equality of additive effects of the genes as considered by Breese (1956) with an additional restriction $p_a = q_a = p_b = q_b = \frac{1}{2}$. The tendency to positive assortative mating will yield the mating types with the corresponding frequencies as given below :-

<u>Mating type</u>	<u>Frequency</u>
AABB x AABB	$p_a^2 p_b^2$
AABb x AABb	$2p_a^2 p_b q_b$
AAbb x AAbb	$p_a^2 q_b^2$
AaBB x AaBB	$2p_a q_a p_b^2$
AaBb x AaBb	$4p_a q_a p_b q_b$
Aabb x Aabb	$2p_a q_a q_b^2$
aaBB x aaBB	$q_a^2 p_b^2$
aaBb x aaBb	$2q_a^2 p_b q_b$
aabb x aabb	$q_a^2 q_b^2$

2.11 Calculation of Means, Variances and Covariance

Let $d_a, d_b, -d_a$ and $-d_b$ measure the departures of AA, BB, aa and bb respectively from the mid-parent. The frequencies,

mean values and within family variances for various mating types are obtained as given in the following table:

Table 10

Mating type	Frequency	Parental Mean	Family Mean	Within family variance
AABB x AABB	$p_a^2 p_b^2$	$d_a + d_b$	$d_a + d_b$	0
AABb x AABb	$2p_a^2 p_b q_b$	d_a	d_a	$\frac{1}{2} d_b^2$
Aabb x Aabb	$p_a^2 q_b^2$	$d_a - d_b$	$d_a - d_b$	0
AaBB x AaBB	$2p_a q_a p_b^2$	d_b	d_b	$\frac{1}{2} d_a^2$
AaBb x AaBb	$4p_a q_a p_b q_b$	0	0	$\frac{1}{2} d_a^2 + \frac{1}{2} d_b^2$
Aabb x Aabb	$2p_a q_a q_b^2$	$-d_b$	$-d_b$	$\frac{1}{2} d_a^2$
aaBB x aaBB	$q_a^2 p_b^2$	$d_b - d_a$	$d_b - d_a$	0
aaBb x aaBb	$2q_a^2 p_b q_b$	$-d_a$	$-d_a$	$\frac{1}{2} d_b^2$
aabb x aabb	$q_a^2 q_b^2$	$-d_a - d_b$	$-d_a - d_b$	0

The following results are obtained from the above table.

$$M_{A_0} = M_{A_1} = (p_a - q_a) d_a + (p_b - q_b) d_b$$

$$1V_{A_1} = W_{A_01} = 2p_a q_a d_a^2 + 2p_b q_b d_b^2$$

$$2V_{A_1} = p_a q_a d_a^2 + p_b q_b d_b^2 .$$

In particular, when $p_a = q_a = p_b = q_b = \frac{1}{2}$ as in F_2 derived from a cross between two true breeding parents, we get results identical to those obtained under selfing F_2 with no dominance.

$$\begin{aligned} \text{i.e., } M_{A_0} &= M_{A_1} = 0 \\ {}_1V_{A_1} &= {}_V_{A_0 1} = \frac{1}{4} (d_a^2 + d_b^2) \\ {}_2V_{A_1} &= \frac{1}{4} (d_a^2 + d_b^2) \end{aligned}$$

2.2 'A' is completely dominant over 'a' and there is no dominance in B-b.

In this case, the nine possible genotypes can be assorted phenotypically into six intra-mating groups as (i) AABB, AaBB (ii) AABb, AaBb (iii) AAbb, Aabb (iv) aaBB (v) aaBb and (vi) aabb. The tendency to positive assortative mating will yield the mating types with corresponding frequencies as given below :-

<u>Mating type</u>	<u>Frequency</u>
AABB x AABB	$p_a^4 p_b^4 / p_a(1+q_a)p_b^2$
AABB x AaBB	$4p_a^3 q_a p_b^4 / p_a(1+q_a)p_b^2$
AaBB x AaBB	$4p_a^2 q_a^2 p_b^4 / p_a(1+q_a)p_b^2$
AABb x AABb	$4p_a^4 p_b^2 q_b^2 / 2p_a(1+q_a)p_b q_b$
AABb x AaBb	$16p_a^3 q_a p_b^2 q_b^2 / 2p_a(1+q_a) p_b q_b$
AaBb x AaBb	$16p_a^2 q_a^2 p_b^2 q_b^2 / 2p_a(1+q_a) p_b q_b$
AAbb x AAbb	$p_a^4 q_b^4 / p_a(1+q_a) q_b^2$
AAbb x Aabb	$4p_a^3 q_a q_b^4 / p_a(1+q_a) q_b^2$
Aabb x Aabb	$4p_a^2 q_a^2 q_b^4 / p_a(1+q_a) q_b^2$
aaBB x aaBB	$q_a^2 p_b^2$
aaBb x aaBb	$2q_a^2 p_b q_b$
aabb x aabb	$q_a^2 q_b^2$

where $p_a(1+q_a)p_b^2$, $2p_a(1+q_a)p_b q_b$ and $p_a(1+q_a) q_b^2$ are the total frequencies of groups (i), (ii) and (iii) respectively.

2.21 Calculation of Means, Variances and Covariance

Let d_a , d_b , h_a , $-d_a$ and $-d_b$ measure the departures of AA, BB, Aa, aa and bb respectively from the mid-parent. The frequencies, family means, parental mean values and the within family variances of the above mating types are given

in the following table :-

Table 11

Mating type	Frequency	Family Mean	Parental Mean	Within family variance
AABB x AABB	k_2/k	$d_a + d_b$	$d_a + d_b$	0
AABB x AaBB	$4k_1 k_2/k$	$\frac{1}{2}(d_a + h_a) + d_b$	$\frac{1}{2}(d_a + h_a) + d_b$	$\frac{1}{4}(d_a - h_a)^2$
AaBB x AaBB	$4k_1^2 k_2/k$	$\frac{1}{2}h_a + d_b$	$h_a + d_b$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$
aaBb x aaBb	$2k_2^2/k$	d_a	d_a	$\frac{1}{2}d_b^2$
AABb x AaBb	$8k_1 k_2^2/k$	$\frac{1}{2}(d_a + h_a)$	$\frac{1}{2}(d_a + h_a)$	$\frac{1}{4}(d_a - h_a)^2 + \frac{1}{2}d_b^2$
AaBb x AaBb	$8k_1^2 k_2^2/k$	$\frac{1}{2}h_a$	h_a	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2 + \frac{1}{2}d_b^2$
AAbb x AAbb	k_2^3/k	$d_a - d_b$	$d_a - d_b$	0
AAbb x Aabb	$4k_1 k_2^3/k$	$\frac{1}{2}(d_a + h_a) - d_b$	$\frac{1}{2}(d_a + h_a) - d_b$	$\frac{1}{4}(d_a - h_a)^2$
Aabb x Aabb	$4k_1^2 k_2^3/k$	$\frac{1}{2}h_a - d_b$	$h_a - d_b$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$
aaBB x aaBB	$k_1 k_2^2 (1 + 2k_1)/k$	$d_b - d_a$	$d_b - d_a$	0
aaBb x aaBb	$2k_1^2 k_2^2 (1 + 2k_1)/k$	$-d_a$	$-d_a$	$\frac{1}{2}d_b^2$
aabb x aabb	$k_1^2 k_2^3 (1 + 2k_1)/k$	$-d_a - d_b$	$-d_a - d_b$	0

Where $k = \frac{p_a(1+q_a)p_b q_b}{p_a^4 p_b^4}$, $k_1 = q_a / p_a$ and $k_2 = q_b / p_b$

are introduced to reduce the algebra involved in calculating various statistics.

The following results are obtained:

$$M_{A0} = (p_a - q_a)d_a + 2p_a q_a h_a + (p_b - q_b) d_b$$

$$M_{A1} = (p_a - q_a) d_a + \frac{2p_a q_a}{1 + q_a} h_a + (p_b - q_b) d_b$$

$$1V_{A1} = \frac{p_a q_a (3q_a + 1)}{1 + q_a} d_a^2 + \frac{p_a q_a (1 + q_a - 4p_a q_a)}{(1 + q_a)^2} h_a^2 \\ + \frac{2p_a q_a (3q_a - 1)}{1 + q_a} d_a h_a + 2p_b q_b d_b^2$$

$$2V_{A1} = p_a q_a d_a^2 + \frac{p_a q_a}{1 + q_a} h_a^2 - \frac{2p_a^2 q_a}{1 + q_a} d_a h_a + p_b q_b d_b^2$$

$$W_{A01} = \frac{p_a q_a (3q_a + 1)}{1 + q_a} d_a^2 + \frac{p_a q_a (1 + q_a - 4p_a q_a)}{1 + q_a} h_a^2 \\ + \frac{2p_a q_a [2q_a (1 + q_a) - 1]}{1 + q_a} d_a h_a + 2p_b q_b d_b^2$$

In particular, when $p_a = q_a = p_b = q_b = \frac{1}{2}$, we get

$$M_{A0} = \frac{1}{2} h_a$$

$$M_{A1} = \frac{1}{2} h_a$$

$$V_{A0} = \frac{1}{2} (d_a^2 + d_b^2) + \frac{1}{2} h_a^2$$

$$1V_{A1} = \frac{5}{12} d_a^2 + \frac{1}{2} d_b^2 + \frac{1}{18} h_a^2 + \frac{1}{6} d_a h_a$$

$$2V_{A1} = \frac{1}{2} d_a^2 + \frac{1}{2} d_b^2 + \frac{1}{6} h_a^2 - \frac{1}{6} d_a h_a$$

Therefore,

$$V_{A1} = \frac{1}{2} d_a^2 + \frac{1}{2} d_b^2 + \frac{2}{9} h_a^2$$

$$W_{A01} = \frac{5}{12} d_a^2 + \frac{1}{2} d_b^2 + \frac{1}{12} h_a^2 + \frac{1}{6} d_a h_a$$

Comparing V_{A_0} and V_{A_1} we find that the coefficient of d_a^2 is increased from $\frac{1}{4}$ to $\frac{1}{3}$ and the coefficient of d_b^2 is increased from $\frac{1}{4}$ to $\frac{2}{3}$ whereas the coefficient of h_a^2 is decreased from $\frac{1}{4}$ to $\frac{2}{9}$.

Also when $p_a = p_b = \frac{2}{3}$ and $q_a = q_b = \frac{1}{3}$ the first rank variance is given by

$$1V_{A_1} = \frac{1}{3} d_a^2 + \frac{4}{9} d_b^2 + \frac{1}{18} h_a^2, \text{ so that the } d_a h_a \text{ vanishes.}$$

2.3 'A' is completely dominant over 'a' and 'B' is completely dominant over 'b'

In this case, the nine possible genotypes can be assorted phenotypically into four intra-mating groups as (i) AABB, AABb, AaBB, AaBb (ii) AAbb, Aabb (iii) aaBB, aaBb and (iv) aabb. In addition if we assume the equality of d increments there would be three intra-mating groups. This situation already considered by Breese (1956) with additional restriction $p_a = q_a = p_b = q_b = \frac{1}{2}$ will not be dealt with here. The tendency to positive assortative mating will yield the mating types with the corresponding frequencies as given below :-

<u>Mating type</u>	<u>Frequency</u>
AABB x AABB	$p_a^4 p_b^4 / p_a p_b (1+q_a)(1+q_b)$
AABB x AABb	$4p_a^4 p_b^3 q_b / p_a p_b (1+q_a)(1+q_b)$
AABB x AaBB	$4p_a^3 q_a p_b^4 / p_a p_b (1+q_a)(1+q_b)$
AABB x AaBb	$8p_a^3 q_a p_b^3 q_b / p_a p_b (1+q_a)(1+q_b)$
AABb x AABb	$4p_a^4 p_b^2 q_b^2 / p_a p_b (1+q_a)(1+q_b)$
AABb x AaBB	$8p_a^3 q_a p_b^3 q_b / p_a p_b (1+q_a)(1+q_b)$
AABb x AaBb	$16p_a^3 q_a p_b^2 q_b^2 / p_a p_b (1+q_a)(1+q_b)$
AaBB x AaBB	$4p_a^2 q_a^2 p_b^4 / p_a p_b (1+q_a)(1+q_b)$
AaBB x AaBb	$16p_a^2 q_a^2 p_b^3 q_b / p_a p_b (1+q_a)(1+q_b)$
AaBb x AaBb	$16p_a^2 q_a^2 p_b^2 q_b^2 / p_a p_b (1+q_a)(1+q_b)$
Aabb x Aabb	$p_a^4 q_b^4 / p_a (1+q_a) q_b^2$
Aabb x Aabb	$4p_a^3 q_a q_b^4 / p_a (1+q_a) q_b^2$
Aabb x Aabb	$4p_a^2 q_a^2 q_b^4 / p_a (1+q_a) q_b^2$
aaBB x aaBB	$q_a^4 p_b^4 / q_a^2 p_b (1+q_b)$
aaBB x aaBb	$4q_a^4 p_b^3 q_b / q_a^2 p_b (1+q_b)$
aaBb x aaBb	$4q_a^4 p_b^2 q_b^2 / q_a^2 p_b (1+q_b)$
aabb x aabb	$q_a^2 q_b^2$

where $p_a p_b (1+q_a)(1+q_b)$ is the total frequency of the first intra-mating group, $p_a(1+q_a)q_b^2$ that of the second and $q_a^2 p_b(1+q_b)$ is that of the third.

2.31 Calculation of Means, Variances and Covariance

Let $d_a, d_b, h_a, h_b, -d_a$ and $-d_b$ measure the departures of AA, BB, Aa, Bb; aa and bb respectively from the mid-parent. The frequencies, family means, parental mean values and the within family variances for the above mating types are given in Table 12.

Table 12

Mating type	Frequency	Family Mean	Parental Mean	Within family variance
AABB x AABB	$1/k$	$d_a + d_b$	$d_a + d_b$	0
AABB x AABb	$4k_2/k$	$d_a + \frac{1}{2}(d_b + h_b)$	$d_a + \frac{1}{2}(d_b + h_b)$	$\frac{1}{4}(d_b - h_b)^2$
AABB x AaBB	$4k_1/k$	$\frac{1}{2}(d_a + h_a) + d_b$	$\frac{1}{2}(d_a + h_a) + d_b$	$\frac{1}{4}(d_a - h_a)^2$
AABB x AaBb	$8k_1k_2/k$	$\frac{1}{2}(d_a + h_a + d_b + h_b)$	$\frac{1}{2}(d_a + h_a + d_b + h_b)$	$\frac{1}{4}(d_a - h_a)^2 + \frac{1}{4}(d_b - h_b)^2$
AABb x AABB	$4k_2^2/k$	$d_a + \frac{1}{2}h_b$	$d_a + h_b$	$\frac{1}{4}d_b^2 + \frac{1}{4}h_b^2$
AABb x AaBB	$8k_1k_2/k$	$\frac{1}{2}(d_a + h_a + d_b + h_b)$	$\frac{1}{2}(d_a + h_a + d_b + h_b)$	$\frac{1}{4}(d_a - h_a)^2 + \frac{1}{4}(d_b - h_b)^2$
AABb x AaBb	$16k_1k_2^2/k$	$\frac{1}{2}(d_a + h_a + h_b)$	$\frac{1}{2}(d_a + h_a) + h_b$	$\frac{1}{4}(d_a - h_a)^2 + \frac{1}{4}(d_b^2) + \frac{1}{4}(h_b^2)$
AaBB x AaBB	$4k_1^2/k$	$\frac{1}{2}h_a + d_b$	$h_a + d_b$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$
AaBB x AaBb	$16k_1^2k_2/k$	$\frac{1}{2}(h_a + d_b + h_b)$	$h_a + \frac{1}{2}(d_b + h_b)$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2 + \frac{1}{4}(d_b - h_b)^2$
AaBb x AaBb	$16k_1^2k_2^2/k$	$\frac{1}{2}(h_a + h_b)$	$h_a + h_b$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2 + \frac{1}{4}d_b^2 + \frac{1}{4}h_b^2$
AAbb x AAbb	$k_2^2(1+2k_2)/k$	$d_a = d_b$	$d_a - d_b$	0
AAbb x Aabb	$4k_2^2k_1(1+2k_2)/k$	$\frac{1}{2}(d_a + h_a) - d_b$	$\frac{1}{2}(d_a + h_a) - d_b$	$\frac{1}{4}(d_a - h_a)^2$
Aabb x Aabb	$4k_2^2k_1^2(1+2k_2)/k$	$\frac{1}{2}h_a - d_b$	$h_a - d_b$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$
aaBB x aaBB	$k_1^2(1+2k_1)/k$	$d_b - d_a$	$d_b - d_a$	0
aaBB x aaBb	$4k_1^2k_2(1+2k_1)/k$	$\frac{1}{2}(d_b + h_b) - d_a$	$\frac{1}{2}(d_b + h_b) - d_a$	$\frac{1}{4}(d_b - h_b)^2$
aaBb x aaBb	$4k_1^2k_2^2(1+2k_1)/k$	$\frac{1}{2}h_b - d_a$	$h_b - d_a$	$\frac{1}{4}d_b^2 + \frac{1}{4}h_b^2$
aabb x aabb	$\frac{2}{k}k_1^2k_2^2(1+2k_1)(1+2k_2)$	$-d_a - d_b$	$-d_a - d_b$	0

where $k = p_a p_b (1+q_a)(1+q_b) / p_a^4 p_b^4$, $k_1 = q_a / p_a$ and

$k_2 = q_b / p_b$. The k 's are introduced for simplification of the algebra. The following results after converting back to p 's and q 's are obtained,

$$M_{A0} = (p_a - q_a)d_a + 2p_a q_a h_a + (p_b - q_b)d_b + 2p_b q_b h_b$$

$$M_{A1} = (p_a - q_a)d_a + \frac{2p_a q_a}{1+q_a} h_a + (p_b - q_b)d_b + \frac{2p_b q_b}{1+q_b} h_b$$

$$1^V_{A1} = \frac{p_a q_a (3q_a + 1)}{1 + q_a} d_a^2 + \frac{p_a q_a (1+q_a - 4p_a q_a)}{(1+q_a)^2} h_a^2 +$$

$$\frac{2p_a q_a (3q_a - 1)}{1 + q_a} d_a h_a + \frac{p_b q_b (3q_b + 1)}{1+q_b} d_b^2 +$$

$$\frac{p_b q_b (1 + q_b - 4p_b q_b)}{(1 + q_b)^2} h_b^2 + \frac{2p_b q_b (3q_b - 1)}{1 + q_b} d_b h_b$$

$$2^V_{A1} = p_a q_a d_a^2 + \frac{p_a q_a}{1+q_a} h_a^2 - \frac{2p_a^2 q_a}{1+q_a} d_a h_a$$

$$+ p_b q_b d_b^2 + \frac{p_b q_b}{1+q_b} h_b^2 - \frac{2p_b^2 q_b}{1+q_b} d_b h_b$$

$$W_{A01} = \frac{p_a q_a (3q_a + 1)}{1 + q_a} d_a^2 + \frac{p_a q_a (1+q_a - 4p_a q_a)}{1 + q_a} h_a^2$$

$$+ \frac{2p_a q_a \sqrt{2q_a(1+q_a) - 1}}{1 + q_a} d_a h_a + \frac{p_b q_b (3q_b + 1)}{1 + q_b} d_b^2$$

$$+ \frac{p_b q_b (1+q_b - 4p_b q_b)}{1 + q_b} h_b^2 + \frac{2p_b q_b \sqrt{2q_b(1+q_b) - 1}}{1 + q_b} d_b h_b$$

In particular, when $p_a = q_a = p_b = q_b = \frac{1}{2}$ as in F_2 , we get

$$M_{A_0} = \frac{1}{2}(h_a + h_b)$$

$$M_{A_1} = \frac{1}{2}(h_a + h_b)$$

$$1V_{A_1} = \frac{5}{12}(d_a^2 + d_b^2) + \frac{1}{18}(h_a^2 + h_b^2) + \frac{1}{6}(d_a h_a + d_b h_b)$$

$$2V_{A_1} = \frac{1}{4}(d_a^2 + d_b^2) + \frac{1}{6}(h_a^2 + h_b^2) - \frac{1}{6}(d_a h_a + d_b h_b)$$

$$W_{A_0 1} = \frac{5}{12}(d_a^2 + d_b^2) + \frac{1}{12}(h_a^2 + h_b^2) + \frac{1}{6}(d_a h_a + d_b h_b)$$

In this case, the total variance is given by

$$V_{A_1} = \frac{5}{9}(d_a^2 + d_b^2) + \frac{2}{9}(h_a^2 + h_b^2) \text{ as against the}$$

parental variance

$$V_{A_0} = \frac{1}{2}(d_a^2 + d_b^2) + \frac{1}{2}(h_a^2 + h_b^2)$$

It is interesting to note that though each of the first and second rank variances involve the product term $d_a h_a$ and $d_b h_b$, the total genetic variance does not. Further, comparing V_{A_1} and V_{A_0} we find that positive assortative mating with complete dominance for either of the genes leads to increased additive genetic variance, but decreased variance due to dominance action.

With $p_a = p_b = \frac{1}{2}$ and $q_a = q_b = \frac{1}{2}$, we find that in the first rank variance the product term disappears and the value is given by $1V_{A_1} = \frac{1}{3}(d_a^2 + d_b^2) + \frac{1}{18}(h_a^2 + h_b^2)$.

2.4 'a' is completely dominant over 'A' and
'B' is completely dominant over 'b'

In this case, the nine possible genotypes can be assorted phenotypically into four intra-mating groups as (i) AaBB, AaBb, aaBB, aaBb (ii) AaBB, AaBb (iii) Aabb, aabb and (iv) AAAbb. The tendency to positive assortative mating will yield the mating types with the corresponding frequencies as given in Table below:

<u>Mating type</u>	<u>Frequency</u>
AaBB x AaBB	$4p_a^2 q_a^2 p_b^4 / (1+p_a) q_a p_b (1+q_b)$
AaBB x aaBB	$4p_a q_a^3 p_b^4 / (1+p_a) q_a p_b (1+q_b)$
AaBB x AaBb	$16p_a^2 q_a^2 p_b^3 q_b / (1+p_a) q_a p_b (1+q_b)$
AaBB x aaBb	$8p_a q_a^3 p_b^3 q_b / (1+p_a) q_a p_b (1+q_b)$
aaBB x aaBB	$q_a^4 p_b^4 / (1+p_a) q_a p_b (1+q_b)$
aaBB x AaBb	$8p_a q_a^3 p_b^3 q_b / (1+p_a) q_a p_b (1+q_b)$
aaBB x aaBb	$4q_a^4 p_b^3 q_b / (1+p_a) q_a p_b (1+q_b)$
AaBb x AaBb	$16p_a^2 q_a^2 p_b^2 q_b^2 / (1+p_a) q_a p_b (1+q_b)$
AaBb x aaBb	$16p_a q_a^3 p_b^2 q_b^2 / (1+p_a) (1+q_b) q_a p_b$
aaBb x aaBb	$4q_a^4 p_b^2 q_b^2 / (1+p_a) (1+q_b) q_a p_b$
AABB x AABB	$p_a^4 p_b^4 / p_a^2 p_b (1+q_b)$
AABB x AABb	$4p_a^4 p_b^3 q_b / p_a^2 p_b (1+q_b)$
AABb x AABb	$4p_a^4 p_b^2 q_b^2 / p_a^2 p_b (1+q_b)$
Aabb x Aabb	$4p_a^2 q_a^2 q_b^4 / (1+p_a) q_a q_b^2$
Aabb x aabb	$4p_a q_a^3 q_b^4 / (1+p_a) q_a q_b^2$
aabb x aabb	$q_a^4 q_b^4 / (1+p_a) q_a q_b^2$
AAbb x AAbb	$p_a^2 q_b^2$

where $(1+p_a)q_a p_b(1+q_b)$, $p_a^2 p_b(1+q_b)$ and $(1+p_a)q_a q_b^2$ are the total frequencies of the intra-mating groups (i), (ii) and (iii) respectively.

2.41 Calculation of Means, Variances and Covariance

Let d_a , d_b , h_a , h_b , $-d_a$ and $-d_b$ measure the departures of AA, BB, Aa, Bb, aa and bb from the mid-parent. The frequencies, family means, parental mean values and the within family variances for the above mating types are given in Table 13.

Table 13

Mating type	Frequency	Family Mean	Parental Mean value	Within family variance
AaBB x AaBB	$4k_1^2 / k$	$\frac{1}{2}h_a + d_b$	$h_a + d_b$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$
AaBB x aaBB	$4k_1^3 / k$	$\frac{1}{2}(h_a - d_a) + d_b$	$\frac{1}{2}(h_a - d_a) + d_b$	$\frac{1}{4}(d_a + h_a)^2$
AaBB x AaBb	$16k_1^2 k_2 / k$	$\frac{1}{2}(h_a + d_b + h_b)$	$h_a + \frac{1}{2}(d_b + h_b)$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$ $+ \frac{1}{4}(d_b - h_b)^2$
AaBB x aaBb	$8k_1^3 k_2 / k$	$\frac{1}{2}(h_a - d_a + d_b + h_b)$	$\frac{1}{2}(h_a - d_a)$ $+ \frac{1}{2}(d_b + h_b)$	$\frac{1}{4}(d_a + h_a)^2$ $+ \frac{1}{4}(d_b - h_a)^2$
aaBB x aaBB	k_1^4 / k	$d_b - d_a$	$d_b - d_a$	0
aaBB x AaBb	$8k_1^3 k_2 / k$	$\frac{1}{2}(h_a - d_a + d_b + h_b)$	$\frac{1}{2}(h_a - d_a)$ $+ \frac{1}{2}(d_b + h_b)$	$\frac{1}{4}(d_a + h_a)^2$ $+ \frac{1}{4}(d_b - h_b)^2$
aaBB x aaBb	$4k_1^4 k_2 / k$	$\frac{1}{2}(d_b + h_b) - d_a$	$\frac{1}{2}(d_b + h_b) - d_a$	$\frac{1}{4}(d_b - h_b)^2$
AaBb x AaBb	$16k_1^2 k_2^2 / k$	$\frac{1}{2}(h_a + h_b)$	$h_a + h_b$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$ $+ \frac{1}{4}d_b^2 + \frac{1}{4}h_b^2$
AaBb x aaBb	$16k_1^3 k_2^2 / k$	$\frac{1}{2}(h_a - d_a + h_b)$	$\frac{1}{2}(h_a - d_a) + h_b$	$\frac{1}{4}(d_a + h_a)^2$ $+ \frac{1}{4}d_b^2 + \frac{1}{4}h_b^2$
aaBb x aaBb	$4k_1^4 k_2^2 / k$	$\frac{1}{2}h_b - d_a$	$h_b - d_a$	$\frac{1}{4}d_b^2 + \frac{1}{4}h_b^2$
AABB x AABB	$k_1(2+k_1) / k$	$d_a + d_b$	$d_a + d_b$	0
AABB x AABb	$4k_1 k_2 (2+k_1) / k$	$d_a + \frac{1}{2}(d_b + h_b)$	$d_a + \frac{1}{2}(d_b + h_b)$	$\frac{1}{4}(d_b - h_b)^2$
AABb x AABb	$4k_1 k_2^2 (2+k_1) / k$	$d_a + \frac{1}{2}h_b$	$d_a + h_b$	$\frac{1}{4}d_b^2 + \frac{1}{4}h_b^2$
Aabb x Aabb	$4k_1^2 k_2^2 (1+2k_2) / k$	$\frac{1}{2}h_a - d_b$	$h_a - d_b$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$
Aabb x aabb	$4k_1^3 k_2^2 (1+2k_2) / k$	$\frac{1}{2}(h_a - d_a) - d_b$	$\frac{1}{2}(h_a - d_a) - d_b$	$\frac{1}{4}(d_a + h_a)^2$
aabb x aabb	$k_1^4 k_2^2 (1+2k_2) / k$	$-d_a - d_b$	$-d_a - d_b$	0
Aabb x AAbb	$k_1 k_2^2 (2+k_1)(1+2k_2) / k$	$d_a - d_b$	$d_a - d_b$	0

where $k = (1+p_a)q_a p_b (1+q_b) / p_a^4 p_b^4$, $k_1 = q_a / p_a$ and $k_2 = q_b / p_b$, are introduced to reduce the algebra involved in calculating various statistics.

The following results are obtained after converting back into p's and q's.

$$M_{A0} = (p_a - q_a)d_a + 2p_a q_a h_a + (p_b - q_b)d_b + 2p_b q_b h_b$$

$$M_{A1} = (p_a - q_a)d_a + \frac{2p_a q_a}{1+p_a} h_a + (p_b - q_b)d_b + \frac{2p_b q_b}{1+q_b} h_b$$

$$\begin{aligned} 1^V_{A1} = & \frac{p_a q_a (3p_a + 1)}{1 + p_a} d_a^2 + \frac{p_a q_a (1 + p_a - 4p_a q_a)}{(1 + p_a)^2} h_a^2 \\ & - \frac{2p_a q_a (3p_a - 1)}{(1 + p_a)} d_a h_a + \frac{p_b q_b (3q_b + 1)}{(1 + q_b)} d_b^2 \\ & + \frac{p_b q_b (1 + q_b - 4p_b q_b)}{(1 + q_b)^2} h_b^2 + \frac{2p_b q_b (3q_b - 1)}{(1 + q_b)} d_b h_b \end{aligned}$$

$$\begin{aligned} 2^V_{A1} = & p_a q_a d_a^2 + \frac{p_a q_a}{1 + p_a} h_a^2 + \frac{2p_a q_a^2}{1 + p_a} d_a h_a \\ & + p_b q_b d_b^2 + \frac{p_b q_b}{1 + q_b} h_b^2 + \frac{2p_b^2 q_b}{1 + q_b} d_b h_b \end{aligned}$$

$$\begin{aligned} W_{A01} = & \frac{p_a q_a (3p_a + 1)}{1 + p_a} d_a^2 + \frac{p_a q_a (1 + p_a - 4p_a q_a)}{1 + p_a} h_a^2 \\ & - \frac{2p_a q_a [2p_a (1 + p_a) - 1]}{1 + p_a} d_a h_a + \frac{p_b q_b (3q_b + 1)}{1 + q_b} d_b^2 \\ & + \frac{p_b q_b (1 + q_b - 4p_b q_b)}{1 + q_b} h_b^2 + \frac{2p_b q_b [2q_b (1 + q_b) - 1]}{1 + q_b} d_b h_b \end{aligned}$$

In particular with $p_a = q_a = p_b = q_b = \frac{1}{2}$,
we get

$$M_{A_0} = \frac{1}{2} (h_a + h_b)$$

$$M_{A_1} = \frac{1}{2} (h_a + h_b)$$

$$1V_{A_1} = \frac{5}{12} (d_a^2 + d_b^2) + \frac{1}{18} (h_a^2 + h_b^2) + \frac{1}{6} (d_b h_b - d_a h_a)$$

$$2V_{A_1} = \frac{1}{2} (d_a^2 + d_b^2) + \frac{1}{6} (h_a^2 + h_b^2) + \frac{1}{6} (d_a h_a - d_b h_b)$$

$$W_{A_01} = \frac{5}{12} (d_a^2 + d_b^2) + \frac{1}{12} (h_a^2 + h_b^2) + \frac{1}{6} (d_b h_b - d_a h_a)$$

In this case also all the conclusions drawn in the previous section (2.3) will hold good. The only change in this case is that the sign of the product term $d_a h_a$ is changed.

2.5 Results with any number of loci

The results obtained in the previous as well as in the present chapters suggest interesting generalisation to any number of loci. Provided the genes involved are independent in action and distribution, it has been found that the contribution of each of the genes involved to the means, variances and covariance depends only on the dominance situation characteristic of that gene, being unaffected by the dominance situation of the other genes and further that these contributions are simply additive. The contribution is also similar in the form if two genes are exhibiting the same type of dominance.

If each of the genes A-a, B-b, C-c, occurring respectively, with gene frequencies p_a, p_b, p_c, \dots in a random

mating population exhibits no dominance, the positive assortative mating would result in the following expressions for the first and second degree statistics.

$$M_{A_0} = M_{A_1} = \sum_a (p_a - q_a) d_a$$

$$1^V_{A_1} = W_{A_0 1} = \sum_a 2p_a q_a d_a^2$$

$$2^V_{A_1} = \sum_a p_a q_a d_a^2$$

where \sum means summation over all genes.

In particular, if positive assortative mating is resorted to in F_2 , we get

$$1^V_{A_1} = W_{A_0 1} = \frac{1}{2}D$$

$$2^V_{A_1} = \frac{1}{4}D$$

where $D = \sum_a d_a^2$, as given by Mather (1949)

If each of the genes involved exhibits complete dominance in the positive direction, the positive assortative mating in a random mating population would result in the following expressions for various first and second degree statistics.

$$M_{A_0} = \sum_a (p_a - q_a) d_a + \sum_a 2p_a q_a h_a$$

$$M_{A_1} = \sum_a (p_a - q_a) d_a + \sum_a \frac{2p_a q_a}{1 + q_a} h_a$$

$$1^V_{A_1} = \sum_a \frac{p_a q_a (3q_a + 1)}{1 + q_a} d_a^2 + \sum_a \frac{p_a q_a (1 + q_a - 4p_a q_a)}{(1 + q_a)^2} h_a^2$$

$$+ \sum_a \frac{2p_a q_a (3q_a - 1)}{1 + q_a} d_a h_a$$

$$\begin{aligned}
 2V_{A1} &= \sum_a p_a q_a d_a^2 + \sum_a \frac{p_a q_a}{1+q_a} h_a^2 - \sum_a \frac{2p_a^2 q_a}{1+q_a} d_a h_a \\
 W_{A01} &= \sum_a \frac{p_a q_a (3q_a + 1)}{1+q_a} d_a^2 + \sum_a \frac{p_a q_a (1+q_a - 4p_a q_a)}{1+q_a} h_a^2 \\
 &\quad + \sum_a \frac{2p_a q_a [2q_a (1+q_a) - 1]}{1+q_a} d_a h_a
 \end{aligned}$$

In particular, if the random mating population is an F_2 , we get

$$\begin{aligned}
 V_{A1} &= 1V_{A1} + 2V_{A2} \\
 &= \left[\frac{5}{12} \sum_a d_a^2 + \frac{1}{18} \sum_a h_a^2 + \frac{1}{6} \sum_a d_a h_a \right] \\
 &\quad + \left[\frac{1}{4} \sum_a d_a^2 + \frac{1}{6} \sum_a h_a^2 - \frac{1}{6} \sum_a d_a h_a \right] \\
 &= \frac{2}{3} \sum_a d_a^2 + \frac{2}{9} \sum_a h_a^2 \\
 &= \frac{2}{3} D + \frac{2}{9} H, \text{ in the notation of Mather (1949).}
 \end{aligned}$$

In this particular case, we can also express the various second degree statistics in terms of D and H, but the definition of D would change from one statistic to another. Thus

$$\begin{aligned}
 1V_{A1} &= \frac{5}{12} D' + \frac{7}{180} H \quad \text{where } D' = \sum_a (d_a + \frac{1}{5} h_a)^2 \\
 2V_{A1} &= \frac{1}{4} D'' + \frac{5}{36} H \quad \text{where } D'' = \sum_a (d_a - \frac{1}{5} h_a)^2 \\
 \text{and } W_{A01} &= \frac{5}{12} D' + \frac{1}{15} H.
 \end{aligned}$$

CHAPTER IIIThe Effect of Linkage

When two genes are located on the same chromosome, they have a tendency to remain together during the process of inheritance rather than assort independently of each other. This tendency is known as "linkage". With two gene pairs A-a and B-b, when the genes come from the same parent (AABB x aabb) they tend to remain together and enter the same gamete. The linkage between A and B is then said to be in "coupling phase", whereas if these genes come from different parents (AAbb x aaBB) they tend to remain apart and enter different gametes. This is known as "repulsion phase" of linkage. The intensity of linkage is measured by p , the probability of recombination with which the homologous chromosomes exchange parts at the time of meiosis or in other words the probability of crossing over.

In the following discussion we assume that there is no epistatic interaction and that the population is either a random mating population with $p_a = q_a = p_b = q_b = \frac{1}{2}$ or it is an F_2 derived from a cross between two true breeding parents. With the linkage in coupling phase the ten possible genotypes occur with frequencies as given below.

<u>Genotype</u>	<u>Frequency</u>
AB / AB	$\frac{1}{4}q^2$
AB / Ab	$\frac{1}{2}pq$
Ab / Ab	$\frac{1}{4}p^2$
AB / aB	$\frac{1}{2}pq$
AB / ab	$\frac{1}{4}q^2$
Ab / aB	$\frac{1}{2}p^2$
Ab / ab	$\frac{1}{2}pq$
aB / aB	$\frac{1}{4}p^2$
aB / ab	$\frac{1}{2}pq$
ab / ab	$\frac{1}{4}q^2$

where $q = (1-p)$, p being the recombination fraction.

We consider the following three conditions of dominance:

- (i) No dominance
- (ii) 'A' is completely dominant over 'a' and there is no dominance in B-b.
- (iii) 'A' is completely dominant over 'a' and 'B' is completely dominant over 'b'.

3.1 No dominance

The ten genotypes can be assorted phenotypically into nine intra-mating groups since the two genotypes AB/ab and Ab/aB give the same phenotypic expression of a double heterozygote. The tendency to positive assortative mating yields the mating types with frequencies as given below.

<u>Mating type</u>	<u>Frequency</u>
AB/AB x AB/AB	$\frac{1}{4}q^2$
AB/Ab x AB/Ab	$\frac{1}{2}pq$
Ab/Ab x Ab/Ab	$\frac{1}{4}p^2$
AB/aB x AB/aB	$\frac{1}{2}pq$
AB/ab x AB/ab	$\frac{q^4}{2(p^2+q^2)}$
AB/aB x Ab/aB	$\frac{2p^2q^2}{2(p^2+q^2)}$
Ab/aB x Ab/aB	$\frac{p^4}{2(p^2+q^2)}$
Ab/ab x Ab/ab	$\frac{1}{2}pq$
aB/aB x aB/aB	$\frac{1}{4}p^2$
aB/ab x aB/ab	$\frac{1}{2}pq$
ab/ab x ab/ab	$\frac{1}{4}q^2$

3.11 Calculation of Means, Variances and Covariance

Let d_a , d_b , $-d_a$ and $-d_b$ measure the departures of AA, BB, aa and bb respectively from the mid-parent. The frequencies, mean values and within family variances are obtained as given in Table 14.

Table 14

Mating type	Frequency	Parental Means	Family Means	Within family variance
AB/AB x AB/AB	$\frac{1}{4}q^2$	d_a+d_b	d_a+d_b	0
AB/Ab x AB/Ab	$\frac{1}{2}pq$	d_a	d_a	$\frac{1}{4}d_b^2$
Ab/Ab x Ab/Ab	$\frac{1}{4}p^2$	d_a-d_b	d_a-d_b	0
AB/aB x AB/aB	$\frac{1}{2}pq$	d_b	d_b	$\frac{1}{4}d_a^2$
AB/ab x AB/ab	$q^4/2(p^2+q^2)$	0	0	$\frac{1}{4}(d_a^2+d_b^2) + (q-p)d_a d_b$
AB/ab x Ab/aB	$2p^2q^2/2(p^2+q^2)$	0	0	$\frac{1}{4}(d_a^2 + d_b^2)$
Ab/aB x Ab/aB	$p^4/2(p^2+q^2)$	0	0	$\frac{1}{4}(d_a^2+d_b^2) - (q-p)d_a d_b$
Ab/ab x Ab/ab	$\frac{1}{2}pq$	$-d_b$	$-d_b$	$\frac{1}{4}d_a^2$
aB/aB x aB/aB	$\frac{1}{4}p^2$	d_b-d_a	d_b-d_a	0
aB/ab x aB/ab	$\frac{1}{2}pq$	$-d_a$	$-d_a$	$\frac{1}{4}d_b^2$
ab/ab x ab/ab	$\frac{1}{4}q^2$	$-d_a-d_b$	$-d_a-d_b$	0

The following results are obtained:

$$M_{A_0} = M_{A_1} = 0$$

$$1V_{A_1} = W_{A_01} = \frac{1}{4} [d_a^2 + d_b^2 + 2(q-p)d_a d_b]$$

$$2V_{A_1} = \frac{1}{4} [d_a^2 + d_b^2 + 2(q-p)^2 d_a d_b]$$

Comparing these results with those obtained with no linkage

(vide 2.1), it is observed that the linkage has no effect on the mean values but it increases the variances and covariances. The increase in ${}_1V_{A_1}$ and $W_{A_0_1}$ is, however, more than that in ${}_2V_{A_1}$. It may again be noticed that these results are parallel to those obtained by Mather (1949) under selfing where the definition of D change in the second rank variance in exactly the same manner as found above.

3.2 'A' is completely dominant over 'a' and there is no dominance in B-b

In this case, the ten possible genotypes can be assorted phenotypically into six intra-mating groups as (i) AB/AB, AB/aB (ii) AB/Ab, AB/ab, Ab/aB (iii) Ab/Ab, Ab/ab (iv) aB/aB (v) aB/ab and (vi) ab/ab. The tendency to positive assortative mating will yield the mating types with the corresponding frequencies as given below.

<u>Mating type</u>	<u>Frequency</u>
AB/AB x AB/AB	$q^3/4(1+p)$
AB/AB x AB/aB	$pq^2/(1+p)$
AB/aB x AB/aB	$p^2q/(1+p)$
AB/Ab x AB/Ab	$p^2q^2/2(1-pq)$
AB/Ab x AB/ab	$pq^3/(1-pq)$
AB/Ab x Ab/aB	$p^3q/(1-pq)$
AB/ab x AB/ab	$q^4/2(1-pq)$
AB/ab x Ab/AB	$p^2q^2/(1-pq)$
Ab/aB x Ab/aB	$p^4/2(1-pq)$
Ab/Ab x Ab/Ab	$p^3/4(1+q)$
Ab/Ab x Ab/ab	$p^2q/(1+q)$
Ab/ab x Ab/ab	$pq^2/(1+q)$
aB/aB x aB/aB	$\frac{1}{4}p^2$
aB/ab x aB/ab	$\frac{1}{2}pq$
ab/ab x ab/ab	$\frac{1}{4}q^2$

3.21 Calculation of Means, Variances and Covariance

Let d_a , d_b , h_a , $-d_a$ and $-d_b$ measure the departures of AA, BB, Aa, aa and bb respectively from the mid-parent. The frequencies, mean values and within family variances are obtained as given in Table 15.

Table 15

Mating type	Frequency	Parental Mean	Family Mean	Within family variance
AB/AB x AB/AB	$q^3/4(1+p)$	$d_a + d_b$	$d_a + d_b$	0
AB/AB x AB/aB	$pq^2/(1+p)$	$\frac{1}{2}(d_a + h_a) + d_b$	$\frac{1}{2}(d_a + h_a) + d_b$	$\frac{1}{4}(d_a - h_a)^2$
AB/aB x AB/aB	$p^2q/(1+p)$	$h_a + d_b$	$\frac{1}{2}h_a + d_b$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$
AB/Ab x AB/Ab	$p^2q^2/2(1-pq)$	d_a	d_a	$\frac{1}{4}d_b^2$
AB/Ab x AB/ab	$pq^3/(1-pq)$	$\frac{1}{2}(d_a + h_a)$	$\frac{1}{2}(d_a + h_a)$	$\frac{1}{4}(d_a - h_a)^2 + \frac{1}{4}d_b^2 +$ $\frac{1}{2}(q-p)d_b(d_a - h_a)$
AB/Ab x Ab/aB	$p^3q/(1-pq)$	$\frac{1}{2}(d_a + h_a)$	$\frac{1}{2}(d_a + h_a)$	$\frac{1}{4}(d_a - h_a)^2 + \frac{1}{4}d_b^2 -$ $\frac{1}{2}(q-p)d_b(d_a - h_a)$
AB/ab x AB/ab	$q^4/2(1-pq)$	h_a	$\frac{1}{2}h_a$	$\frac{1}{4}(d_a^2 + d_b^2) + (q-p)d_a d_b$
AB/ab x Ab/aB	$p^2q^2/(1-pq)$	h_a	$\frac{1}{2}h_a$	$\frac{1}{4}(d_a^2 + d_b^2)$
Ab/aB x Ab/aB	$p^4/2(1-pq)$	h_a	$\frac{1}{2}h_a$	$\frac{1}{4}(d_a^2 + d_b^2) - (q-p)d_a d_b$
Ab/Ab x Ab/Ab	$p^3/4(1+q)$	$d_a - d_b$	$d_a - d_b$	0
Ab/Ab x Ab/ab	$p^2q/(1+q)$	$\frac{1}{2}(d_a + h_a) - d_b$	$\frac{1}{2}(d_a + h_a) - d_b$	$\frac{1}{4}(d_a - h_a)^2$
Ab/ab x Ab/ab	$pq^2/(1+q)$	$h_a - d_b$	$\frac{1}{2}h_a - d_b$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$
aB/aB x aB/aB	$\frac{1}{4}p^2$	$d_b - d_a$	$d_b - d_a$	0
aB/ab x aB/ab	$\frac{1}{4}pq$	$-d_a$	$-d_a$	$\frac{1}{4}d_b^2$
ab/ab x ab/ab	$\frac{1}{4}q^2$	$-d_a - d_b$	$-d_a - d_b$	0

From Table 15 the following results are obtained:

$$M_{A0} = \frac{1}{2} h_a$$

$$M_{A1} = \frac{1}{4} \left[\frac{2+pq(3-8pq)}{(2+pq)(1-pq)} \right] h_a$$

$$= \frac{1}{4} \left[1 + \frac{pq [2 + pq + 2(q-p)^2]}{(2+pq)(1-pq)} \right] h_a$$

$$1^V A_1 = \frac{4 - pq(6-5pq)}{4(2+pq)(1-pq)} d_a^2 + \frac{[2+pq(3-8pq)][2-pq(5-6pq)]}{16(2+pq)^2(1-pq)^2} h_a^2$$

$$+ \frac{pq(4-7pq)}{2(2+pq)(1-pq)} d_a h_a + \frac{1}{2} d_b^2 + (q-p) d_a d_b + \frac{(q-p)pq}{2+pq} h_a d_b$$

$$2^V A_1 = \frac{1}{2} d_a^2 + \frac{2 + pq(3-8pq)}{8(2+pq)(1-pq)} h_a^2 - \frac{pq(4-7pq)}{2(2+pq)(1-pq)} d_a h_a$$

$$+ \frac{1}{2} d_b^2 + \frac{(q-p)^2}{2} d_a d_b - \frac{(q-p)^2 pq}{2(1-pq)} h_a d_b$$

Therefore,

$$V A_1 = 1^V A_1 + 2^V A_1$$

$$= \left[\frac{1}{2} + \frac{(2-13pq + 20p^2q^2)}{12(2+pq)(1-pq)} \right] d_a^2 + \frac{1}{2} d_b^2$$

$$+ \left[\frac{3}{16} + \frac{pq(16-52pq + 62p^2q^2 - 35p^3q^3)}{16(2+pq)^2(1-pq)^2} \right] h_a^2$$

$$+ \frac{1}{2}(q-p)(1+2q) d_a d_b + \frac{(q-p)p^2q(1+5p-2p^2)}{2(2+pq)(1-pq)} h_a d_b$$

$$\begin{aligned}
 VA_{O1} = & \frac{4 - pq(6-5pq)}{4(2+pq)(1-pq)} d_a^2 + \frac{2-pq(5-6pq)}{8(2+pq)(1-pq)} h_a^2 \\
 & + \frac{pq(4-7pq)}{2(2+pq)(1-pq)} d_a h_a + \frac{1}{8} d_b^2 + (q-p) d_a d_b + \frac{3(q-p) pq}{2(2+pq)} h_a d_b
 \end{aligned}$$

It may be observed that the mean value MA_1 , has a minimum of $\frac{1}{2} h_a$ which is achieved when the genes are completely linked ($p=0$) whereas it takes the value $\frac{1}{2} h_a$ with no linkage ($p = 0.5$). With intermediate linkage it takes a value greater than $\frac{1}{2} h_a$ but less than $\frac{1}{2} h_a$. Thus the effect of linkage, in the presence of dominance, is to effect the mean value, the effect being to reduce the mean value of the previous generation to a greater extent. In this respect, therefore, the linkage is reinforcing the effect of positive assortative mating in decreasing the mean value. In regard to the total genetic variance VA_q it may be noted that the coefficient of d_a^2 takes a minimum value of $\frac{1}{4}$ with no linkage and a maximum value of $\frac{3}{8}$ with complete linkage ($p = 0$), and that the coefficient of h_a^2 has got a minimum value of $\frac{3}{16}$ with complete linkage and a maximum of $\frac{2}{9}$ with no linkage. So the effect of linkage is to increase the additive genetic variation but to decrease the dominance action. Considering the coefficient of d_b^2 it is found that it remains the same as in the case when there is no linkage, which is expected since there is no dominance in the gene B-b. The coefficient of $h_a d_b$ will vanish for no linkage as well as for complete linkage whereas the coefficient of $d_a d_b$ will vanish for no linkage, but would take the value $-\frac{3}{2}$ when the linkage is complete. It is also interesting to note that the expressions for the variances with complete linkage are given by

$$1V_{A_1} = \frac{1}{8} (d_a + d_b)^2 + \frac{1}{16} h_a^2$$

$$2V_{A_1} = \frac{1}{4} (d_a + d_b)^2 + \frac{1}{8} h_a^2$$

$$V_{A_1} = \frac{3}{8} (d_a + d_b)^2 + \frac{3}{16} h_a^2$$

$$V_{A_0} = \frac{1}{8} (d_a + d_b)^2 + \frac{1}{8} h_a^2$$

These results show that when the linkage is complete, between two pairs of genes, one showing complete dominance in the positive direction and the other showing no dominance, the effect of positive assortative mating is exactly identical to that of selfing. Also, the two pairs of genes act as a single gene in expressing their additive and dominance effects.

3.3 'A' is completely dominant over 'a' and 'B' is completely dominant over 'b'

In this case, the ten possible genotypes can be assorted phenotypically into four intra-mating groups as

- (i) AB/AB, AB/Ab, AB/ab, Ab/aB, AB/aB
- (ii) Ab/Ab, Ab/ab
- (iii) aB/aB, aB/ab, and
- (iv) ab/ab

The tendency to positive assortative mating will yield the mating types with the corresponding frequencies as given below:

<u>Mating type</u>	<u>Frequency</u>
AB/AB x AB/AB	$q^4/4(2+q^2)$
AB/AB x AB/Ab	$pq^3/(2+q^2)$
AB/AB x AB/aB	$pq^3/(2+q^2)$
AB/AB x AB/ab	$q^4/(2+q^2)$
AB/AB x Ab/aB	$p^2q^2/(2+q^2)$
AB/Ab x AB/Ab	$p^2q^2/(2+q^2)$
AB/Ab x AB/aB	$2p^2q^2/(2+q^2)$
AB/Ab x AB/ab	$2pq^3/(2+q^2)$
AB/Ab x Ab/aB	$2p^3q/(2+q^2)$
AB/aB x AB/aB	$p^2q^2/(2+q^2)$
AB/aB x AB/ab	$2pq^3/(2+q^2)$
AB/aB x Ab/aB	$2p^3q/(2+q^2)$
AB/ab x AB/ab	$q^4/(2+q^2)$
AB/ab x Ab/aB	$2p^2q^2/(2+q^2)$
Ab/aB x Ab/aB	$p^4/(2+q^2)$
Ab/Ab x Ab/Ab	$p^3/4(1+q)$
Ab/Ab x Ab/ab	$p^2q/(1+q)$
Ab/ab x Ab/ab	$pq^2/(1+q)$
aB/aB x aB/aB	$p^3/4(1+q)$
aB/aB x aB/ab	$p^2q/(1+q)$
aB/ab x aB/ab	$pq^2/(1+q)$
ab/ab x ab/ab	$\frac{1}{4}q^2$

3.31 Calculation of Means, Variances and Covariance

Let d_a , d_b , h_a , h_b , $-d_a$ and $-d_b$ measure the departures of AA, BB, Aa, Bb, aa and bb respectively from the mid-parent. The frequencies, mean values and the within family variances

for various mating types are obtained as given in the following Table:

Table 16

Mating type	Frequency	Parental Mean	Family Mean	Within family variance
AB/AB x AB/AB	$q^4/4(2+q^2)$	d_a+d_b	d_a+d_b	0
AB/AB x AB/Ab	$pq^3/(2+q^2)$	$d_a+\frac{1}{2}(d_b+h_b)$	$d_a+\frac{1}{2}(d_b+h_b)$	$\frac{1}{4}(d_b-h_b)^2$
AB/AB x AB/aB	$pq^3/(2+q^2)$	$\frac{1}{2}(d_a+h_a)+d_b$	$\frac{1}{2}(d_a+h_a)+d_b$	$\frac{1}{4}(d_a-h_a)^2$
AB/AB x AB/ab	$q^4/(2+q^2)$	$\frac{1}{2}(d_a+h_a+d_b+h_b)$	$\frac{1}{2}(d_a+h_a+d_b+h_b)$	$\frac{1}{4}(d_a-h_a)^2+\frac{1}{4}(d_b-h_b)^2+$ $\frac{1}{2}(q-p)(d_a-h_a)(d_b-h_b)$
AB/AB x Ab/aB	$p^2q^2/(2+q^2)$	$\frac{1}{2}(d_a+h_a+d_b+h_b)$	$\frac{1}{2}(d_a+h_a+d_b+h_b)$	$\frac{1}{4}(d_a-h_a)^2+\frac{1}{4}(d_b-h_b)^2-$ $\frac{1}{2}(q-p)(d_a-h_a)(d_b-h_b)$
AB/Ab x AB/Ab	$p^2q^2/(2+q^2)$	d_a+h_b	$d_a+\frac{1}{2}h_b$	$\frac{1}{4}d_b^2 + \frac{1}{4}h_b^2$
AB/Ab x AB/aB	$2p^2q^2/(2+q^2)$	$\frac{1}{2}(d_a+h_a+d_b+h_b)$	$\frac{1}{2}(d_a+h_a+d_b+h_b)$	$\frac{1}{4}(d_a-h_a)^2+\frac{1}{4}(d_b-h_b)^2$
AB/Ab x AB/ab	$2pq^3/(2+q^2)$	$\frac{1}{2}(d_a+h_a)+h_b$	$\frac{1}{2}(d_a+h_a+h_b)$	$\frac{1}{4}(d_a-h_a)^2+\frac{1}{4}d_b^2+\frac{1}{4}h_b^2 +$ $\frac{1}{2}(q-p)d_b(d_a-h_a)$
AB/Ab x Ab/aB	$2p^3q/(2+q^2)$	$\frac{1}{2}(d_a+h_a)+h_b$	$\frac{1}{2}(d_a+h_a+h_b)$	$\frac{1}{4}(d_a-h_a)^2+\frac{1}{4}d_b^2+\frac{1}{4}h_b^2-$ $\frac{1}{2}(q-p)d_b(d_a-h_a)$
AB/aB x AB/aB	$p^2q^2/(2+q^2)$	h_a+d_b	$\frac{1}{2}h_a+d_b$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$
AB/aB x AB/ab	$2pq^3/(2+q^2)$	$h_a+\frac{1}{2}(d_b+h_b)$	$\frac{1}{2}(h_a+d_b+h_b)$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2 + \frac{1}{4}(d_b-h_b)^2$ $+ \frac{1}{2}(q-p)d_a(d_b-h_b)$
AB/aB x Ab/aB	$2p^3q/(2+q^2)$	$h_a+\frac{1}{2}(d_b+h_b)$	$\frac{1}{2}(h_a+d_b+h_b)$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2 + \frac{1}{4}(d_b-h_b)^2$ $-\frac{1}{2}(q-p)d_a(d_b-h_b)$

Table 16 continued

Mating type	Frequency	Parental Mean	Family Mean	Within family variance
AB/ab x AB/ab	$q^4/(2+q^2)$	h_a+h_b	$\frac{1}{2}(h_a+h_b)$	$\frac{1}{2}d_a^2+\frac{1}{2}h_a^2+\frac{1}{2}d_b^2+\frac{1}{2}h_b^2 +$ $(q-p)\left[d_a d_b + \right.$ $\left. \frac{1}{2}(q-p)h_a h_b \right]$
AB/ab x Ab/aB	$2p^2q^2/(2+q^2)$	h_a+h_b	$\frac{1}{2}(h_a+h_b)$	$\frac{1}{2}d_a^2+\frac{1}{2}h_a^2+\frac{1}{2}d_b^2+\frac{1}{2}h_b^2$
Ab/aB x Ab/aB	$p^4/(2+q^2)$	h_a+h_b	$\frac{1}{2}(h_a+h_b)$	$\frac{1}{2}d_a^2+\frac{1}{2}h_a^2+d_b^2+\frac{1}{2}h_b^2 -$ $(q-p)\left[d_a d_b + \right.$ $\left. \frac{1}{2}(q-p)h_a h_b \right]$
Ab/Ab x Ab/Ab	$p^3/4(1+q)$	d_a-d_b	d_a-d_b	0
Ab/Ab x Ab/ab	$p^2q/(1+q)$	$\frac{1}{2}(d_a+h_a)-d_b$	$\frac{1}{2}(d_a+h_a)-d_b$	$\frac{1}{2}(d_a-h_a)^2$
Ab/ab x Ab/ab	$pq^2/(1+q)$	h_a-d_b	$\frac{1}{2}h_a-d_b$	$\frac{1}{2}d_a^2+\frac{1}{2}h_a^2$
aB/aB x aB/aB	$p^3/4(1+q)$	d_b-d_a	d_b-d_a	0
aB/aB x aB/ab	$p^2q/(1+q)$	$\frac{1}{2}(d_b+h_b)-d_a$	$\frac{1}{2}(d_b+h_b)-d_a$	$\frac{1}{2}(d_b-h_b)^2$
aB/ab x aB/ab	$pq^2/(1+q)$	h_b-d_a	$\frac{1}{2}h_b-d_a$	$\frac{1}{2}d_b^2+\frac{1}{2}h_b^2$
ab/ab x ab/ab	$\frac{1}{2}q^2$	$-d_a-d_b$	$-d_a-d_b$	0

The following results are obtained from the above Table.

$$M_{A0} = \frac{1}{2}(h_a + h_b)$$

$$M_{A1} = \frac{1+q(3-2pq)}{2(1+q)(2+q^2)}(h_a+h_b) = \frac{1}{2} \left[1 + \frac{q(5-8q+4q^2)-1}{2(1+q)(2+q^2)} \right] (h_a+h_b)$$

$$\begin{aligned}
1V_{A1} = & \frac{4+q^2(7-q)}{4(1+q)(2+q^2)} (d_a^2+d_b^2) + \frac{(1+3q-2pq^2)(p+2q^2+pq^2)}{4(1+q)^2(2+q^2)^2} (h_a^2+h_b^2) \\
& + \frac{q(1+q+3p^2)}{2(1+q)(2+q^2)} (d_a h_a + d_b h_b) + \frac{(q-p)(4+q^2)}{2(2+q^2)} d_a d_b \\
& + \left[\frac{1-q^2(p-q)}{2(2+q^2)} - \frac{(1+3q-2pq^2)^2}{2(1+q)^2(2+q^2)^2} \right] h_a h_b \\
& + \frac{q(q-p)(2-pq)}{2(1+q)(2+q^2)} (d_a h_b + h_a d_b)
\end{aligned}$$

$$\begin{aligned}
2V_{A1} = & \frac{1}{4}(d_a^2+d_b^2) + \frac{4-p(3+2q^2)}{4(1+q)(2+q^2)} (h_a^2+h_b^2) - \frac{q(1+q+3p^2)}{2(1+q)(2+q^2)} (d_a h_a + d_b h_b) \\
& + \frac{1}{4}(q-p)^2 d_a d_b + \frac{(q-p) \left[q^2 + (q-p)(1-2pq) \right]}{2(2+q^2)} h_a h_b \\
& - \frac{q(q-p)^2(1+p)}{2(2+q^2)} (d_a h_b + h_a d_b).
\end{aligned}$$

Therefore,

$$\begin{aligned}
V_{A1} = & \frac{1}{4} \left[1 + \frac{p(q-\frac{1}{2})^2}{(1+q)(2+q^2)} \right] (d_a^2 + d_b^2) \\
& + \left[\frac{2}{9} + \frac{(5-26q+55q^2-80q^3+94q^4-56q^5+8q^6)}{36(1+q)^2(2+q^2)^2} \right] (h_a^2+h_b^2) \\
& + \left[\frac{\{(1-pq^2+q^3)+(q-p)^2(4q^3-5q^2+4q-1)\}}{2(2+q^2)} - \frac{(1+3q-2pq^2)^2}{2(1+q)^2(2+q^2)^2} \right] h_a h_b \\
& + \frac{(q-p)(1+2q+q^3)}{(2+q^2)} d_a d_b + \frac{pq(2-q^2)(q-p)}{(1+q)(2+q^2)} (d_a h_b + h_a d_b).
\end{aligned}$$

$$\begin{aligned}
 W_{A01} &= \frac{4+q^2(7-q)}{2(1+q)(2+q^2)} (d_a^2 + d_b^2) + \frac{p+q^2(3-q)}{4(1+q)(2+q^2)} (h_a^2 + h_b^2) \\
 &+ \frac{q(1+q+3p^2)}{2(1+q)(2+q^2)} (d_a h_a + d_b h_b) + \frac{(q-p)(4+q^2)}{2(2+q^2)} d_a d_b \\
 &+ \frac{(2q^2-1)(q^2+1) + (q-1)(q^2+q-2)}{2(1+q)(2+q^2)} h_a h_b - \\
 &\quad \frac{q(q-p)(1+q^2)}{2(1+q)(2+q^2)} (d_a h_b + h_a d_b)
 \end{aligned}$$

In this case it may be observed that the mean takes a value of $\frac{1}{2}$ with no linkage and also with complete linkage. With intermediate linkage, however, the mean is always reduced. Examining the total variance, it may be noted that the coefficients of d_a^2 and h_a^2 takes the values $\frac{2}{3}$ and $\frac{2}{9}$ with no linkage and also with complete linkage. Similar is the case with d_b^2 and h_b^2 . With intermediate linkage, it is found that the coefficients of d_a^2 and d_b^2 are greater than $\frac{2}{3}$. The coefficient increases from 0.667 to 0.669 as p takes values from 0.50 to 0.19 and decreases from 0.669 to 0.67 again as p takes values from 0.19 to 0. Similar is the case with the coefficient of h_a^2 and h_b^2 for intermediate values of p . The expression for the total genetic variance when there is complete linkage will reduce to the form

$$\begin{aligned}
 V_{A1} &= \frac{2}{3} (d_a^2 + d_b^2 + 2d_a d_b) + \frac{2}{9} (h_a^2 + h_b^2 + 2h_a h_b) \\
 &= \frac{2}{3} (d_a + d_b)^2 + \frac{2}{9} (h_a + h_b)^2 \\
 &= \frac{2}{3} d_a'^2 + \frac{2}{9} h_a'^2, \text{ where } d_a' = d_a + d_b \text{ and } h_a' = h_a + h_b.
 \end{aligned}$$

Therefore, from this it can be concluded that when there is complete linkage, both the genes will combine together to act as a single gene.

CHAPTER - IV

Effect of Positive Assortative Mating with Selection

In the previous chapters we have considered the effects of positive assortative mating without any selection on the genotypes. In the natural populations, however, assortative mating is almost always accompanied by selection and is then considered as a force for evolutionary change. In any practical breeding programme also, any system of mating is combined with selection to achieve maximum genetic improvement. In this chapter, therefore, we have considered the effects of positive assortative mating combined with selection on genotypes.

Consider a large random mating population with one locus A-a (gene frequencies as p and $q = 1-p$ for A and a respectively) segregating. Suppose that the recessive individuals (aa) are entirely eliminated from the population, and that only the dominants are allowed to mate and reproduce. The proportions of various genotypes in the population before and after selection would be as follows :-

	Zygotic proportions		
	AA	Aa	aa
Before selection	p^2	$2pq$	q^2
After selection	$\frac{p^2}{p^2+2pq}$	$\frac{2pq}{p^2+2pq}$	0
	= $p/(1+q)$	$2q/(1+q)$	0

In the selected population, the positive assortative mating is resorted to. The results obtained under conditions of no dominance and complete dominance in the positive direction are discussed below.

4.1 No dominance

In this case both the genotypes AA and Aa will be phenotypically recognisably distinct. The tendency to positive assortative mating will yield the mating types with the corresponding frequencies as given below:

<u>Mating type</u>	<u>Frequency</u>
AA x AA	$p / (1+q)$
Aa x Aa	$2q / (1+q)$

4.11 Calculation of Means, Variances and Covariance

Let d_a measure the departure of AA from the mid-parent. The values given in the table below are obtained against both the mating types.

Table 17

Mating type	Frequency	Parental Mean	Family Mean	Within family variance
AA x AA	$p / (1+q)$	d_a	d_a	0
Aa x Aa	$2q / (1+q)$	0	0	$\frac{1}{2}d_a^2$

The following results are obtained:

$$M_{A_0} = (p-q)d_a$$

$$M_{A_0}^S = M_{A_1} = \frac{p}{1+q} d_a, \text{ where } M_{A_0}^S \text{ denotes}$$

the mean of the
parental selected
population.

$$1^V_{A_1} = W_{A_0 1} = \frac{2pq}{(1+q)^2} d_a^2$$

$$2^V_{A_1} = \frac{q}{1+q} d_a^2$$

Therefore, the total genetic variance is given by

$$\begin{aligned} V_{A_1} &= 1^V_{A_1} + 2^V_{A_1} \\ &= \frac{2pq}{(1+q)^2} d_a^2 + \frac{q}{1+q} d_a^2 \\ &= \frac{q(2+p)}{(1+q)^2} d_a^2 \end{aligned}$$

The total genetic variance obtained with selection against recessives and positive assortative mating, given no dominance, behaves in a significant manner. It is always greater than $2pq d_a^2$, the total genetic variance in the parental generation, but compared with the variance obtained under positive assortative mating with no selection i.e. $3pq d_a^2$, it is smaller except for values of p nearer to zero. This variance increases with p slowly, attains a maximum at $p = 0.4$ and decreases thereafter. The effect of positive assortative mating combined with selection, in this case, therefore, is increased genetic variability but the increase is much less than would be obtained if selection is dropped.

4.2 'A' is completely dominant over 'a'

In this case both the genotypes AA and Aa will be phenotypically same. So there will be only one intra-mating group. The tendency to assortative mating will yield the mating types with the corresponding frequencies as given below:

<u>Mating type</u>	<u>Frequency</u>
AA x AA	$p^2 / (1+q)^2$
AA x Aa	$4pq / (1+q)^2$
Aa x Aa	$4q^2 / (1+q)^2$

4.21 Calculation of Means, Variances and Covariance

Let d_a and h_a measure the departure of AA and Aa respectively from the mid-parent. The values given in the following table are obtained against various mating types.

Table 18

<u>Mating type</u>	<u>Frequency</u>	<u>Parental Mean</u>	<u>Family Mean</u>	<u>Within family variance</u>
AA x AA	$p^2 / (1+q)^2$	d_a	d_a	0
AA x Aa	$4pq / (1+q)^2$	$\frac{1}{2}(d_a+h_a)$	$\frac{1}{2}(d_a+h_a)$	$\frac{1}{4}(d_a-h_a)^2$
Aa x Aa	$4q^2 / (1+q)^2$	h_a	$\frac{1}{2}h_a$	$\frac{1}{4}d_a^2 + \frac{1}{4}h_a^2$

The following results are obtained:

$$M_{A_0} = (p-q)d_a + 2pq h_a$$

$$M_{A_0}^2 = \frac{p}{1+q} d_a + \frac{2q}{1+q} h_a$$

$$M_{A1} = \frac{p}{1+q} d_a + \frac{2q}{(1+q)^2} h_a$$

$$1V_{A1} = \frac{pq}{(1+q)^2} d_a^2 + \frac{p^2q}{(1+q)^4} h_a^2 - \frac{2p^2q}{(1+q)^3} d_a h_a$$

$$2V_{A1} = \frac{q}{1+q} d_a^2 + \frac{q}{(1+q)^2} h_a^2 - \frac{2pq}{(1+q)^2} d_a h_a$$

Therefore, the total variance is given by

$$V_{A1} = \frac{2q}{(1+q)^2} d_a^2 + \frac{2q(1+q^2)}{(1+q)^4} h_a^2 - \frac{4pq}{(1+q)^3} d_a h_a$$

$$W_{A01} = \frac{pq}{(1+q)^2} d_a^2 + \frac{p^2q}{(1+q)^3} h_a^2 - \frac{2pq}{(1+q)^3} d_a h_a$$

In particular when $p = q = \frac{1}{2}$,

$$M_{A0} = \frac{1}{2} h_a$$

$$M_{A0}^S = \frac{1}{2} d_a + \frac{1}{2} h_a$$

$$M_{A1} = \frac{1}{2} d_a + \frac{4}{9} h_a$$

$$1V_{A1} = \frac{1}{9} d_a^2 + \frac{2}{81} h_a^2 - \frac{2}{27} d_a h_a$$

$$2V_{A1} = \frac{1}{9} d_a^2 + \frac{2}{9} h_a^2 - \frac{2}{9} d_a h_a$$

$$W_{A01} = \frac{1}{9} d_a^2 + \frac{1}{27} h_a^2 - \frac{4}{27} d_a h_a$$

$$V_{A1} = \frac{4}{9} d_a^2 + \frac{20}{81} h_a^2 - \frac{8}{27} d_a h_a$$

Comparing M_{A1} with that obtained without selection it may be noted that the mean value is larger in this case. In the mean value without selection there was no d_a term and the coefficient of h_a was $\frac{1}{2}$. But in this case we see that the term

containing d_a also is there and that the coefficient of h_a is $\frac{4}{9}$. Compared with the parent population the effect of selection with assortative mating is to increase the mean value. In this respect, therefore, it may be desirable to combine selection always with positive assortative mating to counteract the depressing effect on the mean value expected under this type of mating. In regard to the total genetic variance it can be seen that for the simple case of $d_a = h_a = 1$, it is $32/81$ as against $8/9$ obtained when positive assortative mating is resorted to without any selection and is, therefore, considerably smaller. Compared with the parental variance of $\frac{1}{2}$ (obtained by putting $d_a = h_a = 1$ in $\frac{1}{2}d_a^2 + \frac{1}{2}h_a^2$), it is found to have decreased to almost half of the parental variance. It is, therefore, concluded that provided the action of a gene is in the dominant phase, the effect of assortative mating with selection against recessives is to decrease the total genetic variability.

S U M M A R Y

The effect of positive assortative mating on genetic variance and covariance has been studied under varying conditions of dominance. The study deals separately with the situations (i) one locus segregating and (ii) any number of loci segregating; assuming in each case, arbitrary gene frequencies. With one locus segregating, the effect of repeated positive assortative mating has also been dealt with giving general results for a population subject to this type of mating for 'n' generations. The consequences, if two loci segregating are linked have also been worked out assuming half as gene frequencies in each case. The effect of selection combined with positive assortative mating when one locus is segregating with arbitrary gene frequencies has also been investigated.

With one locus segregating and when dominance is not operating, it is found that while the positive assortative mating does not effect the mean value it increases the total genetic variance in such a way that the within family variance is halved. When dominance is operating, the mean value, however, decreases. The total genetic variance in this case, however, depends on 'p', the frequency of dominant allelomorph and decreases or increases from generation to generation according as 'p' is less than or greater than 0.3. The covariance between family means and parental mean values in successive generations is also affected only when 'p' is greater than 0.3.

With any number of loci segregating, provided the genes involved are independent in action and distribution, it has been

found that the contribution of each of the genes involved to the means, variances and covariance depends only on the dominance situation characteristic of that gene, being unaffected by the dominance situation of the other genes and further that these contributions are simply additive. The contribution is also similar in form if two genes are exhibiting the same type of dominance.

In regard to the effect of linkage, when there is no dominance, it is found that linkage has no effect on the mean values, but it affects the variances and the covariance. The results in this case are parallel to those obtained by Mather (1949) under selfing, that is the definition of 'D' changes in the second rank variance. In the presence of dominance, however, the effect of linkage is to reduce the mean value of the previous generation to a greater extent. When the linkage is complete, between two pairs of genes, one of which shows complete dominance in the positive direction while the other shows no dominance, the two linked genes act as a single gene in expressing their additive and dominance effects, but the effect of positive assortative mating on genetic variability is not the same as found with one locus segregating, but is that as found under selfing. When both the genes show complete dominance in positive direction, and the linkage is complete, the two genes act as a single gene and the effect of positive assortative mating is now the same as found with one locus segregating.

In the absence of dominance, the effect of positive assortative mating combined with selection against recessives is found to increase the genetic variability but the increase is much less than would be obtained if selection is dropped. In the presence of dominance in positive direction, however, it is found that the effect of positive assortative mating with selection against recessives is to increase the mean value, but to decrease the total genetic variability to a considerable extent.

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