

QUANTITATIVE ANALYSIS OF A CROSS BETWEEN POPULATIONS AND THEIR DERIVED GENERATIONS

José Branco de Miranda Filho

ABSTRACT

Formulas are presented for the biometrical interpretation of means and genetic variances of generations resulting from a cross between two random mating populations. A simple model with one locus and two alleles under the additive-dominance gene action was considered; epistasis was neglected when extended for multiple loci. Besides the formulations for generation means, two other parameters were considered: b , half the contrast for the comparison of parent population means; or the effect of selection if the parents come from a divergent selection program; and h , the mid-parent heterosis of a quantitative trait in the population cross. Formulas for estimating b and h and for the appropriate tests of hypothesis are given based on the least square procedure. The theoretical patterns of variation of b and h and the difference between them are shown graphically.

The expected genetic variances within generations (parents included) are given according to the model, by varying allele frequencies and levels of dominance. It is expected that the values and formulas will be useful for the interpretation of studies on segregating generations following a cross between two random mating populations.

INTRODUCTION

The genetic structure of random mating populations for quantitative traits in terms of means and variances is well discussed by several authors (Falconer, 1960; Cockerham, 1963, Hallauer and Miranda Filho, 1988).

For a cross between two populations, the first characterization of genetic variance and of partition into its additive and dominance components was given by

Stuber and Cockerham (1966). Hallauer and Miranda Filho (1988) also provide the basis for the interpretation of the mean and genetic variance in a population cross, following a simple model based on additive-dominance gene effects, without epistasis.

Mather and Jinks (1971) give formula for the interpretation of the means and variances in the cross (F_1 generation) between two inbred lines and advanced generations (F_2 and backcrosses). The purpose of this communication is to provide formulas for the interpretation of the means and genetic variances in two random mating populations and derived generations (F_1 , F_2 and backcrosses). Two other parameters were included: b , half the difference between the population means; and h , the mid-parent heterosis. Formulas for their estimation and for the pertinent tests of hypothesis were developed through the least square procedure.

MATERIAL AND METHODS

We assumed two random mating populations in Hardy-Weinberg equilibrium with allele frequencies $p(B):q(b)$ in population P_1 and $r(B):s(b)$ in population P_2 , so that the genotypic arrays are $p^2(BB):2pq(Bb):q^2(bb)$ and $r^2(BB):2rs(Bb):s^2(bb)$, respectively, at one locus (B,b) level. The following generations, derived from the population cross ($P_1 \times P_2$), were considered: F_1 (first generation cross), F_2 (F_1 random mated), and backcrosses $B_1 = F_1 \times P_1$ and $B_2 = F_1 \times P_2$; parents (P_1 and P_2) also were included. A simple additive-dominance model was assumed, so that the genotypic values are represented by $u + a$, $u + d$, and $u - a$, for BB , Bb and bb , respectively; u is the mean between the two homozygotes, a is half the difference between the homozygotes and d is a deviation due to dominance.

In the analysis of generation means, the formulas for the analysis of variance, estimation of parameters and tests of hypothesis were derived by the least square procedure.

RESULTS AND DISCUSSION

The genotypic arrays relative to the six populations (parents included) are as shown in Table I.

The population means at one locus level are then expressed according to the following relations:

$$\bar{P}_1 = u + (p-q)a + 2pqd$$

$$\bar{P}_2 = u + (r-s)a + 2rsd$$

Table I - Genotypic arrays within populations (generations) for one locus with two alleles.

Generation*	Genotypes		
	BB	Bb	bb
P_1	p^2	$2pq$	q^2
P_2	r^2	$2rs$	s^2
F_1	pr	$ps + qr$	qs
F_2	$\frac{1}{4}(p+r)^2$	$\frac{1}{2}(p+r)(q+s)$	$\frac{1}{4}(q+s)^2$
B_1	$\frac{1}{2}p(p+r)$	$pq + \frac{1}{2}(ps + qr)$	$\frac{1}{2}q(q+s)$
B_2	$\frac{1}{2}r(p+r)$	$rs + \frac{1}{2}(ps + qr)$	$\frac{1}{2}s(q+s)$

* P_1, P_2 : parents; F_1, F_2 : first and second generation of the hybrid cross; B_1, B_2 : backcrosses $F_1 \times P_1$ and $F_1 \times P_2$, respectively.

$$\begin{aligned} \bar{F}_1 &= u + (pr - qs)a + (ps + pq)d &= \frac{1}{2}(\bar{P}_1 + \bar{P}_2) + h \\ \bar{F}_2 &= u + (pr - qs)a + \frac{1}{2}(pq + rs + ps + qr)d &= \frac{1}{2}(\bar{P}_1 + \bar{P}_2) + \frac{1}{2}h \\ \bar{B}_1 &= u + \frac{1}{4}[3(p - q) + (r - s)]a + \frac{1}{2}(2pq + ps + pr)d &= \frac{1}{4}(3\bar{P}_1 + \bar{P}_2) + \frac{1}{2}h \\ \bar{B}_2 &= u + \frac{1}{4}[(p - q) + 3(r - s)]a + \frac{1}{2}(2rs + ps + qr)d &= \frac{1}{4}(\bar{P}_1 + 3\bar{P}_2) + \frac{1}{2}h \end{aligned}$$

where h is the mid-parent heterosis. The right hand formulas are similar to those given by Mather and Jinks (1971) for generations derived from a cross between two inbred lines. For random mating populations they also can be derived from the general procedure for prediction of generation means as given by Vencovsky (1970; op. cit. Hallauer and Miranda Filho, 1988). A similar formulation was used by Vencovsky and Zinsly (1969) for the study of generation means ($\bar{P}_1, \bar{P}_2, \bar{F}_1, \bar{F}_2$ and \bar{B}_1) and to predict the second backcross generation for yield and popping expansion in a popcorn breeding program.

By taking m_0 (the average of the parents) as a reference, the following general model can be used for the analysis of population means:

$$Y_i = m_0 + \theta_{1i}b + \theta_{2i}h + \bar{e}_i \quad (\text{Model 1})$$

where Y_i represents the means of one of the six population already defined; b is the deviation (negative or positive) of parents (P_1 and P_2) from their average value (m_0); h is the mid-parent heterosis; θ_1 and θ_2 are the coefficients of b and h , according to the expected genetic structure of the population means; and \bar{e}_i is the error associated with the i^{th} mean (over R replications). Such a model is similar to that given by Mather and Jinks (1971) for the genetic analysis of generations derived from the cross of inbred lines, where b and h are replaced by a (half the difference between homozygotes) and d (dominance deviation), respectively).

Therefore, using the least square procedure for the estimation of parameters, the matrix equation ($Y = X\beta + \epsilon$) is similar to that given by Mather and Jinks (1971):

$$X = \begin{vmatrix} 1 & -1 & 0 \\ 1 & 1 & 0 \\ 1 & 0 & 1 \\ 1 & 0 & \frac{1}{2} \\ 1 & \frac{1}{2} & \frac{1}{2} \\ 1 & \frac{1}{2} & \frac{1}{2} \end{vmatrix} \quad \hat{\beta} = \begin{vmatrix} \hat{m}_0 \\ \hat{b} \\ \hat{h} \end{vmatrix} \quad Y = \begin{vmatrix} Y_1 \\ Y_2 \\ Y_3 \\ Y_4 \\ Y_5 \\ Y_6 \end{vmatrix} = \begin{vmatrix} \bar{P}_1 \\ \bar{P}_2 \\ \bar{F}_1 \\ \bar{F}_2 \\ \bar{B}_1 \\ \bar{B}_2 \end{vmatrix}$$

The solution of the normal equations, $\hat{\beta} = (X'X)^{-1} X'Y$, leads to the following estimates, as similarly by Pereira *et al.* (1989) for the model of Mather and Jinks (1971):

Estimates

$$\hat{m}_0 = \frac{1}{17} (7 T_1 - 10 T_3)$$

$$\hat{b} = \frac{2}{5} T_2$$

$$\hat{h} = \frac{1}{17} (24 T_3 - 10 T_1)$$

Values of T_1 , T_2 and T_3

$$T_1 = \bar{P}_1 + \bar{P}_2 + \bar{F}_1 + \bar{F}_2 + \bar{B}_1 + \bar{B}_2$$

$$T_2 = (\bar{P}_2 - \bar{P}_1) + \frac{1}{2} (\bar{B}_2 - \bar{B}_1)$$

$$T_3 = \bar{F}_1 + \frac{1}{2} (\bar{F}_2 + \bar{B}_1 + \bar{B}_2)$$

The effects b and h increase or decrease in the same direction when changing p and r in the joint distribution of gene frequencies. In fact, $b = (r-p) [a + (1-p-r) d] = \frac{1}{2} (r-p) (\alpha_1 + \alpha_2)$ and $h = (r-p)^2 d = \frac{1}{2} (r-p) (\alpha_1 - \alpha_2)$, where α_1 and α_2 are the average effects of gene substitution for the populations P_1 and P_2 , respectively. Figure 1 shows the pattern of variation of both b and h for some combinations of allele frequencies. The difference between b and h is: $D = (r-p) [a + (1-2r)d] = (r-p) \alpha_2$, and its variation is shown in Figure 2 for several combinations of allele frequencies ($p \leq 0.5$; $r \leq 1$; $p < r$) and levels of dominance. Obviously $D = 0$ for $p = r$ in any instance, and in the particular case of complete dominance $D = 0$ also for $r = 1$ for any value of p ; therefore, in that case for any p and increasing r , D increases up to a maximum and then decreases to zero when $r = 1$.

If P_1 and P_2 come from divergent selection of the same base population, then b is a measure of the effectiveness of selection, on the assumption that selection is equally effective for increasing or decreasing the trait: in this case, \hat{m}_0 is an estimate of the original population mean. Another hypothesis that may be considered is that selection has been equally effective in changing allele frequency by an amount Δ in both direction, and then the original population mean (m'_0) is changed by $b_1 = -2\Delta\alpha_0 - \frac{1}{2} h$ in the downward selection and by $b_2 = 2\Delta\alpha_0 - \frac{1}{2} h$ in the upward selection, where α_0 is the average effect of gene substitution with reference to the original population and $h = (2\Delta)^2 d$. Under this hypothesis the appropriate model should be:

$$Y_i = m'_0 + 2 \theta_{1i} \Delta \alpha_0 + (\theta_{2i} - \frac{1}{2}) h + \bar{e}_i \tag{Model 2}$$

It can be shown that: $m'_0 = m_0 + \frac{1}{2} h$, and it follows that $2\Delta\alpha = b$, where b is the change in the population mean, as defined for Model 1. It can be shown that \hat{h} does not change in relation to Model 1. In the same way, the sums of squares due to parameters in the model are the same for both models herein considered, whose underlying assumptions are: i) symmetric response in the population mean (Model 1); ii) symmetric change in allele frequency (Model 2). The only differences lie in the estimate of the original population mean, m_0 (average of divergent parents) in Model 1 and $m'_0 = m_0 + \frac{1}{2} h$ in Model 2; and the expected change in the population mean is b in Model 1 and b_1 (downward) and b_2 (upward) in Model 2.

It can be shown that, under the assumption of symmetric change in allele frequency, the difference between b and h is $D = 2 \Delta (\alpha_0 - 2\Delta d) = 2 \Delta \alpha_2$, where α_2 is the average effect of gene substitution in the upward selected population with allele frequency $p_0 + \Delta$.

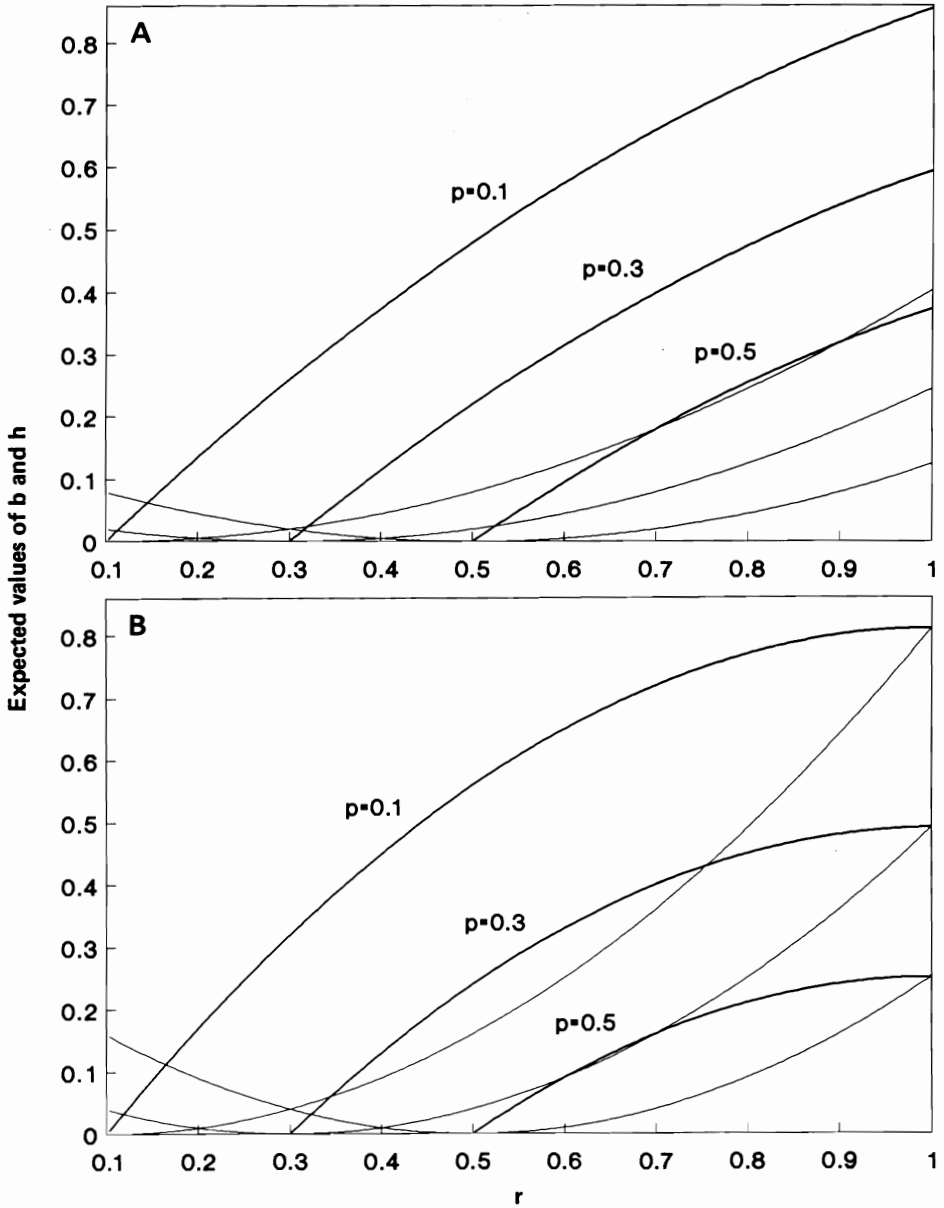


Figure 1 - Expected values of b (thick lines) and h (thin lines) for some combinations of allele frequencies (p and r) and two levels of dominance: A - partial dominance ($a = 1$; $d = 0.5$); B - complete dominance ($a = 1$; $d = 1$).

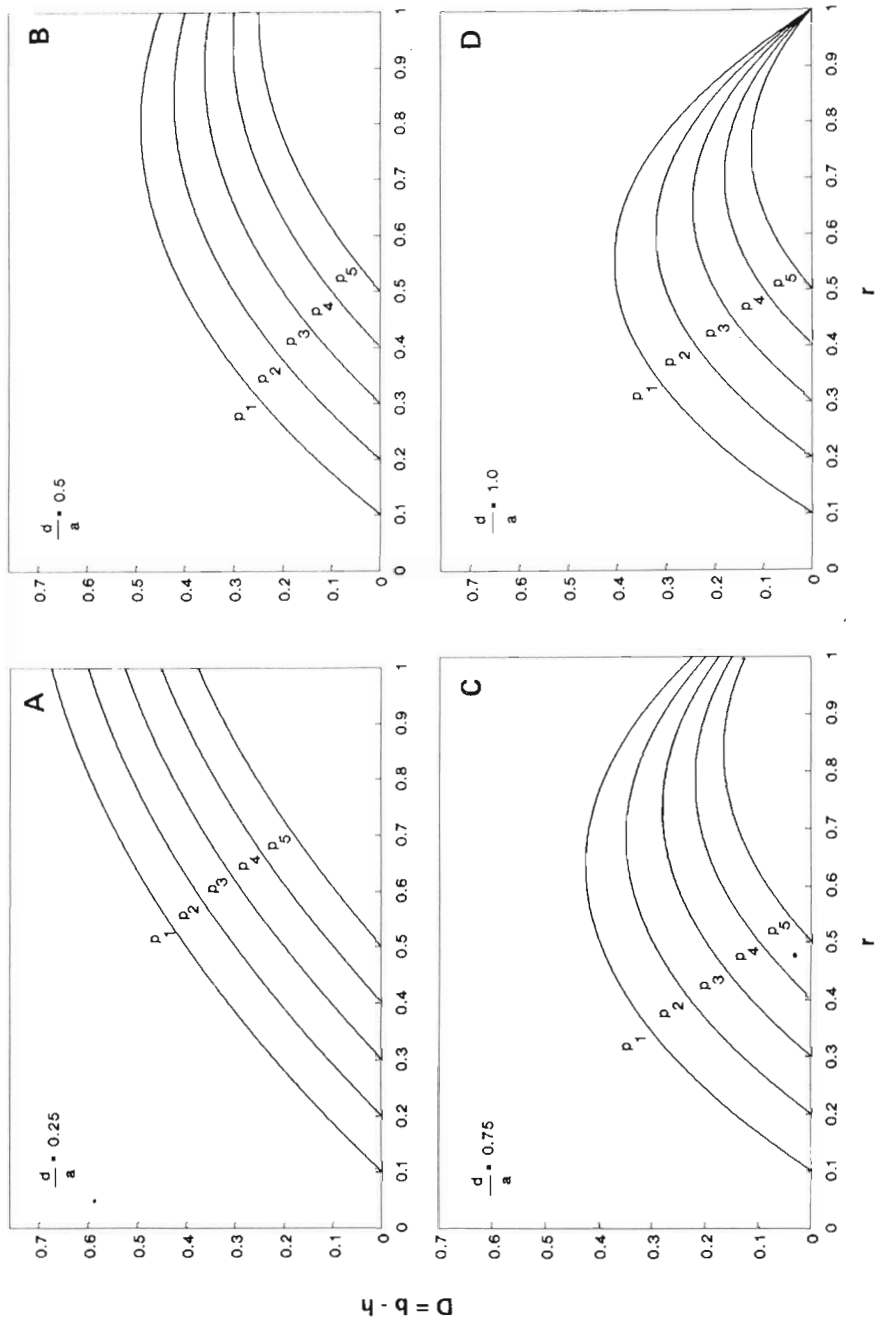


Figure 2 - Pattern of variation of the difference $D = b - h$ for some combinations of allele frequencies, p ($p_1 = 0.1; p_2 = 0.2; p_3 = 0.3; p_4 = 0.4; p_5 = 0.5$) and r ($0 r 1$) and levels of dominance ($d/a: 0.25; 0.50; 0.75; 1.00$).

In the analysis of variance, usually a preliminary analysis is performed according to the experimental design, mainly to provide an estimate of the error variance. In the analysis of variance for the adopted model according to the least square procedure, the sums of squares are obtained as shown in Table II.

Table II - Analysis of variance for generation means according to the least square procedure.

Source	d.f.	Sums of squares	Mean squares	F
Total (uncorrected)	6	$\sum_1 Y_1^2$		
Parameters (m, b, h)	3	$\frac{1}{85} (35 T_1^2 + 34 T_2^2 + 120 T_3^2 - 100 T_1 T_3)$		
$\hat{b}/\hat{m}, \hat{h}$	1	$\frac{2}{5} T_2^2$	M_1	M_1/M_4
$\hat{h}/\hat{m}, \hat{b}$	1	$\frac{1}{102} (5T_1 - 12T_3)^2$	M_2	M_2/M_4
Deviations	3	SS (Total) - SS ($\hat{m}, \hat{b}, \hat{h}$)	M_3	M_3/M_4
Error	5 (r - 1)	--	M_4	

Standard error of the estimates: $s_{\hat{b}} = 0.6325 \bar{\sigma}$; $s_{\hat{h}} = 1.1882 \bar{\sigma}$, where $\bar{\sigma}$ is estimated by the square root of the error means square (for treatment means).

Because b and h are orthogonal contrasts, the test for the null hypothesis $b = 0$ and $h = 0$ can alternatively be performed by the t test, as

$$t_{\hat{b}} = \hat{b} (5R/2 \hat{\sigma}^2)^{\frac{1}{2}} \quad \text{and} \quad t_{\hat{h}} = \hat{h} (17R/24 \hat{\sigma}^2)^{\frac{1}{2}}$$

which are the square roots of the corresponding F's.

The total genetic variances expressed in different generations are functions of allele frequencies and the average effects of gene substitution, $\alpha_1 = [a + (1-2p)d]$ and $\alpha_2 = [a + (1-2r)d]$, whose reference equilibrium populations are P_1 and P_2 , respectively. Then, at one locus level, we have:

$$V(P_1) = 2 pq \alpha_1^2 + (2pqd)^2$$

$$V(P_2) = 2 rs \alpha_2^2 + (2rsd)^2$$

$$V(F_1) = pq \alpha_2^2 + rs \alpha_1^2 + (2pqd)(2rsd)$$

$$V(F_2) = \frac{1}{2}(p+r)(q+s) \left[\frac{\alpha_1 + \alpha_2}{2} \right]^2 + \left[\frac{1}{2}(p+r)(q+s)d \right]^2$$

$$V(B_1) = \frac{1}{4}(p+r)(q+s) \alpha_1^2 + pq \left[\frac{\alpha_1 + \alpha_2}{2} \right]^2 + pq(p+r)(q+s)d^2$$

$$V(B_2) = \frac{1}{4}(p+r)(p+s) \alpha_2^2 + rs \left[\frac{\alpha_1 + \alpha_2}{2} \right]^2 + rs(p+r)(q+s)d^2$$

For F_2 , B_1 and B_2 , the quantity $\frac{\alpha_1 + \alpha_2}{2}$ can be written as:

$[a + (1-p-r)d] = \alpha_{12}$, which is the average effect of gene substitution as defined for the F_2 population. For multilocus traits, the above formulations must be extended by summation over loci.

Table III shows the expected genetic variance within generations for one locus with two alleles and several allele frequencies for no dominance ($d/a = 0$) and complete dominance ($d/a = 1$). The values for P_1 and P_2 are also shown in Figure 3, where partial dominance ($d/a = 0.75; 0.50; 0.25$) was also considered. The same figure may represent both P_1 and P_2 , depending only on the allele frequency considered (p or r); therefore some comparisons between P_1 and P_2 can be obtained directly from the same figure. For example, under complete dominance, the variance of P_1 or $V(P_1)$ at $p = 0.4$ is smaller than the variance of P_2 , or $V(P_2)$, only in the range of $0.2 < r < 0.4$; it follows that under the assumption of $p < r$, $V(P_1)$ is always higher than $V(P_2)$ for $p = 0.3$.

Table IV shows the range of allele frequency (r) in P_2 such that $V(P_1)$ is smaller than $V(P_2)$, for some values of p (allele frequency in P_1). The maximum variances for P_1 and P_2 and the corresponding allele frequencies (at maximum) for several levels of dominance can be seen in Figure 3, but their patterns of variation are shown directly in Figure 4.

The variances shown in Table IV for generations other than P_1 and P_2 are also shown in Figure 5 for no dominance and in Figure 6 for complete dominance.

Table III - Expected total genetic variance*within generations for no dominance ($a = 1$; $d = 0$) and complete dominance ($a = d = 1$) at one locus level and several combinations of allele frequencies (p and r).

p	r	No dominance						Complete dominance					
		P ₁	P ₂	F ₁	F ₂	B ₁	B ₂	P ₁	P ₂	F ₁	F ₂	B ₁	B ₂
0.1	0.1	180	180	180	180	180	180	616	616	616	616	616	616
	0.3	180	420	300	320	250	370	616	1000	932	922	806	986
	0.5	180	500	340	420	300	460	616	750	990	1000	932	910
	0.7	180	420	300	480	330	450	616	328	788	922	994	590
	0.9	180	180	180	500	340	340	616	40	328	750	990	190
0.3	0.1	420	180	300	320	370	250	1000	616	932	922	986	806
	0.3	420	420	420	420	420	420	1000	1000	1000	1000	1000	1000
	0.5	420	500	460	480	450	490	1000	750	910	922	974	840
	0.7	420	420	420	500	460	460	1000	328	664	750	910	510
	0.9	420	180	300	480	450	330	1000	40	260	538	806	154
0.5	0.1	500	180	340	420	460	300	750	616	990	1000	910	932
	0.3	500	420	460	480	490	450	750	1000	910	922	840	974
	0.5	500	500	500	500	500	500	750	750	750	750	750	750
	0.7	500	420	460	480	490	450	750	328	510	538	640	422
	0.9	500	180	340	420	460	300	750	40	190	328	510	116
0.7	0.1	420	180	300	480	450	330	328	616	788	922	590	994
	0.3	420	420	420	500	460	460	328	1000	664	750	510	910
	0.5	420	500	460	480	450	490	328	750	510	538	422	640
	0.7	420	420	420	420	420	420	328	328	328	328	328	328
	0.9	420	180	300	320	370	250	328	40	116	154	226	78
0.9	0.1	180	180	180	500	340	340	40	616	328	750	190	990
	0.3	180	420	300	480	330	450	40	1000	260	538	154	806
	0.5	180	500	340	420	300	460	40	750	190	328	116	510
	0.7	180	420	300	320	250	370	40	328	116	154	78	226
	0.9	180	180	180	180	180	180	40	40	40	40	40	40

*Values multiplied by 10^3 .

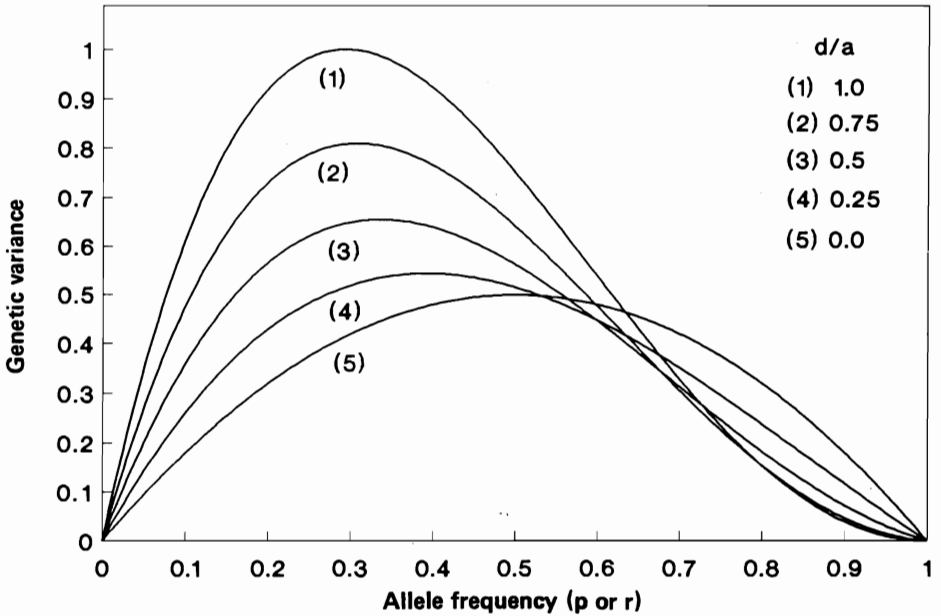


Figure 3 - Expected total genetic variance within populations (P_1 or P_2) for several levels of dominance (d/a : 1.00; 0.75; 0.50; 0.25; 0.00) and varying allele frequencies (p for P_1 , or r for P_2).

By analysing such figures, some comparisons of interest can be drawn; for example, for $p = 0.3$ and $r = 0.5$, under complete dominance it is expected that $V(P_1) > V(P_2)$; $V(F_2) > V(F_1)$; $V(B_1) > V(B_2)$; or comparing all together $V(P_1) > V(B_1) > V(F_2) > V(F_1) > V(B_2) > V(P_2)$.

Other specific comparisons can be drawn from the tables and figures presented in this paper and may eventually help the interpretation of experimental results in the study of segregating generations following a cross between two random mating populations.

Table IV - Range for the allele frequency (r) in P_2 for several allele frequencies (p) in P_1 such that $V(P_1) < V(P_2)$, for complete, partial and no dominance.

P	Complete dominance		Partial dominance		No dominance	
	$V(P_1)$	Range for r	$V(P_1)$	Range for r	$V(P_1)$	Range for r
0.1	0.6156	$0.1 < r < 0.564$	0.3609	$0.1 < r < 0.665$	0.18	$0.1 < r < 0.9$
0.2	0.9216	$0.2 < r < 0.400$	0.5665	$0.2 < r < 0.496$	0.32	$0.2 < r < 0.8$
0.3	0.9996	$r \cong 0.0^*$	0.6489	$0.3 < r < 0.373$	0.42	$0.3 < r < 0.7$
0.4	0.9216	$0.4 > r > 0.200$	0.6384	$0.4 > r > 0.276$	0.48	$0.4 < r < 0.6$
0.5	0.7500	$0.5 > r > 0.134$	0.5625	$0.5 > r > 0.197$	0.50	---
0.6	0.5376	$0.6 > r > 0.083$	0.4464	$0.6 > r > 0.134$	0.48	$0.6 > r > 0.4$
0.7	0.3276	$0.7 > r > 0.046$	0.3129	$0.7 > r > 0.083$	0.42	$0.7 > r > 0.3$
0.8	0.1536	$0.8 > r > 0.020$	0.1824	$0.8 > r > 0.045$	0.32	$0.8 > r > 0.2$
0.9	0.0396	$0.9 > r > 0.005$	0.0729	$0.9 > r > 0.017$	0.18	$0.9 > r > 0.1$

Levels of dominance: complete ($a = d = 1$), partial ($a = 1; d = 0.5$), no dominance ($a = 1; d = 0$).

*Too short an interval to be detected.

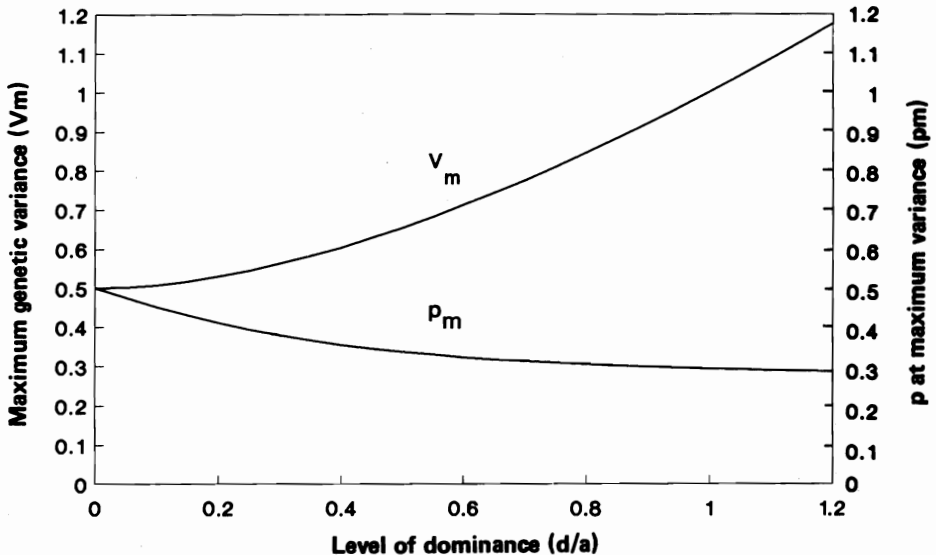


Figure 4 - Expected maximum variances and the corresponding allele frequencies within populations (P_1 or P_2) for several levels of dominance.

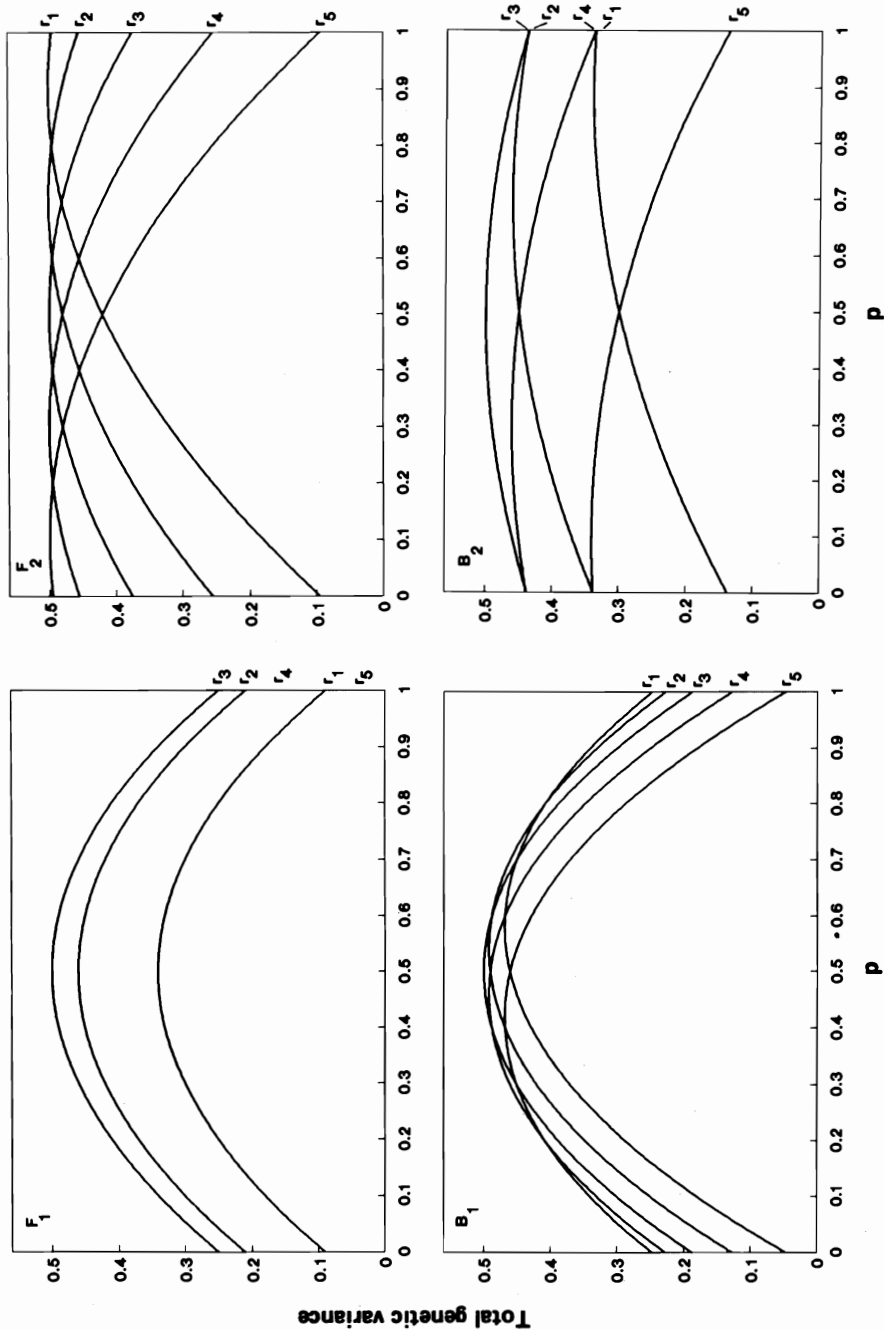


Figure 5 - Expected total genetic variance for generations F_1 , F_2 , B_1 and B_2 for no dominance ($a = 1$; $d = 0$) and varying allele frequencies p ($0 \leq p \leq 1$) and r ($r_1 = 0.1$; $r_2 = 0.3$; $r_3 = 0.5$; $r_4 = 0.7$; $r_5 = 0.9$).

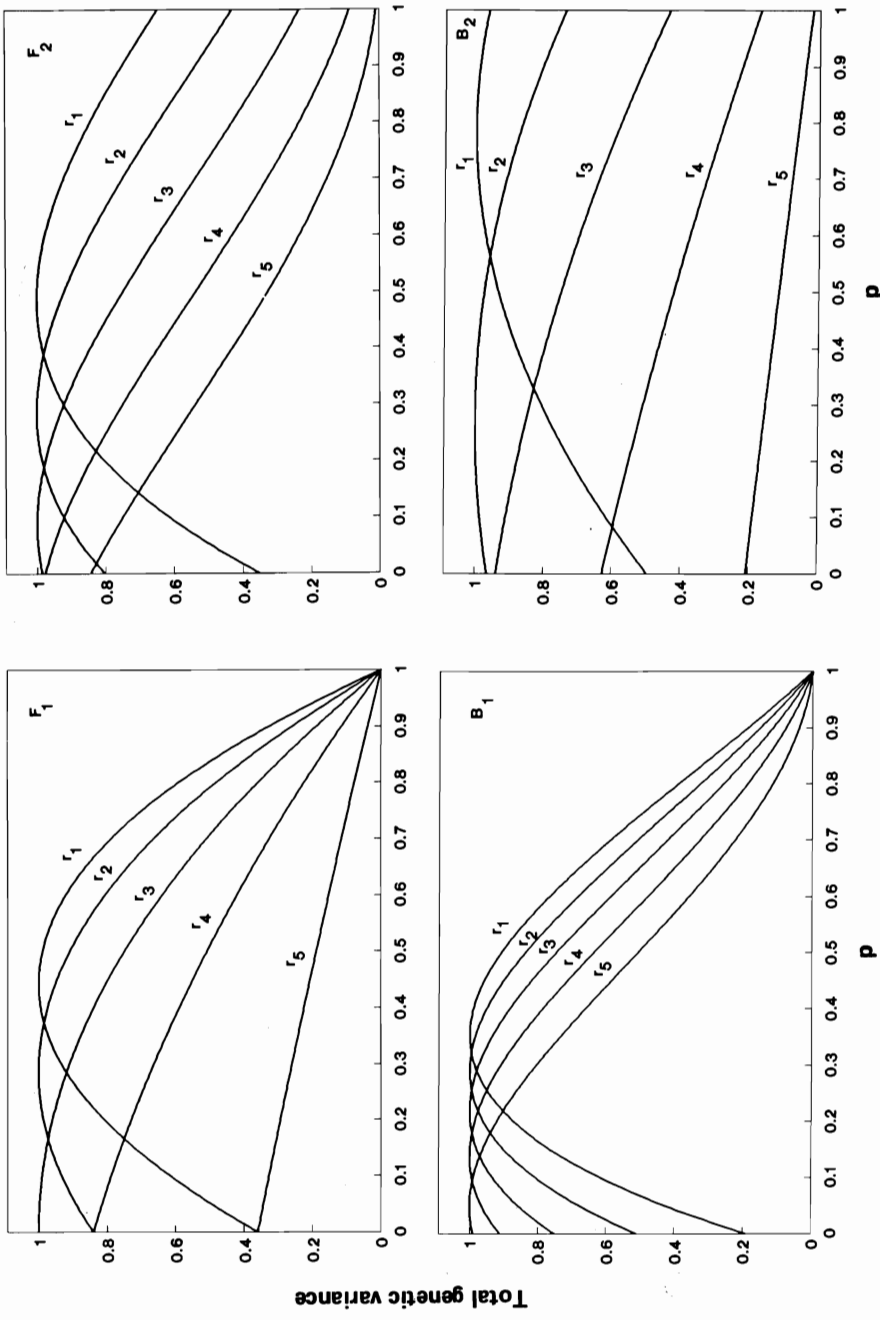


Figure 6 - Expected total genetic variance for generations F_1, F_2, B_1 and B_2 for complete dominance ($a = 1; d = 1$) and varying allele frequencies p ($0 \leq p \leq 1$) and r ($r_1 = 0.1; r_2 = 0.3; r_3 = 0.5; r_4 = 0.7; r_5 = 0.9$).

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RESUMO

São apresentadas fórmulas para a interpretação biométrica de médias e variâncias genéticas de gerações obtidas do cruzamento de duas populações panmíticas. Foi considerado um modelo simples com um loco e dois alelos sob ação gênica aditiva-dominante sem epistase. Além das formulações para médias de gerações, dois outros parâmetros foram considerados: b , um contraste para a comparação das médias das populações parentais, ou para medir o efeito da seleção se os pais provêm de um programa de seleção divergente; e h , a heterose de um caráter quantitativo no híbrido interpopulacional. São dadas fórmulas para estimação de b e h e para os testes de hipóteses apropriados, com base na análise de dados experimentais pelo processo dos quadrados mínimos. O padrão de variação de b e h e da diferença entre eles são mostrados graficamente em bases teóricas.

As variâncias genéticas esperadas dentro de gerações são dadas de acordo com o modelo adotado, variando-se as frequências alélicas e os níveis de dominância. Espera-se que os valores e fórmulas sejam úteis para a interpretação de resultados experimentais no estudo de gerações segregantes obtidas do cruzamento de duas populações panmíticas.

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