GENETIC VARIANCE AND ASSORTATIVE MATING

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1. Introduction

The partitioning of the phenotypic variation in a trait controlled by polygenes into various components under different systems of mating is of utmost importance to a plant or animal breeder. Mather (1949) showed how a partition into three important compoents *viz.* additive, dominance and environmental can be affected in selfed and biparental populations derived from a cross between two true breeding parents and also in randomly breeding population under equilibrium. Hayman (1953) and Rajagopalan (1958) did the same for sib mating. Breese (1956) examined such a partitioning under positive assortative mating when each gene is segregating independently and is represented by two alleles having equal frequencies and the environmental fluctuations are considered negligible. He further suggested that such a type of mating system may profitably have wider use as a technique in plant or animal breeding, especially where inbreeding methods are impracticable or undesirable. Rao (1964) extended Breese's procedure to cover cases when each gene is represented by two alleles having arbitrary gene frequencies and when genes located on the same chromosome are linked. The consequence of resorting to positive assortative mating over a number of generations with one locus segregating were also investigated. In this paper, some of these results are described and the behaviour of genetic variability under positive assortative mating is discussed.

2. One Locus Segregating

Consider a random mating population in equilibrium with frequencies p for gene A and q for a, so that the three genotypes AA, Aa and aa have frequencies respectively as p^2, $2pq$ and q^2. Also let d_a, h_a, and $-d_a$ measure the departure of the values of AA, Aa and

aa respectively from the mid-parent. The mean value and variance of the parental generation for one locus are then given by

$$M_{Ao}^{(1)} = (p-q) \, d_a + 2pq \, h_a \qquad \dots(1)$$

$$V_{Ao}^{(1)} = \tfrac{1}{2} \, D^{(1)} + \tfrac{1}{2} \, F^{(1)} + \tfrac{1}{4} \, H^{(1)} \qquad \dots(2)$$

where

$$D^{(1)} = 4pq \, d^2_a$$
$$F^{(1)} = 8pq \, (q-p) \, d_a h_a$$
$$H^{(1)} = 8pq \, (1-2pq) \, h^2_a.$$

The effects of assortative mating depend upon how similar are the phenotypes of the parents to be mated in regard to the character under study. As Wright (1921) suggested, it depends on the degree of determination by heredity and the phenotypic correlation for the character between the parents. It is assumed here that the environmental fluctuations are negligible (as for instance in a highly heritable character) so that by resorting to assortative mating almost perfect genetic correlation between the mates is achieved. With this assumption, the phenotypic assortment of the three genotypes in the population would depend upon whether A is dominant over a or not and in the former case whether it is complete with reinforcing or complete with opposing dominance. When there is no dominance, the three genotypes are phenotypically recognisably distinct and there are three intra-mating groups *viz.* (1) AA, (2) Aa and (3) aa occurring with frequencies p^2, $2pq$ and q^2 respectively. This is exactly what happens under selfing and therefore need not be dealt with here. With complete dominance, the two phases of reinforcing and opposing dominance are exactly opposite, so that the results for the latter case can be obtained from the former by replacing 'q' by 'p' and changing the sign of d_a. It would therefore suffice to consider the case of complete reinforcing dominance only.

2·1 Mean value and variability after one generation of mating system

With complete reinforcing dominance, AA and Aa are not phenotypically recognisably distinct so that there are two intra-mating groups *viz.* (*i*) AA, Aa and (*ii*) aa occurring in the ratio $p(1+q) : q^2$. The tendency to positive assortative mating would

yield the four mating types with frequencies, family mean values and within family variances as shown in table 1.

TABLE 1

Frequencies, mean values and variances of families

Type of mating	Frequency	Family mean	Family variance
$AA \times AA$	$p^3/(1+q)$	d_a	o
$AA \times Aa$	$4p^2q/(1+q)$	$\frac{1}{2}(d_a+h_a)$	$\frac{1}{4}(d_a-h_a)^2$
$Aa \times Aa$	$4pq^2/(1+q)$	$\frac{1}{2}h_a$	$\frac{1}{2}d_a{}^2+\frac{1}{4}h_a{}^2$
$aa \times aa$	q^2	$-d_a$	o

2·11. Mean value

The mean value of the population resulting from positive assortative mating would be given by

$$M^{(1)}_{A1}=(p-q)\,d_a+\frac{2pq}{(1+q)}\,h_a. \qquad \ldots(3)$$

The comparison of (1) and (3) shows that the mean value has decreased by $\dfrac{2pq^2}{(1+q)}h_a$. It may be seen that in the resulting population the three genotypes AA, Aa and aa would occur with frequencies $p/(1+q)$, $2pq/(1+q)$ and $2q^2/(1+q)$ respectively so that the heterozygotes decrease by $2pq^2/(1+q)$. The decrease in the mean value is thus directly proportional to the decrease in the proportion of heterozygosity.

2·12. Variances

The types of progenies obtained under the given system of mating yield two second degree statistics viz. (*i*) the variance of family means (1st rank variance, $_1V_{A1}$) and (*ii*) the mean variance within families (2nd rank variance, $_2V_{A1}$). These are given by

$$_1V^{(1)}_{A1}=\frac{1+3q}{4(1+q)}\,D^{(1)}+\frac{3q-1}{4(1+q)\,(q-p)}\,F^{(1)}+\frac{1+q-4pq}{8(1-2pq)(1+q)^2}\,H^{(1)}$$
$$\ldots(4)$$

$$_2V^{(1)}_{A1}=\frac{1}{4}\,D^{(1)}+\frac{p}{4(1+q)(p-q)}\,F^{(1)}+\frac{1}{8(1+q)(1-2pq)}\,H^{(1)}$$
$$\ldots(5)$$

$$V^{(1)}_{A1} = {}_1V^{(1)}_{A1} + {}_2V^{(1)}_{A1}$$

$$= \frac{1+2q}{2(1+q)}\ D^{(1)} + \frac{1}{2(1+q)}\ F^{(1)} + \frac{1-q+2q^2}{4(1-2pq)(1+q)^2}\ H^{(1)}$$

$$\text{...(6)}$$

Since complete reinforcing dominance is assumed, $d_a = h_a$, so that the variance

$$V^{(1)}_{A1} = \frac{2q(2q+1)}{(1+q)^2}\ D^{(1)}$$

as compared to the initial total variance

$$V^{(1)}_{A0} = q(1+q)\ D^{(1)}$$

obtained by putting $d_a = h_a$ in (2). Hence $V^{(1)}_{A1}$ is greater or less than $V^{(1)}_{A0}$ according as $(1+q-3q^2-q^3)$ is positive or negative respectively. It follows that $V^{(1)}_{A1} \gtrless V^{(1)}_{A0}$ as $q \gtrless q_0$ where q_0 lies between 0·6 and 0·7. This shows that in the presence of dominance, positive assortative mating leads to increased variability only when the frequency of recessive allele q is not well above 0·6. However, if the coefficient of $D^{(1)}$ consisting the additive genetic portion of the variance is compared in $V^{(1)}_{A0}$ and $V^{(1)}_{A1}$, it is found that assortative mating leads to increased variability the increase being $2pq^2/(1+q)$.

2·2. Mean value and variability after two generations of mating system

Since in $A1$ the three genotypes AA, Aa and aa occur with frequancies $p/(1+q)$, $2pq/(1+q)$ and $2q^2/(1+q)$ respectively, the tendency to positive asssortative mating would yield the four mating types $AA \times AA$, $AA \times Aa$, $Aa \times Aa$ and $aa \times aa$ with corresponding family means and variances as given in Table 1 but with frequencies as $p/(1+q)$ $(1+2q)$, $4pq/(1+q)$ $(1+2q)$, $4pq^2/(1+q)$ $(1+2q)$ and $2q^2/(1+q)$ respectively.

2·21. Mean value

The mean value of the resulting population would be given by

$$M^{(1)}_{A2} = (p-q)\,d_a + \frac{2pq}{1+2q}h_a. \qquad \text{...(7)}$$

Comparing (3) and (7), it is found that the mean value has decreased by $2pq^2/(1+q)(1+2q)$ which is again proportional to the decrease in heterozygosity since in $A2$ the three genotypes AA, Aa and aa would occur with frequencies $p/(1+q)/(1+2q)$, $2pq/(1+2q)$ and $3q^2/(1+2q)$ respectively.

2·22. Variances

The two variances are given by

$$_1V^{(1)}_{A2} = \frac{(1-16q-8pq)}{4(1+q)(1+2q)} D^{(1)} + \frac{(6q-4pq-1)}{4(1+q)(1+2q)(q-p)} F^{(1)}$$
$$+ \frac{(1+2q-4pq)}{8(1+2q)^2(1-2pq)} H^{(1)} \quad \dots(8)$$

$$_2V^{(1)}_{A2} = \frac{1}{4(1+q)} D^{(1)} + \frac{1}{4(1+q)(1+2q)(p-q)} F^{(1)}$$
$$+ \frac{1}{8(1+2q)(1-2pq)} H^{(1)} \quad \dots(9)$$

$$V^{(1)}_{A2} = {}_1V^{(1)}_{A2} + {}_2V^{(1)}_{A2}$$
$$= \frac{(1+4q)}{2(1+2q)} D^{(1)} + \frac{1}{2(1+2q)} F^{(1)} + \frac{(1+2q^2)}{4(1+2q)^2(1-2pq)} H^{(1)}$$
$$\dots(10)$$

With $d_a = h_a$, the total variance is given by

$$V^{(1)}_{A2} = \frac{3q(1+3q)}{(1+2q)^2} D^{(1)}.$$

Hence

$$V^{(1)}_{A2} \gtrless V^{(1)}_{A0}$$

according as

$$(1+2q-4q^2-2q^3) \lessgtr 0$$

and

$$V^{(1)}_{A2} \gtrless V^{(1)}_{A1}$$

according as

$$(1+3q-3q^2-7q^3) \gtrless 0.$$

It is thus found that

$$V^{(1)}_{A2} > V^{(1)}_{A1} > V^{(1)}_{A0}$$

if
$$q < q_0$$

and

$$V_{A2}^{(1)} < V_{A1}^{(1)} < V_{A0}^{(1)}$$

if
$$q > q_0$$

where q_0 lies between 0.6 and 0.7. Comparing only the additive genetic portion of the total variability in

$$V_{A1}^{(1)} \quad \text{and} \quad V_{A2}^{(1)}$$

it is found that this has increased by $2pq^2/(1+q)(1+2q)$.

With $d_a = h_a$, comparing $_1V_{A1}^{(1)}$ and $_2V_{A1}^{(1)}$ with $_1V_{A2}^{(1)}$ and $_2V_{A2}^{(1)}$ respectively it is found that $_1V_{A2}^{(1)}$ is always higher than $_1V_{A1}^{(1)}$ and $_2V_{A2}^{(1)}$ is always lower than $_2V_{A1}^{(1)}$ except for $q=0$ and 1 when both are equal. The maximum differences in both the cases occur when q lies between 0.6 and 0.7.

2·3. Mean value and variability after 'n' generations

2·31. Mean value

The mean of the population resulting from positive assortative mating for n generations is given by

$$M_{An}^{(1)} = (p-q)d_a + \frac{2pq}{1+nq}h_a. \qquad \qquad ...(11)$$

In the limit as $n \to \infty$.

$$M_A^{(1)} = (p-q)\,d_a.$$

2·32. Variances

The two variances are given by

$$_1V_{An}^{(1)} = \frac{[\{1+(n-2)q\}\,(1+2nq)+2nq(1+nq)]}{4(1+\overline{n-1}\,q)\,(1+nq)}\,D^{(1)} +$$

$$\frac{[1+(n-2)\,q-2\,(p-q(1+\overline{n-1}\,q)]}{4(1+\overline{n-1}\,q)(1+nq)\,(q-p)}\,F^{(1)} +$$

$$\frac{(1+nq-4pq)}{8(1+nq)^2(1-2pq)}\,H^{(1)} \qquad \qquad ...(12)$$

$$_2V_{An}^{(1)} = \frac{1}{4(1+\overline{n-1}\,q)}\,D^{(1)} + \frac{(1+\overline{n-2}\,q)}{4(1+\overline{n-1}\,q)(1+nq)(p-q)}\,F^{(1)} +$$

$$\frac{1}{8(1+nq)(1-2pq)}\,H^{(1)}. \qquad \qquad ...(13)$$

In the limit as $n \to \infty$, we get the following results

$$_1V_A^{(1)} = D^{(1)}$$

$$_2V_A^{(1)} = 0.$$

Thus after the mating system is allowed to practice for an infinitely large number of generations, all the variance tends to appear in tho variance of family means.

3. TWO LINKED LOCI SEGREGATING

Consider two genetic factors $A-a$ and $B-b$ from a random mating population with frequencies as $\frac{1}{2}$ each for the genes A, a, B and b and let 'r' be the recombination fraction when the linkage is in coupling phase so that the ten genotypes AB/AB, AB/Ab, Ab/Ab, AB/aB, AB/ab, Ab/aB, Ab/ab, aB/aB, aB/ab and ab/ab have frequencies respectively as $t^2/4$, $rt/2$, $r^2/4$, $rt/2$, $t^2/2$, $r^2/2$, $rt/2$, $r^2/4$, $rt/2$ and $t^2/4$ where $t = 1 - r$. Denoting d_a, h_a and $-d_a$ as usual, the mean value and variance of the parental generation for two linked loci are then given by

$$M_{Ao}^{(2)} = \frac{1}{2}(h_a + h_b) \qquad \qquad ...(14)$$

$$V_{Ao}^{(2)} = \frac{1}{2} D^{(2)} + \frac{1}{4} H^{(2)} + \frac{1}{2}(1-2r) D^{(2)\prime} + \frac{1}{2}(1-2r)^2 H^{(2)\prime}$$

$$...(15)$$

where

$$D^{(2)} = (d_a^2 + d_b^2)$$

$$H^{(2)} = (h_a^2 + h_b^2)$$

$$D^{(2)\prime} = 2 d_a d_b$$

and

$$H^{(2)\prime} = h_a h_b.$$

It is assumed here that the environmental fluctuations are negligible and that the genes are equal in effect. With this assumption the phenotypic assortment of the ten gehotypes in the population would depend upon the dominance situation in the two genetic factors. We shall consider two cases *viz.* when either of the two gene pairs show (a) no dominance and (b) complete dominance.

3·1. No dominance

When there is no dominance in both factors and both the factors show equal effect, the ten genotypes can be assorted phenotypically into five intra·mating groups *viz.* (i) AB/AB (ii) AB/Ab, AB/aB (iii) Ab/Ab, AB/ab, Ab/aB, aB/aB (iv) Ab/ab, aB/ab and (v) ab/ab. The tendency to positive assortative mating would yield the eighteen mating types with frequencies, family means and within family variances as shown in Table 2.

TABLE 2
Frequencies, mean values and variances of families

Mating type	Frequency	Family mean	Family variances
$AB/AB \times AB/AB$	$t^2/4$	(d_a+d_b)	o
$AB/Ab \times AB/Ab$	$rt/4$	d_a	$\frac{1}{2} d_b^2$
$AB/Ab \times AB/aB$	$rt/2$	$\frac{1}{2}(d_a+d_b)$	$\frac{1}{4}(d_a^2+d_b^2)$
$AB/aB \times AB/aB$	$rt/4$	d_b	$\frac{1}{2} d_a^2$
$Ab/Ab \times Ab/Ab$	$r^4/8(2r^2+t^2)$	(d_a-d_b)	o
$Ab/Ab \times AB/ab$	$r^2t^2/2(2r^2+t^2)$	$\frac{1}{2}(d_a-d_b)$	$\frac{1}{4}(d_a^2+d_b^2)+\frac{1}{2}(t-r) d_a d_b$
$Ab/Ab \times Ab/aB$	$r^4/2(2r^2+t^2)$	$\frac{1}{2}(d_a-d_b)$	$\frac{1}{4}(d_a^2+d_b^2)-\frac{1}{2}(t-r) d_a d_b$
$AB/ab \times AB/ab$	$t^4/2(2r^2+t^2)$	o	$\frac{1}{2}(d_a^2+d_b^2)+(t-r) d_a d_b$
$AB/ab \times Ab/aB$	$r^2t^2/(2r^2+t^2)$	o	$\frac{1}{2}(d_a^2+d_b^2)$
$Ab/aB \times Ab/aB$	$r^4/2(2r^2+t^2)$	o	$\frac{1}{2}(d_a^2+d_b^2)-(t-r) d_a d_b$
$aB/aB \times aB/aB$	$r^4/8(2r^2+t^2)$	$(-d_a+d_b)$	o
$Ab/Ab \times aB/aB$	$r^4/4(2r^2+t^2)$	o	o
$AB/ab \times aB/aB$	$r^2t^2/2(2r^2+t^2)$	$-\frac{1}{2}(d_a-d_b)$	$\frac{1}{4}(d_a^2+d_b^2)+\frac{1}{2}(t-r)d_a d_b$
$Ab/aB \times aB/aB$	$r^4/2(2r^2+t^2)$	$-\frac{1}{2}(d_a-d_b)$	$\frac{1}{4}(d_a^2+d_b^2)-\frac{1}{2}(t-r)d_a d_b$
$Ab/ab \times Ab/ab$	$rt/4$	$-d_b$	$\frac{1}{2} d_a^2$
$Ab/ab \times aB/ab$	$rt/2$	$-\frac{1}{2}(d_a+d_b)$	$\frac{1}{4}(d_a^2+d_b^2)$
$aB/ab \times aB/ab$	$rt/4$	$-d_a$	$\frac{1}{2} d_b^2$
$ab/ab \times ab/ab$	$t^2/4$	$-(d_a+d_b)$	o

3·11. Mean value

The mean value of the population resulting from positive assortative mating would be given by

$$M_{A1}^{(2)}=0. \qquad \qquad \qquad ...(16)$$

From this it can be concluded that positive assortative mating has no effect on the mean value when the two gene pairs are linked and when there is no dominance in both the gene pairs.

3·12. Variances

$$_1V_{A1}^{(2)} = \frac{1+t)}{4} \ D^{(2)} + \frac{(2t-r)}{4} \ D^{(2)'} \qquad \ldots(17)$$

$$_2V_{A1}^{(2)} = \frac{1}{4} \ D^{(2)} + \frac{(t-r)^2}{4} \ D^{(2)'} \qquad \ldots(18)$$

$$V_{A1}^{(:)} = \frac{(2+t)}{4} \ D^{(2)} + \frac{t(4t-1)}{4} \ D^{(2)'} \qquad \ldots(19)$$

Since equal gene effects are assumed, $d_a = d_b$, so that

$$V_{A1}^{(2)} = \frac{(8t^2 - t + 2)}{4} \ D^{(2)}$$

compared to the initial total variance

$$V_{Ao}^{(2)} = \frac{(3-4r)}{2} \ D^{(2)}$$

obtained by putting $d_a = d_b$ and $h_a = h_b = 0$ in (15). It can be easily seen that for all admissible values of r, $V_{A1}^{(2)}$ is greater than $V_{A0}^{(2)}$. This shows that in the presence of linkage and in the absence of dominance, positive assortative mating always leads to increased variability.

For $r = 0·5$, the expressions (17) and (18) become

$$_1V_{A1}^{(2)} = \frac{3}{8} \ D^{(2)} + \frac{1}{8} \ D^{(:)'} \qquad \ldots(20)$$

$$_2V_{A1}^{(2)} = \frac{1}{4} \ D^{(2)} \qquad \ldots(21)$$

which are in agreement with those given by Breese (1956).

For $r = 0$, the expressions (17) and (18) reduce to

$$_1V_{A1}^{(2)} = \frac{1}{2} (d_a + d_b)^2$$

$$_2V_{A1}^{(2)} = \frac{1}{4} (d_a + d_b)^2$$

which are the same as expected for one genetic factor under selfing (Mather, 1949).

For comparing (17) and (18) with (20) and (21), (17) and (18) can be written in the following form :

$$_1V_{A1}^{(2)} = \left[\frac{3}{8} + \frac{2t-1}{8} \right] D^{(2)} + \left[\frac{1}{8} + \frac{3(2t-1)}{8} \right] D^{(2)'}$$

$$_2V_{A1}^{(2)} = \frac{1}{4} D^{(2)} + \frac{(t-r)^2}{4} D^{(2)'}.$$

From the above expressions it can be easily seen that for all permissible values of r, both the first and second rank variances are more in the presence of linkage than those expected in the absence of linkage.

3·2. Complete dominance in either factors

With complete reinforcing dominance in both the gene pairs, the ten genotypes can be assorted phenotypically into three intra-mating groups viz. (i) AB/AB, AB/aB, AB/Ab, AB/ab, Ab/aB (ii) Ab/Ab, Ab/ab, aB/aB, aB/ab and (iii) ab/ab. The tendency to positive assortative mating would yield the twenty-six mating types with frequencies, family means and within family variances as shown in Table 3.

3·21. Mean value

The mean of the population resulting from positive assortative mating when there is complete reinforcing dominance in both the gene pairs would be given by

$$M_{A1}^{(2)} = \left[\frac{5}{12} + \frac{(t-r)(t^2-3t-1)}{6(1+t)(2+t^2)} \right] (h_a + h_b). \qquad \ldots(22)$$

It can be seen that the mean takes a maximum value of $5/12$ and a manimum value of $1/3$. This means that as the recombination value decreases from 0 5 to 0 0, the mean value decreases from $5/12$ to $1/3$. In other words, in the presence of dominance the effect of linkage is to depress the mean value of the original population given by (14) more than that expected in the absence of linkage. The action of positive assortative mating in decreasing the mean value is, therefore, more prominent when the two factors are closely linked. This is quite in contrast with the regular inbreeding systems, where linkage does not affect the mean value at all.

TABLE 3. *Frequencies, mean values and variances of families*

Mating type	Frequency	Family mean	Family variance
$AB/AB \times AB/AB$	$t^1/4(2+t^2)$	(d_a+d_b)	0
$AB/AB \times AB/aB$	$rt^3/(2+t^2)$	$\frac{1}{2}(d_a+h_a)+d_b$	$\frac{1}{4}(d_a-h_a)^2$
$AB/AB \times AB/Ab$	$rt^3/(2+t^2)$	$d_a+\frac{1}{2}(d_b+h_b)$	$\frac{1}{4}(d_b-h_b)^2$
$AB/AB \times AB/ab$	$t^4/(2+t^2)$	$\frac{1}{2}(d_a+h_a+d_b+h_b)$	$\frac{1}{4}(d_a-h_a)^2+\frac{1}{4}(d_b-h_b)^2+$ $\frac{1}{2}(t-r)(d_a-h_a)(d_b-h_b)$
$AB/AB \times Ab/aB$	$r^2t^2/(2+t^2)$	$\frac{1}{2}(d_a+h_a+d_b+h_b)$	$\frac{1}{4}(d_a-h_a)^2+\frac{1}{4}(d_b-h_b)^2-$ $\frac{1}{2}(t-r)(d_a-h_a)(d_b-h_b)$
$AB/aB \times AB/aB$	$r^2t^2/(2+t^2)$	$\frac{1}{2}h_a+d_b$	$\frac{1}{2}d_a^2+\frac{1}{4}h_a^2$
$AB/aB \times AB/Ab$	$r^2t^2/(2+t^2)$	$\frac{1}{2}(d_a+h_a+d_b+h_b)$	$\frac{1}{4}(d_a-h_a)^2+\frac{1}{4}(d_b-h_b)^2$
$AB/aB \times AB/ab$	$rt^3/(2+t^2)$	$\frac{1}{2}(h_a+d_b+h_b)$	$\frac{1}{2}d_a^2+\frac{1}{4}h_a^2+\frac{1}{4}(d_b-h_b)^2+$ $\frac{1}{2}(t-r)d_a(d_b-h_b)$
$AB/aB \times Ab/aB$	$r^3t/(2+t^2)$	$\frac{1}{2}(h_a+d_b+h_b)$	$\frac{1}{2}d_a^2+\frac{1}{4}h_a^2+\frac{1}{4}(d_b-h_b)^2-$ $\frac{1}{2}(t-r)d_a(d_b-h_b)$
$AB/Ab \times AB/Ab$	$r^2t^2/(2+t^2)$	$d_a+\frac{1}{2}h_b$	$\frac{1}{2}d_b^2+\frac{1}{4}h_b^2$
$AB/Ab \times AB/ab$	$rt^3/(2+t^2)$	$\frac{1}{2}(d_a+h_a+h_b)$	$\frac{1}{4}(d_a-h_a)^2+\frac{1}{2}d_b^2+\frac{1}{4}h_b^2+$ $\frac{1}{2}(t-r)d_b(d_a-h_a)$
$AB/Ab \times Ab/aB$	$r^3t/(2+t^2)$	$\frac{1}{2}(d_a+h_a+h_b)$	$\frac{1}{4}(d_a-h_a)^2+\frac{1}{2}d_b^2+\frac{1}{4}h_b^2-$ $\frac{1}{2}(t-r)d_b(d_a-h_a)$
$AB/ab \times AB/ab$	$t^4/(2+t^2)$	$\frac{1}{2}(h_a+h_b)$	$\frac{1}{2}d_a^2+\frac{1}{4}h_a^2+\frac{1}{2}d_b^2+\frac{1}{4}h_b^2+$ $(t-r)[d_ad_b+\frac{1}{2}(t-r)h_ah_b]$
$AB/ab \times Ab/aB$	$r^2t^2/(2+t^2)$	$\frac{1}{2}(h_a+h_b)$	$\frac{1}{2}d_a^2+\frac{1}{4}h_a^2+\frac{1}{2}d_b^2+\frac{1}{4}h_b^2$
$Ab/aB \times Ab/aB$	$r^4/(2+t^2)$	$\frac{1}{2}(h_a+h_b)$	$\frac{1}{2}d_a^2+\frac{1}{4}h_a^2+\frac{1}{2}d_b^2+\frac{1}{4}h_b^2-$ $(t-r)[d_ad_b+\frac{1}{2}(t-r)h_ah_b]$
$Ab/Ab \times Ab/Ab$	$r^3/8(1+t)$	(d_a-d_b)	0
$Ab/Ab \times Ab/ab$	$r^2t/2(1+t)$	$\frac{1}{2}(d_a+h_a)-d_b$	$\frac{1}{4}(d_a-h_a)^2$
$Ab/Ab \times aB/aB$	$r^3/4(1+t)$	(h_a+h_b)	0
$Ab/Ab \times aB/ab$	$r^2t/2(1+t)$	$h_a+\frac{1}{2}(h_b-d_b)$	$\frac{1}{4}(d_b+h_b)^2$
$Ab/ab \times Ab/ab$	$rt^2/2(1+t)$	$\frac{1}{2}h_a-d_b$	$\frac{1}{2}d_a^2+\frac{1}{4}h_a^2$
$Ab/ab \times aB/aB$	$r^2t/2(1+t)$	$\frac{1}{2}(h_a-d_a)+h_b$	$\frac{1}{4}(d_a+h_a)^2$
$Ab/ab \times aB/ab$	$rt^2/(1+t)$	$\frac{1}{2}(h_a-d_a+h_b-d_b)$	$\frac{1}{4}(d_a+h_a)^2+\frac{1}{4}(d_b+h_b)^2$
$aB/aB \times aB/aB$	$r^3/8(1+t)$	(d_b-d_a)	0
$aB/aB \times aB/ab$	$r^2t/2(1+t)$	$\frac{1}{2}(d_b+h_b)-d_a$	$\frac{1}{4}(d_b-h_b)^2$
$aB/ab \times aB/ab$	$r^2t/2(1+t)$	$\frac{1}{2}h_b-d_a$	$\frac{1}{2}d_b^2+\frac{1}{4}h_b^2$
$ab/ab \times ab/ab$	$t^2/4$	$-(d_a+d_b)$	0

3·22. Variances

$$
{}_1V_{A1}^{(2)} = \left[\frac{1}{3} + \frac{(t-r)(1+3t-t^2)}{6(1+t)(2+t)}\right] D^{(2)} +
$$

$$
\left[\frac{19}{288} + \frac{(t-r)(18t^7+9t^6+4t^5+145t^4-200t^3-32t^2+16t-68)}{288(1+t)^2(2+t^2)^2}\right] H^{(2)} +
$$

$$
\left[\frac{1}{12} + \frac{(t-r)(3t^3+t^2+12t+8)}{12(1+t)(2+t^2)}\right] D^{(2)'} +
$$

$$
\left[\frac{1}{24} + \frac{(r-t)(6t^7-6t^6+16t^5-26t^4+4t^3-2t^2-32t+10)}{12(1+t)^2(2+t^2)^2}\right] H^{(2)'} +
$$

$$
\left[\frac{1}{12} + \frac{(t-r)(3t^3+7t^2-6t+2)}{12(1+t)(2+t^2)}\right] B^{(2)} + \frac{t(t-r)(t^2-t+2)}{2(1+t)(2+t^2)} \ B^{(2)'} \quad ...(23)
$$

$$
{}_2V_{A1}^{(2)} = \frac{1}{4}D^{(2)} + \left[\frac{17}{96} + \frac{(t-r)(10-18t+5t^2+3t^3-6t^4)}{96(1+t)(2+t^2)}\right] H^{(2)} +
$$

$$
\frac{(t-r)^2}{4} \ D^{(2)'} + \frac{(t-r)(8t^4-14t^3+13t^2-6t+1)}{2(2+t^2)} \ H^{(2)'} +
$$

$$
\left[\frac{(r-t)(3t^3+7t^2-6t+2)}{12(1+t)(2+t^2)} - \frac{1}{12}\right] B^{(2)} + \frac{t(t-2)(t-r)^2}{2(2+t^2)} \ B^{(2)'} \quad ...(24)
$$

$$
V_{A1}^{(2)} = \left[\frac{7}{12} + \frac{(t-r)(1+3t-t^2)}{6(1+t)(2+t^2)}\right] D^{(2)} +
$$

$$
\left[\frac{35}{144} + \frac{(r-t)(8t^5-88t^4+176t^3+80t^2+32t+8)}{288(1+t)^2(2+t^2)^2}\right] H^{(2)} +
$$

$$
\left[\frac{1}{12} + \frac{(t-r)(3t^4+3t^3+5t^2+9t+1)}{6(1+t)(2+t^2)}\right] D^{(2)'} +
$$

$$
\left[\frac{1}{24} + \frac{(t-r)(48t^8+6t^7+60t^6+40t^5-257t^4+44t^3+32t^2-16t+2)}{12(1+t)^2(2+t^2)^2}\right]
$$

$$
H^{(2)'} + \frac{t(t-r)(1-t)(2-t^2)}{(1+t)(2+t^2)} \ B^{(2)'} \qquad ...(25)
$$

where

$$
B^{(2)} = (d_a h_a + d_b h_b)
$$

$$
B^{(2)'} = (d_a h_b + d_b h_a).
$$

For $r=0{\cdot}5$ (no linkage) these expressions reduce to

$$_1V^{(2)}_{A1}= \frac{1}{3}\ D^{(2)}+\frac{19}{288}\ H^{(2)}+\frac{1}{12}\ D^{(2)'}+\frac{1}{24}\ H^{(2)'}+\frac{1}{12}\ B^{(2)}$$

$$\ldots(26)$$

$$_2V^{(2)}_{A1}= \frac{1}{4}\ D^{(2)}+\frac{17}{96}\ H^{(2)}-\frac{1}{12}\ B^{(2)} \qquad\qquad \ldots(27)$$

$$V^{(2)}_{A1}= \frac{7}{12}\ D^{(2)}+\frac{35}{144}\ H^{(2)}+\frac{1}{12}\ D^{(2)'}+\frac{1}{24}\ H^{(2)'} \qquad \ldots(28)$$

which are in agreement with the expressions given by Breese (1956).

For $r=0$ (complete linkage), (23), (24) and (25) reduce to

$$_1V^{(2)}_{A1}= \frac{5}{12}\ D^{(2)}+\frac{1}{18}\ H^{(2)}+\frac{5}{12}\ D^{(2)'}+\frac{1}{9}\ H^{(2)'}+\frac{1}{6}B^{(2)}+\frac{1}{6}\ B^{(2)}$$

$$\ldots(29)$$

$$_2V^{(2)}_{A1}= \frac{1}{4}\ D^{(2)}+\frac{1}{6}\ H^{(2)}+\frac{1}{4}\ D^{(2)'}+\frac{1}{3}\ H^{(2)'}-\frac{1}{6}\ B^{(2)}-\frac{1}{6}\ B^{(2)}$$

$$\ldots(30)$$

$$V^{(2)}_{A1}= \frac{2}{3}\ D^{(2)}+\frac{2}{9}\ H^{(2)}+\frac{2}{3}\ D^{(2)'}+\frac{4}{9}\ H^{(2)'}\ . \qquad \ldots(31)$$

The expressions (29), (30) and (31) can be written as

$$_1V^{(2)}_{A1}= \frac{5}{12}\ D^{(2)''}+\frac{1}{18}\ H^{(2)''}+\frac{1}{6}\ B^{(2)''} \qquad\qquad \ldots(32)$$

$$_2V^{(2)}_{A1}= \frac{1}{4}\ D^{(2)''}+\frac{1}{6}\ H^{(2)''}-\frac{1}{6}\ B^{(2)''} \qquad\qquad \ldots(33)$$

$$V^{(2)}_{A1}= \frac{2}{3}\ D^{(2)''}+\frac{2}{9}\ H^{(2)''} \qquad\qquad \ldots(34)$$

where

$$D^{(2)''} =(d_a+d_b)^2$$

$$H^{(2)''} =(h_a+h_b)^2$$

$$B^{(2)''} =(d_a+d_b)(h_a+h_b).$$

It can be seen that the coefficient of $D^{(2)''}$, $H^{(2)''}$ and $B^{(2)''}$ in (32), (33) and (34) are the same as those of $d_a{}^2$, $h_a{}^2$ and $d_a h_a$ respectively in (4), (5) and (6) for $p=q=(1/2)$. So it can be concluded that in the case of complete linkage both the genes combine to act as a single gene in expressing their additive and dominance effects,

From (26) and (29) it can be seen that the coefficient of $D^{(2)}$ in the first rank variance takes the minimum value of $1/3$ when there is no linkage and a maximum value of $5/12$ when the linkage is complete. That means as the recombination value decreases from 0.5 to 0.0 the variation due to additive genetic effect increases from $1/3$ to $5/12$. Similarly by studying the coefficient of $H^{(2)}$ in (26) and (29) in the first rank variance it can be seen that as the intensity of linkage increases the variation due to dominance decreases from $19/288$ to $1/18$. In the second rank variance, however, the variance due to additive genetic effect remains same for all intensities of linkage but the variance due to dominance effect decreases from $17/96$ to $1/6$.

Considering the total variance and putting $d_a = d_b = h_a = h_b$, it is observed that as the intensity of linkage increases, the variance increases from $67/36$ to $32/9$. It can, therefore, be concluded that the variance of family means as well as the mean variance within families both are more when the two segregating genes are linked than those expected when genes freely recombine.

SUMMARY

The effect of positive assortative mating on the mean value and the variances has been studied. With one locus segregating, the effect of repeated positive assortative mating has been dealt with giving general results for a population subjected to this type of mating for 'n' generations. The consequences, of two linked loci segregating, have also been studied.

With one locus segregating and when complete dominance is assumed, it is found that the mean value is decreased, the decrease being proportional to the decrease in the heterozygosity. The increase in total variability due to positive assortative mating is, however, found to depend on the gene frequency. If the system of mating is practised for an infinitely large number of generations, the ultimate result is that all the variance tend to appear in the variance of the family means.

When two segregating genetic factors are linked and when there is no dominance it is found that there is no change in the mean value but both the first and second rank variances are more than those expected in the absence of linkage. When dominance is present the linkage affects the mean value in decreasing it. The first and second rank variances both tend to increase due to linkage when complete dominance is assumed for either of the factors.

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