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Components of Variance

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Objectives

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- Learn to model components of genetic variances for purposes of estimating heritability.
- Be able to explain
    - the impact of allele frequencies on genetic components of genotypic variability,
    - the reason estimates of components of genetic variability are limited to the population from which they are estimated,
    - the reason additive variance does not imply additive gene action and
    - how additive genetic variance can arise from genes with any degree of dominance or epistasis.

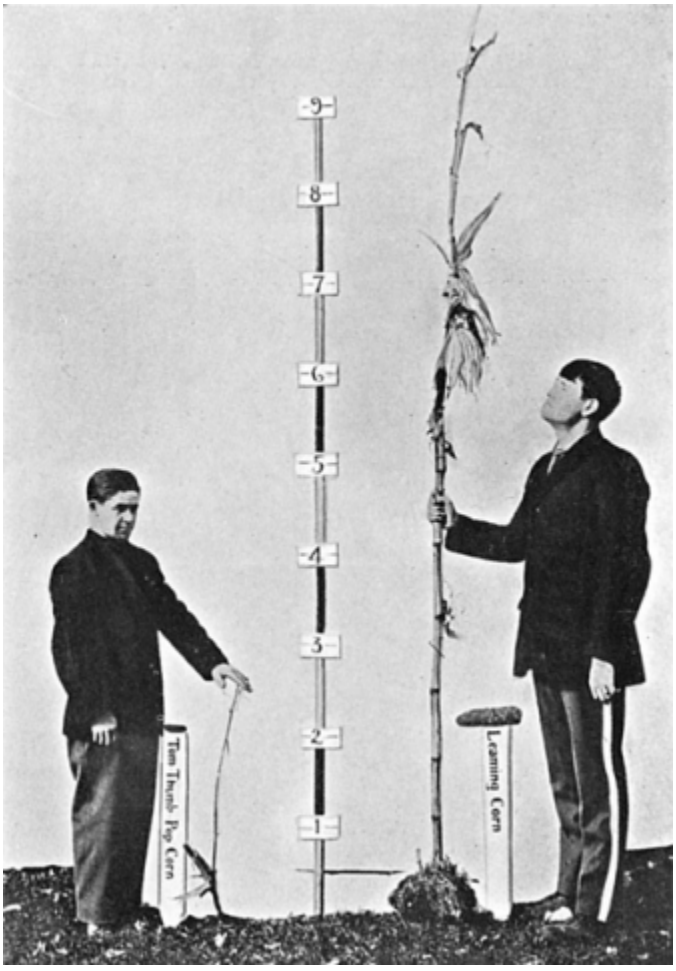

Fig. 1 A short and a tall boy each holding a stalk of corn—one stalk of a race of short corn, the other of tall corn. From "Critique of the Theory of Evolution" (1915) by Thomas Hunt Morgan, available freely at Project Gutenberg. Licensed under Public Domain via Wikimedia Commons.

Phenotypic Components of Variance

Recall that our working model for the phenotype includes genotypic and non-genotypic (environmental) sources of variability:

$$P = \mu + G + E$$

The source of phenotypic variability determines whether selection for the trait will result in a heritable response, i.e., will be passed on to the next generation.

For purposes of making decisions in plant breeding, if two populations have different phenotypic means, we want to know whether the differences are due to different environments, or to different genotypes, or some combination of both. If the differences are due to genotypic differences, then what proportion of the genotypic differences is heritable?

Fig. 2 Comparing phenotypic traits of plant populations at the University of KwaZulu-Natal in South Africa. Photo by Iowa State University.

Algebraic Description

Using simple algebra and our working model, we can show that the phenotypic variance (V_P) within a population is equal to the sum of the genotypic variance (V_G) and environmental variance (V_E), assuming that G and E are independent:

$$V(P) = V(G) + V(E)$$

If the genotypic values and environmental deviations are not independent, the V_p can be increased by twice the covariance of G with E:

$$V(P) = V(G + E))(V(P) = V(G) + V(E) + 2cov(G, E)$$

Genetic Components of Variance

Genetic components of variability can be divided into several subcategories, including additive variance (V_A), dominance variance (V_D), and epistatic variance (V_I). Together, the values for each of these subcategories yield the total amount of genetic variation (V_G) responsible for a particular phenotypic trait:

$$V_P = V_G + V_E$$

Consider the ratio of V_G to V_P . This was originally recognized by statistical geneticists (such as RA Fisher) as the genotypic intra-class correlation. To understand this, consider evaluation of a line *i*, for a phenotype, *Y*. Next imagine that you can evaluate line *i* in repeatedly. Let's designate these repeated measurements as *j*. We can then designate these repeated measurements of the phenotype as Y_{ij}. There is a Covariance among these repeated evaluations that we can represent as

$$Cov(Y_{ij}, Y_{ij'}) = Var(G_i), for\ j \neq j'$$

Explanation of Formula

Thus the correlation among these repeated measures is

$$\rho(Y_{ij}, Y_{ij'}) = \frac{Cov(Y_{ij}, Y_{i,j'})}{\sqrt{Var(Y_{ij})Var(Y_{ij'})}}$$

Equation 1

and because $Var(Y_{i,j}) = V(G_i) + V(E_{ij})$

$$\rho(Y_{ij}, Y_{ij'}) = \frac{V(G_i)}{V(G_i) + V(E_{ij})} = \frac{V(G_i)}{V(P_{ij})}$$

Equation 2

Heritability in the Broad Sense

JL Lush, an animal breeder, also referred to this intra-class correlation coefficient as **heritability in the broad sense** (1937). He wanted to distinguish the application of intra-class correlation to animals from the concept of repeatability. Repeatability as an engineering concept refers to the same measurement procedure, conducted by a single observer, using single measuring instrument, under the same conditions, at a single location, over a short period of time. As a result plant and animal breeders tend to prefer the use of broad sense heritability for the genotypic intra-class correlation, although both plant and animal breeders routinely evaluate a single trait on individual genotypes repeatedly over time and space (locations and years).

Fig. 3 J.L. Lush. Photo by Iowa State University.

Broad-Sense Components

The genetic variance can be recognized as consisting of several components:

$$V_G = V_A + V_D + V_I)$$

where:

$\mathbf{V_A}$ (Additive variance) is the variance of breeding values. This refers to the deviation from the mean phenotype due to inheritance of a particular allele and this allele's relative effect on phenotype, i.e., relative to the mean phenotype of the population;

$\mathbf{V_D}$ (Dominance variance) is the variance due to interactions between alternative alleles at a specific locus;

$\mathbf{V_I}$ (Epistatic variance): is the variance due an interaction between alleles at different loci.

Heritability in the Narrow Sense

Heritability in the narrow sense was defined by JL Lush (1937) to represent the extent to which phenotypes are determined by the genes transmitted from their parents:

$$h^2 = \frac{V_A}{V_P}$$

So, we can now expand our model for the phenotypic variance to include several genetic variance components and environmental variance:

$$V_P = V_A + V_D + V_I + V_E$$

Table 1 Sources of the variance components.

Variance component	Symbol	Source of variation
Phenotypic	V_P	Phenotypic value
Genotypic	V_G	Genotypic Value
Additive	V_A	Breeding Value
Dominance	V_D	Dominance deviation
Interaction	V_I	Interaction deviation
Evironmental	V_E	Non-genetic deviation

Deriving Variance Components

The genetic components of variance are influenced by the gene frequency and the assigned genotypic values *a* and *d*. The information needed to derive V_A and V_D are:

Table 2 Derivation of additive and dominance variance components of genetic variance.

Genotypes	AA	Aa	aa
Frequencies	p^2	2pq	q^2
Coded GV	a	d	-a
Genotypic Value	2q(a-pd) 2q(a-qd)	a(q-p) + d(1-2pq) (q-p)a + 2pqd	-2p(a+qd) -2p(a+pd)
Breeding Value	2qa	(q-p)a	-2pa
Dominance Deviation	$-2q^2d$	2pqd	$-2p^2d$

The variances are thus obtained by squaring the values in the table, multiplying by the frequency of the genotype concerned, and summing over the three genotypes.

$$V_A = 4p^2q^2\alpha^2 + 2pq(q-p)^2\alpha^2 + 4p^2q^2\alpha^2)(= 2pq(2pq + q^2 - 2pq + p^2 + 2pq)\alpha^2)(= 2pq(p^2 + 2pq + q^2)\alpha^2)(= 2pq\alpha^2)(= 2pq[a + d(q-p)]^2)(V_D = d^2(4q^4p^2 + 8p^3q^3 + 4p^4q^2))(= 4p^2q^2d^2(q^2 + 2pq + p^2))(= (2pqd)^2$$

Covariance

If there is no dominance at the locus under consideration (d=0), then:

$$V_A = 2pq\alpha^2$$

If there is complete dominance (d=a), the additive variance becomes

$$V_A = 8pq^3\alpha^2$$

The total genetic variance is

$$V_G = V_A + V_D + 2COV_{AD}$$

where cov_{AD} is the covariance of breeding values with dominance deviations, which can be demonstrated to be zero. Thus,

$$V_G = V_A + V_D)(= 2pq[a + d(q - p)]^2 + [2pqd]^2$$

Component Relationships

The relationships among variance components, gene action and allele frequencies for the two allele case can be graphically represented (Figs. 4, 5, 6).

Additive Gene Action

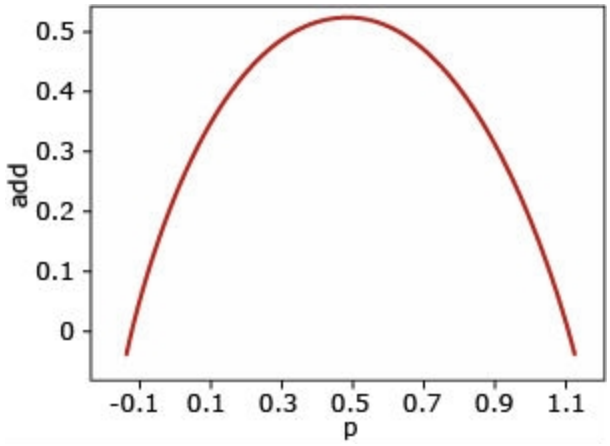

Fig. 4

Additive gene action: There is no dominance (a>0, d=0). In this case, the genetic variance is additive, and it is greatest when p=q=0.5.

Complete Dominance

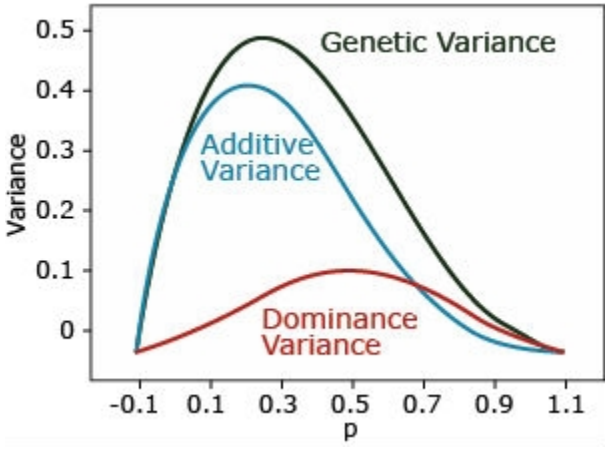

Fig. 5

Complete dominance: (a>0, d=a). The dominance variance is maximal when p=q=0.5. The additive is maximal when p=0.3.

Overdominance

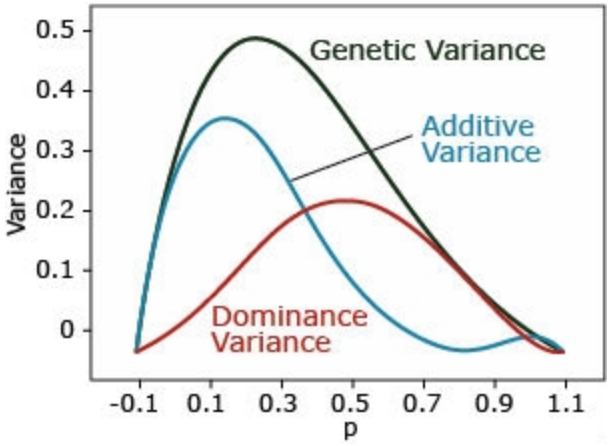

Fig. 6

Overdominance: (a=0, d>0). The dominance variance is the same as in complete dominance.

Principles to Remember

Important principles to remember:

1. All the components of genetic variance are dependent on the gene frequencies.
2. Estimates of components of genetic variances are valid only for the population from which they are estimated.
3. The concept of additive variance does not carry with it the assumption of additive gene action; the existence of additive variance is not an indication that genes act additively.
4. Additive variance can arise from genes with any degree of dominance or epistasis.

Fig. 7 Examining phenotypic traits of maize fields at the University of KwaZulu-Natal,South Africa. Photo by Iowa State University.

Influence of Epistasis

Two Or More Loci: Influence Of Epistasis On Components Of Genetic Variance

When more than one locus is under consideration then deviations due to interactions among loci give rise to additional variance components due to epistatic interactions (V_i).

$$V_I = V_{AA} + V_{AD} + V_{DD} + etc.$$

V_{AA} is additive × additive variance is the interaction between two breeding values.

V_{AD} is additive × dominance variance is the interaction between the breeding value of one locus and the dominance deviation of the other.

V_{DD} is dominance × dominance variance is the interaction between the two dominance deviations

Epistatic Model

A non-intuitive consequence of the epistatic models is that additive variance can arise from purely epistatic genetics. For example, let's consider the special case of an F_2 population, with equal frequencies of two alleles at each of two independently segregating loci. Let's imagine that we know the genotypes at each of these functional loci and analyze the F_2 population using a regression approach for each of the loci and their interactions.

Table 3 Sources of genetic variability and associated df in an analysis of independently segregating loci in an F_2 population based on a regression approach of analysis.

Source of variance	**Df**
Locus A	**2**
Linear (Additive)	1
Quadratic (Dominance)	1
Locus B	**2**
Linear (Additive)	1
Quadratic (Dominance)	1
Epistasis	**4**
Linear A x Linear B (A * A)	1
Linear A x Quadratic B (A * D)	1
Quadratic A x Linear B (D * A)	1
Quadratic A x quadratic B (B * D)	1
Total	**8**

Example 1

Analysis of a phenotype in an F_2 population with equal frequencies of alleles at two functionally polymorphic loci each contributing only additive coded genotypic values from the A locus and a B locus, i.e., $P = \mu + a_A + a_B$, where $\mu=5$, $a_A = 3$ and $a_B=1$.

Table 4 Parameters and their Coded Genotypic values for P (example 1).

Parameter	Value
aA	3
dA	0
aB	1
d_B	0
μ	5

Table 5 Coded Genotypic values for two functional bi-allelic loci in an F_2 population derived from a cross of two inbred lines (example 1).

		A_1A_1	A_1A_2	A_2A_2	Mean
		1/4	1/2	1/4	
B_1B_1	1/4	9	6	3	6
B_1B_2	1/2	8	5	2	5
B_2B_2	1/4	7	4	1	4
Mean		8	5	2	2.75

Table 6 Calculated variances components for the F_2 population described in example 1.

Variance component	Variance
$\delta^2_{A_A}$	4.5
$\delta^2_{A_B}$	0.5

$\delta^2_{D_A}$	0
$\delta^2_{D_B}$	0
δ^2_{AA}	0
δ^2_{AD}	0
δ^2_{DA}	0
δ^2_{DD}	0

Example 2

Analysis of a phenotype in an F_2 population with equal frequencies of alleles at two functionally polymorphic where only single epistatic interaction between the genotypes will produce an altered phenotype, $P = \mu + a_A + a_B + d_A + d_B + e_{AABB}$ where $\mu=0$, $a_A = 0$ and $a_B=0$, $d_A=0$, $d_B=0$, $e_{AABB}=50$.

Table 7 Coded Genotypic values for two functional bi-allelic loci in an F_2 population derived from a cross of two inbred lines (example 2).

		A_1A_1	A_1A_2	A_2A_2	Mean
		1/4	1/2	1/4	
B_1B_1	1/4	0	0	0	0
B_1B_2	1/2	0	0	0	0
B_2B_2	1/4	0	0	50	12.5
Mean		0	0	12.5	3.125

Table 8 Calculated variances components for the F_2 population described in example 2.

Population variances	Population	Percent
Total genetic	**146.484**	**100.0%**
Additive effects	39.063	26.7%
Dominance	19.531	13.3%
Epistasis	87.891	60.0%

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