CHAPTER SIX

Quantitative Inheritance

The simultaneous segregation of many genes that control a quantitative character results in a range of genotypes that cannot be separated into distinct classes. Variation among individuals for a quantitative character also involves the effect of the environment on the phenotypic expression of a genotype. The study of the inheritance of quantitative characters is sometimes referred to as mathematical or statistical genetics because mathematical and statistical concepts are utilized.

CHARACTERIZATION OF A POPULATION

The evaluation of a quantitative character is based on the study of a population of genotypes. A population can be characterized for a trait by use of several different statistics (Falconer, 1981).

Population Mean

One important statistic used to describe a population is the mean performance of the genotypes it contains. A population of 10 genotypes with seed yields of 40, 41, 44, 46, 49, 50, 54, 58, 61, and 63 units would have a mean yield of 50.6 units. Effective selection among genotypes in a population results in a change in the mean population performance.

Falconer (1981) described the mean performance of a population for a single locus with two different alleles as

$$M = a(p - q) + 2dpq$$

where M = population mean
a = value of homozygous genotype
p = frequency of one allele

q = frequency of second allele
d = value of heterozygote

As an illustration of the components of the equation, consider a locus with two alleles, A_1 and A_2, that combine to form the genotypes A_1A_1, A_1A_2, and A_2A_2. The value of each genotype is designated with a symbol: $A_1A_1 = +a$, $A_2A_2 = -a$, and $A_1A_2 = d$. The value of a is the performance of a homozygous genotype minus the average performance of the two homozygous genotypes: $+a$ for $A_1A_1 = A_1A_1 - [(A_1A_1 + A_2A_2)/2]$ and $-a$ for $A_2A_2 = A_2A_2 - [(A_1A_1 + A_2A_2)/2]$. If $A_1A_1 = 20$ and $A_2A_2 = 14$, then $+a$ for $A_1A_1 = 20 - [(20 + 14)/2] = +3$ and $-a$ for $A_2A_2 = 14 - [(20 + 14)/2] = -3$.

The value of d is a measure of the degree of dominance between alleles. It is measured as the difference between the value of the heterozygote and the mean of the homozygotes.

$$d = A_1A_2 - \frac{A_1A_1 + A_2A_2}{2}$$

If the value of A_1A_2 is 19 and the average of the two homozygotes is 17, the value of d is $+2$. d is greater than zero but less than a with partial dominance, d equals a with complete dominance, and d is greater than a with overdominance.

The frequency of an allele in a population can vary from 0 to 1. The sum of the frequencies of alleles at a locus equals 1. For discussion of the population mean, the frequency of allele A_1 will be designated as p and the frequency of A_2 as q.

The values of a and d in a population do not change at a locus, but may vary among loci. Changes in the population mean are a result of changes in gene frequency.

The discussion thus far has dealt with a single locus. For a character controlled by many loci, the mean of a population is equal to the sum of the means for the individual loci, which can be expressed as

$$M = \Sigma [a(p - q) + 2dpq]$$

This expression assumes that there are no epistatic interactions between loci to influence the population mean (Falconer, 1981).

There is no way to measure the values of a, d, p, or q for individual loci of a polygenic character. Nevertheless, an understanding of their role in determining the population mean is helpful for evaluating the impact of selection on population performance.

Genotypic Values

A population can be characterized by the amount and type of genetic variability it contains. Genetic improvement of a quantitative character is based on effective selection among individuals that differ in genotypic value. The variation among

genotypic values represents the genotypic variance of a population. A description of the various types of gene action that determine the genotypic value of individuals in a population will be helpful in understanding the concept of genetic variance.

Genotypic value can be considered on the basis of a single locus or as a function of all loci of an individual that control a quantitative character (Falconer, 1981). The genotypic value of a single locus is equal to

$$G = A + D$$

where G is the genotypic value, A is the breeding value, and D is the dominance deviation. The genotypic value of all loci considered together is expressed as

$$G = A + D + I$$

where A is the sum of breeding values for separate loci, D is the sum of dominance deviations, and I is attributable to the interaction of alleles among loci, referred to as the interaction deviation or epistatic deviation. The type of gene action associated with the breeding value, dominance deviation, and epistatic deviation is an important concept in quantitative genetics.

Breeding Value. The breeding value of an individual is that portion of its genotypic value that determines the mean performance of its progeny (Falconer, 1981). The breeding value of an individual can be measured by mating the individual to a number of random individuals from a population, determining the mean performance of the progeny, subtracting the mean progeny performance from the population mean, and multiplying the deviation by two. The deviation is multiplied by two because half of the genes in the progeny are contributed by the individual and the other half are a random sample from the population with a value equal to the population mean.

The breeding value of an individual is determined by summation of the average effects of its genes, also referred to as the additive effect of genes. The average effect of a gene substitution is the regression coefficient (b) obtained from the linear regression of the genotypic value of an individual locus on the number of alleles of a certain type at that locus (Fisher, 1918,1941). If there is no dominance expressed at a locus, the linear regression line connects the genotypic values of the two homozygotes [Fig. 6-1(a)]. If dominance is expressed, none of the genotypic values will lie directly on the regression line [Fig. 6-1(b)].

Gene frequency in the population to which an individual is mated will influence the average effect of a gene substitution when dominance is present at a locus. If allele A_1 expresses some degree of dominance over A_2, the genotypic value of the heterozygote A_1A_2 will be closer to that of A_1A_1 than to that of A_2A_2. The effect of substituting A_2 for A_1 is greater when A_1A_2 is changed to A_2A_2 than when A_1A_1 is changed to A_1A_2. The average effect of a gene substitution depends, therefore, on the relative frequency of different genotypes in a population. Genotypic frequency in a population is determined by gene frequency.

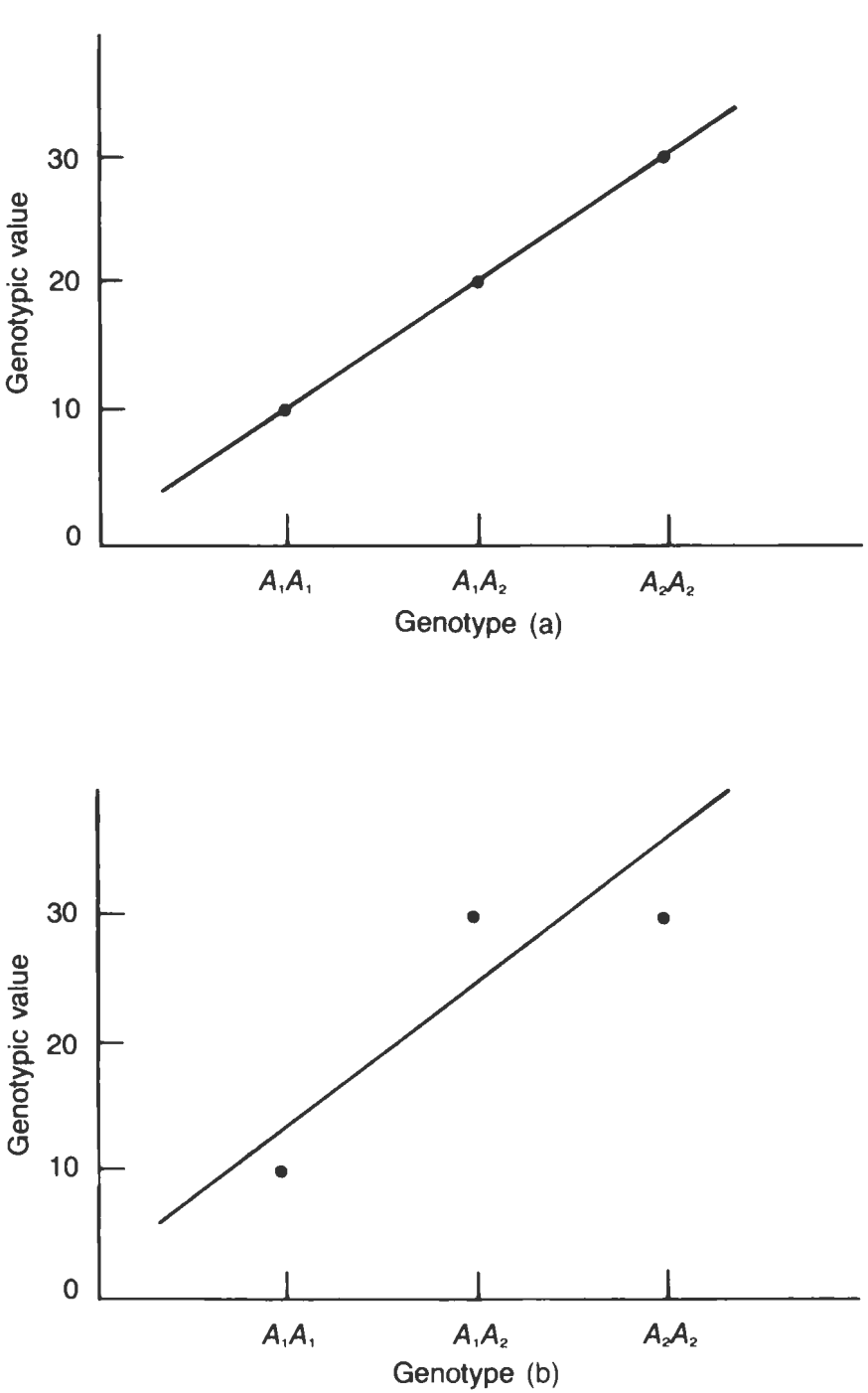


Figure 6-1 Regression of the genotypic value of a locus on the number of favorable alleles at that locus. (a) No dominance. (b) Complete dominance.

The relationship of the average effect of a gene substitution to the degree of dominance at a locus and gene frequency is summarized by the equation

$$\alpha = a + d(q - p)$$

where α = average effect of a gene substitution
a = difference between one homozygote and average of two homozygotes
d = difference between heterozygote and average of two homozygotes
q and p = frequency of alleles in population

The sum of the average effects of genes at all loci controlling a character determines the breeding value of an individual for that character. In the absence of epistasis, the sum of the average effects across loci is equal to the breeding value obtained by mating an individual to a population and measuring the deviation of progeny performance from the population mean.

Dominance Deviation. The dominance deviation (D) at a locus is the difference between the genotypic value (G) and the breeding value (A) of an individual, $D = G - A$ (Falconer, 1981). It represents the interaction of alleles at a locus, or intralocus interaction. The degree of dominance and gene frequency of a population influence genotypic values and breeding values; consequently, they also influence dominance deviations. The relationship among genotypic values, breeding values, and dominance deviations is illustrated in Fig. 6-2.

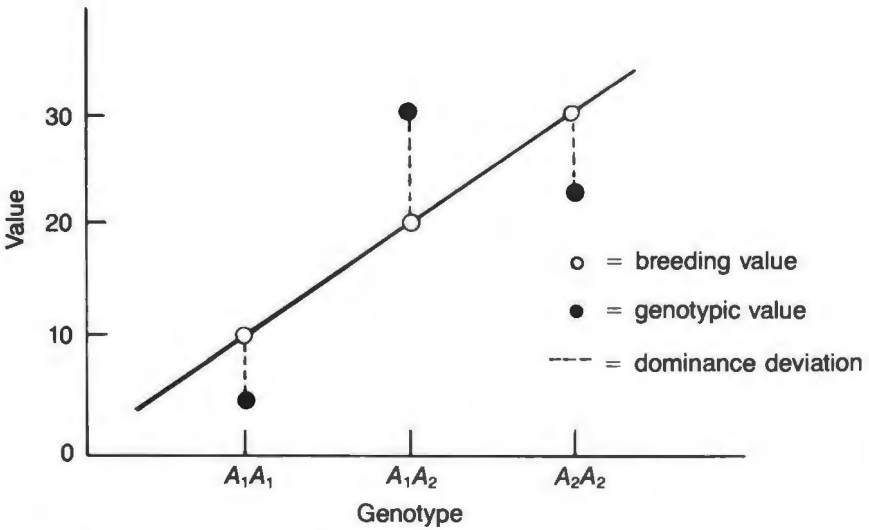


Figure 6-2 Relationship among genotypic value, breeding value, and dominance deviation.

Epistatic Interaction. The genotypic value of an individual for a quantitative character can be influenced by the interaction of alleles and genotypes at different loci, referred to as interlocus interaction. In the absence of epistasis, the genotypic value for all loci controlling a character is equal to the sum of the genotypic values for individual loci. When epistasis is present, the genotypic value for all loci is not accounted for completely by the genotypic values of individual loci.

The types of epistatic interaction described in quantitative genetics for two loci are additive × additive, additive × dominance, and dominance × dominance. For three loci, the number of possible interactions increases and includes additive × additive × additive, additive × additive × dominance, and so forth. In these expressions, "additive" refers to breeding values and "dominance" to dominance deviations. For two loci, additive × additive is the interaction of breeding values at both loci, additive × dominance is the interaction of breeding values at one locus and dominance deviations at the other, and dominance × dominance is the interaction of dominance deviations at both loci.

Epistatic interactions are dependent on the average effects of genes and dominance deviations at individual loci. As a result, they are dependent on the degree of dominance and the gene frequency in the population.

Types of Genotypic Variance

The genotypic variance among individuals in a population can be expressed as

$$\sigma_g^2 = \sigma_A^2 + \sigma_D^2 + \sigma_I^2$$

σ_g^2 represents the total genotypic variance (Falconer, 1981). σ_A^2, the additive variance, is the variation in breeding values among individuals. σ_D^2, the dominance variance, is the variation among individuals for dominance deviations. The epistatic variance, σ_I^2, is the variation associated with differences among individuals for epistatic interactions. The epistatic interaction can be subdivided further into variance components associated with the different types of interlocus interaction, such as additive × additive (σ_{AA}^2), additive × dominance (σ_{AD}^2), additive × additive × additive (σ_{AAA}^2), and so forth.

The magnitude of genetic variance components is unique to the population from which the components are obtained. Genotypic values, breeding values, dominance deviations, and epistatic interactions are influenced by the degree of dominance at a locus and the gene frequency of a population. Consequently, the variation among genotypic values is also a function of degree of dominance and gene frequency. This can be illustrated by considering the genotypic, additive, and dominance variances for one locus. The variance components are defined by the following equations (Falconer, 1981):

$$\sigma_A^2 = 2pq\,[a + d(q - p)]^2$$
$$\sigma_D^2 = (2pqd)^2$$
$$\sigma_g^2 = \sigma_A^2 + \sigma_D^2 = 2pq\,[a + d(q - p)]^2 + (2pqd)^2$$

Substitution of different values for d, p, and q will change the relative magnitudes of σ_A^2, σ_D^2, and σ_g^2 (Falconer, 1981).

ESTIMATION OF GENETIC VARIANCES

There are a number of mating designs that can be used by the plant breeder to estimate the genotypic variance in a population. The mating designs differ in the genetic material evaluated, which determines the extent to which additive, dominance, and epistatic variances can be estimated.

A detailed review of alternative mating designs has been provided by Hallauer and Miranda (1981). Three of the more commonly used mating designs, the diallel, Design I, and Design II, will be used to illustrate the general procedure for estimating genotypic variances.

A number of criteria must be met for each mating design to obtain valid estimates of genotypic variance (Baker, 1978). Failure to meet one or more of these criteria may result in biased estimates of genotypic variance. A primary criterion for the diallel, Design I, and Design II mating designs is that individuals evaluated from a population be a random sample of all possible genotypes.

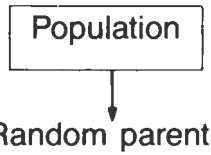
Diallel Design

The genetic material evaluated in the diallel mating design includes random individuals from a population and the progeny obtained by crossing those individuals in all combinations. The matings among individuals may include reciprocal crosses and selfed progeny.

To prepare the genetic material for the diallel, a group of random parents is identified in a population (Fig. 6-3), Self-pollinated seed of each genotype is maintained for evaluation of its performance per se. Each genotype is mated to every other genotype, and the seed from each mating is maintained separately. If the diallel is to include reciprocal crosses, each genotype is used as male and female for each mating and seed from the reciprocal crosses is kept separate.

The number of entries that are evaluated for the diallel mating design is determined by the number of genotypes (parents) sampled from the population. If the number of parents is designated as p, the number of pairwise matings among them is equal to $p(p - 1)/2$. Reciprocal crosses among pairwise combinations doubles the number of matings that must be made, expressed as $p(p - 1)$. If the number of genotypes is equal to 5, the number of pairwise matings is equal to $5(5 - 1)/2 = 10$, and the number of matings with reciprocal crosses is equal to $5(5 - 1) = 20$.

There are four combinations of crosses and selfed progeny of the parents that can be included for evaluation in the diallel mating design: (a) the crosses,



Single crosses without reciprocal matings or selfed progeny

	P_1	P_2	P_3
P_1	-	x	x
P_2	-	-	x
P_3	-	-	-

Single crosses with reciprocal matings

	P_1	P_2	P_3
P_1	-	x	x
P_2	x	-	x
P_3	x	x	-

Single crosses with reciprocal matings and selfed progeny

	P_1	P_2	P_3
P_1	⊗	x	x
P_2	x	⊗	x
P_3	x	x	⊗

Figure 6-3 Derivation of progenies in a diallel mating design. Each parent is mated with every other parent, and reciprocal matings and selfed progeny also can be evaluated.

Table 6-1 Analysis of Variance of Diallel Crosses for $n(n-1)/2$ Crosses of n Parents Where Expected Mean Squares, E(MS), Are Expressed in Terms of Covariances of Relatives

Source	Degrees of Freedom	Mean Squares	Expected Mean Squares
Replications	$r-1$		
Crosses	$[n(n-1)/2]-1$	M_2	$\sigma^2 + r\sigma_c^2$
GCA	$n-1$	M_{21}	$\sigma^2 + r(\text{Cov FS} - 2\text{ Cov HS}) + r(n-2)\text{Cov HS}$
SCA	$n(n-3)/2$	M_{22}	$\sigma^2 + r(\text{Cov FS} - 2\text{ Cov HS})$
Error	$(r-1)\{[n(n-1)/2]-1\}$	M_1	σ^2
Total	$rn-1$		

GCA = general combining ability; SCA = specific combining ability; r, n = number of replications and parents, respectively; M = mean squares; Cov FS, Cov HS = covariance of full-sib families and of half-sib families, respectively.

Source: Hallauer and Miranda, 1981.

(b) the crosses and selfed progeny of the parents, (c) the reciprocal crosses, and (d) the reciprocal crosses and selfed progeny of the parents (Griffing, 1956).

The separation of the genotypic variance that is possible with the diallel cross can be illustrated with an analysis of variance that involves only the crosses (Table 6-1). The variation among crosses in the diallel can be divided into variation among half-sib families and variation among full-sib families. There is one half-sib family for each parent in a diallel. The performance of a half-sib family is determined by averaging the performance of all crosses with one parent in common. The variation among the half-sib families in a diallel is an estimate of general combining ability (GCA). A full-sib family is the mating of two parents; therefore, the number of full-sib families in a diallel equals the number of single crosses that are evaluated. The performance of the full-sib families is used to obtain an estimate of specific combining ability (SCA).

The genetic variance components associated with the covariance of half-sib families (Cov HS) and full-sib families (Cov FS) depends on the inbreeding (F) of the genotypes used as parents in the diallel. When the parents are F_2 or S_0 plants or lines derived from them (F = 0), the genetic variance components are

$$\text{Cov HS} = \tfrac{1}{4}\sigma_A^2 + \tfrac{1}{16}\sigma_{AA}^2 + \text{higher orders of additive epistasis}$$

$$\text{Cov FS} = \tfrac{1}{2}\sigma_A^2 + \tfrac{1}{4}\sigma_D^2 + \tfrac{1}{4}\sigma_{AA}^2 + \text{other forms of additive and dominance epistasis}$$

Assuming there is no epistasis, the Cov HS is multiplied by four to obtain σ_A^2; $\sigma_A^2 = \frac{1}{4}\sigma_A^2 \times 4$. An estimate of σ_D^2 is obtained as

$$\begin{aligned}\sigma_D^2 &= 4\,(\text{Cov FS} - 2\,\text{Cov HS}) \\ &= 4[(\tfrac{1}{2}\sigma_A^2 + \tfrac{1}{4}\sigma_D^2) - 2(\tfrac{1}{4}\sigma_A^2)]\end{aligned}$$

When the parents are random inbred lines from a population (F = 1), the genetic variance components are

$$\text{Cov HS} = \tfrac{1}{2}\sigma_A^2 + \tfrac{1}{4}\sigma_{AA}^2 + \text{higher orders of additive epistasis}$$

$$\text{Cov FS} = \sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2 + \text{higher orders of additive and dominance epistasis}$$

Assuming there is no epistasis, the Cov HS is multiplied by two to obtain σ_A^2; $\sigma_A^2 = \frac{1}{2}\sigma_A^2 \times 2$. An estimate of σ_D^2 is obtained as

$$\text{Cov FS} - 2\,\text{Cov HS} = (\sigma_A^2 + \sigma_D^2) - 2(\tfrac{1}{2}\sigma_A^2)$$

Design I (Nested Design)

Genotypic variance can be subdivided into components by a mating design referred to as Design I or the nested design. Genetic material for this mating

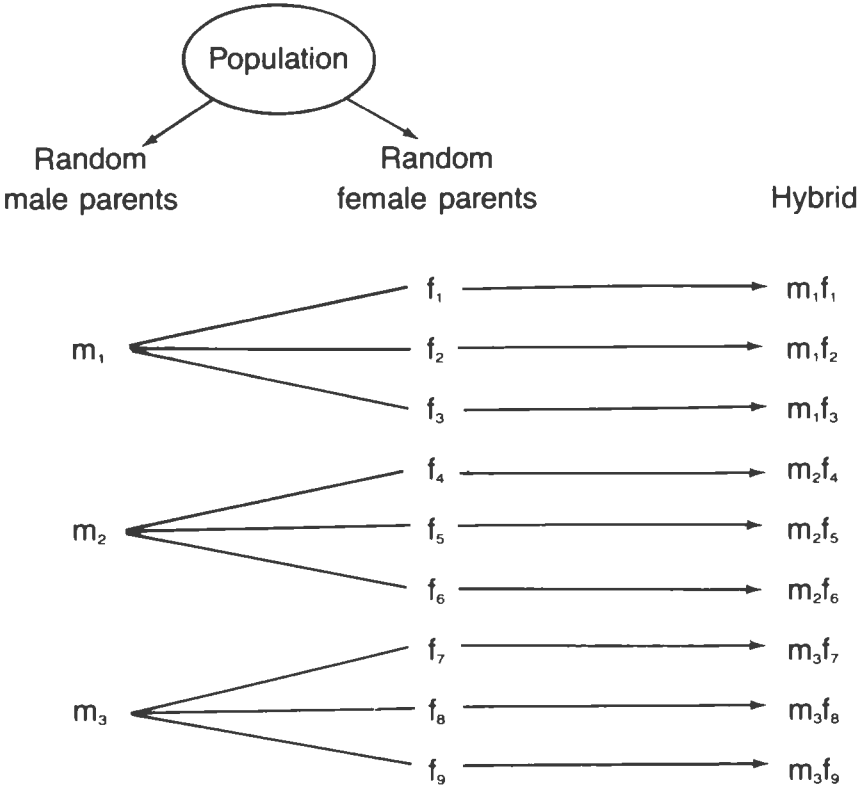


Figure 6-4 Derivation of progenies in a Design I mating design. Each male parent is crossed to different female parents from the population.

design involves crosses among random parents from a population, some of which are designated as males and others as females. Each male plant is mated to an equal number of females (Fig. 6-4). A different group of female parents is used for each male. The number of single crosses formed by the matings is equal to the number of males (p_m) times the number of females (p_f) mated to each male: $p_m \times p_f$. If 10 male parents are each mated to 5 female parents, 50 single crosses are evaluated.

The variation among single crosses is divided into variation among males and variation among females within males (Table 6-2). The expected mean squares for the sources of variation include the covariance of half-sibs (Cov HS) and the covariance of full-sibs (Cov FS). The genetic variance components associated with these covariance terms and their use to obtain estimates of σ_A^2 and σ_D^2 are the same as described for the diallel design (Hallauer and Miranda, 1981).

Table 6-2 Analysis of Variance of Design I Mating Design for One Environment

Source	Degrees of Freedom	Mean Squares	Expected Mean Squares	
			Components of Variance	Covariances of Relatives
Replications	$r-1$			
Males	$m-1$	M_3	$\sigma^2 + r\sigma^2_{f:m} + rf\sigma^2_m$	$\sigma^2 + r(\text{Cov FS} - \text{Cov HS}) + rf\text{Cov HS}$
Females/males	$m(f-1)$	M_2	$\sigma^2 + r\sigma^2_{f:m}$	$\sigma^2 + r(\text{Cov FS} - \text{Cov HS})$
Error	$(r-1)(mf-1)$	M_1	σ^2	σ^2
Total	$rmf-1$			

r, m, and f = number of replications, males, and females within males, respectively; M = mean squares; Cov FS, Cov HS = covariance of full-sib and half-sib families, respectively.

Source: Hallauer and Miranda, 1981.

Design II (Factorial Design)

Design II is a factorial mating design in which some parents from a population are designated as male and others as female. Each male parent is mated to each female, but male parents are not crossed to each other and female parents are not crossed to each other (Fig. 6-5). The number of single crosses included is equal to the number of male parents (p_m) times the number of female parents (p_f) : $p_m \times p_f$. If there were eight male and six female parents, 48 single crosses would be included in the experiment.

Variation among crosses is divided into variation among male parents, variation among female parents, and the interaction of male and female parents (Table 6-3). The covariance among half-sib families can be designated as Cov HS_m when the male parent is common to all crosses and Cov HS_f when the female parent is common to all crosses. The genetic variance components associated with the two covariances are the same. When the parents are noninbred (F = 0),

Cov HS_m and Cov $HS_f = \frac{1}{4}\sigma_A^2 + \frac{1}{16}\sigma_{AA}^2 +$ other forms of additive epistasis

When the parents are inbred (F = 1)

Cov HS_m and Cov $HS_f = \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_{AA}^2 +$ other forms of additive epistasis

The separate covariances for half-sib families of male and female parents provide separate estimates of σ_A^2. An estimate of σ_D^2 is obtained from the relationship Cov FS − (Cov HS_m + Cov HS_f).

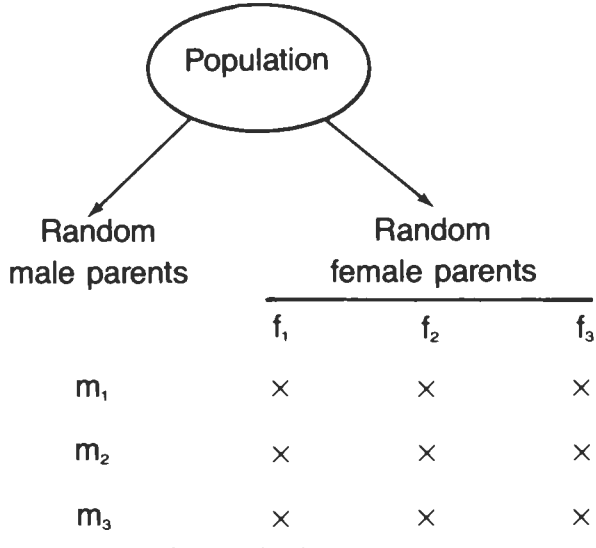


Figure 6-5 Derivation of progenies in a Design II mating design. The male parents are each crossed to the same female parents.

Table 6-3 Analysis of Variance of Design II Mating Design for One Environment

Source	Degrees of Freedom	Mean Squares	Expected Mean Squares	
			Components of Variance	Covariances of Relatives
Replications	$r-1$			
Males	$m-1$	M_4	$\sigma^2 + r\sigma^2_{fm} + rf\sigma^2_m$	$\sigma^2 + r(\text{Cov FS} - \text{Cov HS}_f - \text{Cov HS}_m) + \text{rfCov HS}_m$
Females	$f-1$	M_3	$\sigma^2 + r\sigma^2_{fm} + rm\sigma^2_f$	$\sigma^2 + r(\text{Cov FS} - \text{Cov HS}_f - \text{Cov HS}_m) + \text{rmCov HS}_f$
Males × females	$(m-1)(f-1)$	M_2	$\sigma^2 + r\sigma^2_{fm}$	$\sigma^2 + r(\text{Cov FS} - \text{Cov HS}_f - \text{Cov HS}_m)$
Error	$(r-1)(mf-1)$	M_1	σ^2	σ^2
Total	$rmf-1$			

r, m, and f = number of replications, males, and females, respectively; M = mean squares; Cov FS and Cov HS = covariance of full-sib and half-sib families, respectively.

Source: Hallauer and Miranda, 1981.

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CHAPTER SEVEN

Heritability

The effectiveness of selection for a trait depends on the relative importance of genetic and nongentic factors in the expression of phenotypic differences among genotypes in a population, a concept referred to as heritability. The heritability of a character has a major impact on the methods chosen for population improvement, inbreeding, and other aspects of selection. Single-plant selection may be effective for a character with high heritability and relatively ineffective for one with low heritability. The extent to which replicated testing is required for selection will depend on the heritability of the character.

COMPONENTS OF HERITABILITY

Heritability (h^2) can be defined as the ratio of the genotypic variance (σ_g^2) to the phenotypic variance (σ_{ph}^2); $h^2 = \sigma_g^2 / \sigma_{ph}^2$. The phenotypic variance can be subdivided into components of variance attributable to factors that cause differences in the performance among individuals. This relationship can be expressed as $\sigma_{ph}^2 = \sigma_e^2 + \sigma_{ge}^2 + \sigma_g^2$. The variance component σ_e^2 is a measure of differences among phenotypes caused by the failure to treat each genotype exactly alike, generally referred to as experimental error or environmental variance. σ_{ge}^2 represents differences among phenotypes that are caused by genotype × environment interaction, which is the failure of genotypes to perform the same relative to each other when they are evaluated in different locations and/or years. σ_{ge}^2 is the sum of genotype × location (σ_{gl}^2), genotype × year (σ_{gy}^2), and genotype × location × year (σ_{gly}^2) interaction. Genotype × environment interaction is discussed in more detail in Chap. 18. The genotypic variance, σ_g^2, is the variation caused by genetic differences among individuals. The genotypic variance is the sum of the additive (σ_A^2), dominance (σ_D^2), and epistatic (σ_I^2) variances (Chap. 6).

TYPES OF HERITABILITY

Heritability can be expressed in a broad sense or a narrow sense. Broad-sense heritability is a ratio of the total genotypic variance, including additive, dominance, and epistatic variance, to the phenotypic variance, $\sigma_g^2/\sigma_{ph}^2 = (\sigma_A^2 + \sigma_D^2 + \sigma_I^2)/\sigma_{ph}^2$. Heritability in the narrow sense is a ratio of the additive genetic variance to the phenotypic variance, σ_A^2/σ_{ph}^2. Narrow-sense heritability is the more useful concept because it measures the relative importance of the additive portion of the genetic variance that can be transmitted to the next generation of offspring. This is particularly important when heritability is used to predict gain expected from selection for a character (Chap. 17).

The heritability of a character is not a constant value. Decisions made by the breeder can influence the magnitude of heritability and the amount of genetic improvement obtained from selection. An understanding of the factors that contribute to heritability permits the breeder to develop a breeding program that maximizes genetic improvement with available resources. Because many factors can influence heritabilities, estimates of them should be interpreted with regard to the conditions under which they were obtained.

FACTORS INFLUENCING THE MAGNITUDE OF HERITABILITY ESTIMATES

Population Characterized

Estimates of heritability are influenced by the amount of genotypic variance present for a trait in the population being studied. The number and genetic diversity of parents used to form a population will have a direct bearing on the amount of genetic variation present. A population derived from crosses between many divergent parents is expected to express more genetic variance than a population derived from a few related parents.

The amount of self-pollination in a population will influence the genetic variance among individuals. As the level of inbreeding increases, the magnitude of the genetic variance among individuals increases. Consequently, the heritability estimate obtained from evaluation of F_2 plants can differ from an estimate obtained with F_4 individuals.

Sample of Genotypes Evaluated

Heritability estimates are obtained by evaluating a relatively small number of individuals in a population. If all possible segregates of a population could be evaluated, the true genetic variance of a population could be determined. The number of possible segregates in a population is so large, however, that it is impossible to evaluate them all. For example, the number of possible genotypes

in a diploid species for a character controlled by 10 independent loci with two alleles is $3^{10} = 59{,}049$. Considering that important quantitative characters such as yield are probably controlled by more than 10 loci, only a sample of possible genotypes in a population can be measured. The genetic variance obtained from a sample of individuals is an estimate of the true genetic variance in the population. Consequently, the heritability computed for a sample of genotypes is an estimate of the true heritability of a population.

The relationship between a heritability estimate obtained from a sample of genotypes and the true heritability of a population depends on the manner in which the sample is chosen for evaluation. If the genotypes are chosen at random from all possible members of the population, the genetic variance among the random genotypes is considered a valid estimate of the true genetic variance of the population, and the heritability estimate is considered a valid estimate of the true heritability. Stated in another manner, results obtained with random genotypes are considered applicable to all members of the population.

Valid estimates of the genetic variance and the heritability of a trait cannot be obtained when genotypes are purposely selected from a population rather than chosen at random. Consider a population that has extensive variation for plant height, some of the plants being shorter and others taller than would be acceptable in a cultivar. If the short and tall plants intentionally are not included in a sample obtained from the population, the genetic variance and heritability estimates for plant height obtained with the selected sample would not be representative of the whole population.

When genotypes are a nonrandom sample, results obtained from their evaluation pertain only to those genotypes and cannot be used to infer what would be expected if random genotypes were studied. A breeder may choose to evaluate the genetic variation among selected genotypes and compute the ratio of genetic variation to the phenotypic variation. The ratio is not referred to as heritability. The term repeatability has been used when a nonrandom sample of genotypes is evaluated. It should be noted that repeatability used in this sense has a different meaning than when used to describe the correlation between repeated measurements on the same individual, as discussed by Falconer (1981).

Heritability also has been used to describe the ratio of genotypic to phenotypic variance among random genotypes that are not part of a segregating population. Assume there is a quantitative character for which cultivars of a species have not been evaluated previously. A random group of the cultivars is evaluated, the genotypic and phenotypic variances among them are determined, and a ratio of genotypic to phenotypic variance is computed. In this context, the reference population is cultivars of the species, not a segregating population.

Method of Calculation

The heritability of a character can be computed by a number of methods. The values obtained by different methods will vary to some extent.

Variance Component Method. The method that provides the greatest flexibility for predicting the effectiveness of alternative selection procedures is based on variance components obtained from analysis of variance procedures (Table 7-1). This method is discussed in the chapters dealing with maximizing genetic improvement (Chap. 17) and with genotype × environment interaction (Chap. 18). The components of variance can be used to compute heritability estimates on a single plant, a plot, or an entry-mean basis.

The calculation of heritability in a narrow sense requires an estimate of the additive genetic variance in a population. Several mating designs are available to obtain such estimates, including the diallel, design I, and design II (Chap. 6).

Parent-Offspring Regression. The linear regression of the performance of offspring on that of the parents was proposed by Lush (1940) as a method of estimating heritability. The linear regression model is

$$Y_i = a + bX_i + e_i$$

Table 7-1 Equations for Computing Heritabilities by the Variance Component Method with Four Different Selection Units

Heritability on single-plant basis when selection is based on plants of a population that are not subdivided into plots or blocks

$$h^2 = \frac{\sigma_g^2}{\sigma_w^2 + \sigma^2 + \sigma_{ge}^2 + \sigma_g^2}$$

Heritability on single-plant basis when selection is based on comparison of plants within a plot. Formula also applies when plants of a population are divided into blocks of a grid and the plants within a block are compared with each other without regard to performance of plants in other blocks (Gardner, 1961).

$$h^2 = \frac{\sigma_g^2}{\sigma_w^2 + \sigma_{ge}^2 + \sigma_g^2}$$

Heritability on plot basis

$$h^2 = \frac{\sigma_g^2}{\sigma_w^2/n + \sigma^2 + \sigma_{ge}^2 + \sigma_g^2} = \frac{\sigma_g^2}{\sigma_e^2 + \sigma_{ge}^2 + \sigma_g^2}$$

Heritability on entry-mean basis

$$h^2 = \frac{\sigma_g^2}{\sigma_e^2/rt + \sigma_{ge}^2/t + \sigma_g^2}$$

h^2 = heritability; σ_g^2 = genetic variance; σ_w^2 = variance among plants within a plot; σ^2 = variance among plots or blocks; σ_e^2 = experimental error = $(\sigma_w^2/n) + \sigma^2$; σ_{ge}^2 = genotype × environment interaction; n = number of plants within a plot or block; r = number of replications; t = number of test environments.

where Y_i = performance of offspring of the ith parent

a = mean performance of all parents evaluated

b = linear regression coefficient

X_i = performance of ith parent

e_i = experimental error associated with measurement of X_i

In plant species "parent" refers to a random plant or a line from a population, and "offspring" are half-sib or selfed progeny. A mid-parent–offspring regression also can be used, which is the relationship between the average performance of two parents and their full-sib offspring.

The relationship of the regression coefficient to heritability depends on the type of offspring that is evaluated. The type of offspring also determines if a narrow- or broad-sense heritability is obtained. As an illustration of these principles, consider the evaluation of F_2 plants from a random-mating population with no inbreeding. The evaluation of half-sib progeny from F_2 plants will be considered first. The half-sib seed is obtained by mating an F_2 plant (parent) to a random sample of gametes from F_2 plants in the population. Half of the alleles in the offspring will be from the parent and half from the population. The value of b obtained from the regression of half-sib offspring on their parents is equal to $^1/_2$ the heritability value. The b value is multiplied by two to obtain the heritability estimate, $2b = h^2$.

The equation for the linear regression coefficient is $b = \sigma xy/\sigma_x^2$, where σ^{xy} is the covariance between parents (x) and their offspring (y) and σ_x^2 is the phenotypic variation among the parents. The genetic relationship defined by the covariance determines if the numerator includes only additive genetic variance for narrow-sense heritability or if other types of genetic variance are present for broad-sense heritability. For the covariance of half-sib offspring on their parents, the genetic components include additive variance and additive forms of epistasis, but no dominance. The heritability can be considered narrow-sense unless the amount of additive epistasis is important.

A second type of offspring from F_2 plants is selfed progeny. Random F_2 plants are measured, selfed seed is obtained from each, and the selfed offspring are evaluated. All of the alleles in the offspring are obtained from the parent. The b value obtained from the parent-offspring regression is equal to the heritability, $b = h^2$. The genetic components defined by the covariance of parent and offspring include additive, dominance, and epistasis; therefore, broad-sense heritability is obtained.

A third type of offspring is the full-sib progeny obtained by mating two random F_2 plants. The two F_2 plants of a mating are measured and their average or mid-parent value is determined. The performance of the full-sib progeny is regressed on the mid-parent value. The alleles in the full-sib offspring are obtained from the two parents of a mating, and the regression coefficient is equal to the heritability, $b = h^2$. Additive and additive forms of epistasis are included

in the covariance; therefore, narrow-sense heritability is obtained by mid-parent–offspring regression when additive epistasis is not important.

Use of parent-offspring regression is based on several assumptions: (a) The character of interest has diploid Mendelian inheritance, (b) the population is random-mated, (c) the population is in linkage equilibrium or there is no linkage among loci controlling a character, (d) parents are noninbred, and (e) there is no environmental correlation between the performance of parents and offspring (Vogel et al., 1980). Failure to meet the assumptions can bias the heritability estimates obtained. When the parents are inbred, an adjustment factor can be applied to the heritability estimate (Smith and Kinman, 1965). Environmental correlation between the performance of parents and offspring generally is not a problem when parents and offspring are randomized as independent entries in an experiment. The assumption may not be met if parents and progeny are evaluated in the same plot instead of being randomized within replications (Vogel et al., 1980).

Parent-Offspring Correlation. Correlation of the performance of a parent with that of its offspring was proposed by Frey and Horner (1957) as an alternative to the parent-offspring-regression method for computing heritability. When parents are measured in one season and their offpsring in another, environmental differences between the two seasons can cause the range in phenotypes among the parents to be greater or less than that for the offspring. As a result, heritability percentages obtained by parent-offspring regression could have maximum values greater than 100 percent. To eliminate this effect of environment, the use of standard unit heritabilities obtained by calculating parent-offspring regressions on data coded in terms of standard deviation units was suggested. Such a procedure leads to results equivalent to the coefficient obtained from a simple parent-offspring correlation.

Indirect Estimates of Environmental Variation. A method was proposed by Mahmud and Kramer (1951) to estimate broad-sense heritability on a single-plant basis. The method involves the measurement of a character on F_2 plants of a single-cross population and on the inbred parents used to form the population. The formula these investigators presented for estimating heritability is

$$h^2 = \frac{\sigma^2_{F2} - \sqrt{(\sigma^2_{P1})(\sigma^2_{P2})}}{\sigma^2_{F2}}$$

where h^2 = heritability

σ^2_{F2} = phenotypic variance among F_2 plants

σ^2_{P1} and σ^2_{P2} = phenotypic variances among plants of parents of single-cross population

σ^2_{F2} includes the additive, dominance, and epistatic genetic variance, variation due to genotype × environment interaction, and variation due to environmental effects (experimental error). The environmental variation is estimated by the variation among plants of the inbred parents that are considered genetically homogeneous. The difference between the variance among the F_2 plants and the geometric mean of the variance for the parents is considered an estimate of the genetic variance (σ^2_g).

The variation among genetically homogeneous F_1 plants obtained from a cross between inbred parents also can provide an estimate of environmental variation, in addition to that obtained from the parents. The numerator of the equation becomes

$$\sigma^2_{F2} - \sqrt[3]{(\sigma^2_{P1})(\sigma^2_{P2})(\sigma^2_{F1})}$$

One potential weakness of the method is that environmental variation among F_2 plants may not be equivalent to that of the parents or of the F_1. For species that are subject to extensive inbreeding depression, weak inbred plants may be subject to more environmental variation than vigorous F_2 plants. When heterosis is large, hybrid F_1 plants may be less sensitive to environmental fluctuations than are F_2 plants (Warner, 1952).

Backcross Method. A method for estimating narrow-sense heritability on a single-plant basis was developed by Warner (1952). It involves the measurement of F_2 plants from a cross between inbred parents and F_2 plants from populations developed by backcrossing the single-cross hybrid to each of the inbred parents. The formula used to compute heritability is

$$h^2 = \frac{2(\sigma^2_{F2}) \quad (\sigma^2_{B1} + \sigma^2_{B2})}{\sigma^2_{F2}}$$

where σ^2_{F2} is the variance among F_2 plants of the single-cross population and σ^2_{B1} and σ^2_{B2} are the variances among F_2 plants from the backcrosses of the single-cross F_1 to parent 1 and parent 2. The numerator of the equation represents additive genetic variance, and σ^2_{F2} in the denominator represents the phenotypic variance among plants.

Realized Heritability. The heritability of a character can be estimated by the amount of genetic improvement that is realized by selection within a population (Falconer, 1981). The general formula used is $h^2 = R/S$, where R is the response realized by selection and S is the selection differential. The selection differential is the difference between the mean of individuals selected from a population and the overall mean of the population from which they were selected.

The method can be illustrated by considering the performance of F_2 plants and their F_3 progeny. The mean performance of all F_2 plants can be designated

$\bar{x}_{F2}$, and the mean of selected F_2 plants as $\bar{x}_{s,F2}$. The selection differential in F_2 is

$$S = \bar{x}_{s,F2} - \bar{x}_{F2}$$

The mean performance of all F_3 progeny from F_2 plants can be designated $\bar{x}_{F3}$ and the mean of F_3 progeny from selected F_2 plants as $\bar{x}_{s,F3}$. The realized response from selection is $R = \bar{x}_{s,F3} - \bar{x}_{F3}$. Realized heritability can be summarized as

$$h^2 = \frac{\bar{x}_{s,F3} - \bar{x}_{F3}}{\bar{x}_{s,F2} - \bar{x}_{F2}}$$

Realized heritability can be computed on a single-plant, a plot, or an entry-mean basis. The basis of the heritability depends on the unit used for selection. In the previous illustration, selection among F_2 plants provided an estimate of heritability on a single-plant basis.

An alternative procedure for computing realized heritability involves selection within a population for individuals with high or low values for a trait. The progeny of individuals in each group are evaluated. Realized heritability is expressed as the difference in mean performance of high and low progeny divided by the difference in the mean of the parents. If F_2 plants and their progeny are evaluated, the equation can be expressed as

$$h^2 = \frac{\bar{x}_{high,F3} - \bar{x}_{low,F3}}{\bar{x}_{high,F2} - \bar{x}_{low,F2}}$$

where $\bar{x}_{high,F3}$ = mean performance of F_3 progeny of F_2 plants selected in high group

$\bar{x}_{low,F3}$ = mean performance of F_3 progeny of F_2 plants in low group

$\bar{x}_{high,F2}$ = mean performance of F_2 plants in high group

$\bar{x}_{low,F2}$ = mean performance of F_2 plants in low group

Realized heritability may not provide a valid estimate of the true heritability of a population (Falconer, 1981). Changes in the population unrelated to selection could bias the heritability estimates. These could include systematic changes due to environmental trends, inbreeding depression, and random drift.

Extensiveness of Genotype Evaluation

Selection among genotypes in a plant species can be based on the performance of single plants or on the average performance of progeny of a genotype evaluated in one or more replications, locations, and years. The heritability of a character and the effectiveness of selection are a function of the extensiveness with which

a genotype is evaluated. The heritability of a character may be relatively low when individual plants are evaluated for selection and relatively high when individuals are selected on the basis of the average performance of their progeny when tested in multiple environments. The most useful descriptions of the heritability of a character include information on the extensiveness with which genotypes were evaluated.

Heritability is commonly described on a single plant, a plot, or an entry-mean basis. Heritability on a single-plant basis can be described for selection among or within plots. The heritabilities differ in the extent to which factors other than the additive genetic variance among genotypes contribute to the phenotypic variance. This can be illustrated by examining the equations that are used to compute heritability by the variance component method (Table 7-1).

Heritability is lowest for the selection among single plants in a population that is not subdivided into plots. When single plants within a plot are compared, plot-to-plot variation (σ^2) does not contribute to the phenotypic variation (Hallauer and Miranda, 1981) (Chap. 17). The phenotypic variation on a plot basis is affected by the number of plants per plot whose measurements are averaged to obtain a single value for the character. The largest amount of influence that a breeder can have on the phenotypic variation is for heritability on an entry-mean basis. It is influenced by number of plants per plot, replications, locations, and years over which a genotype is evaluated.

Failure to estimate genotype × location (σ^2_{gl}), genotype × year, (σ^2_{gy}) and genotype × location × year (σ^2_{gly}) interactions can result in an inflated estimate of the genetic variance and heritability of a character (Chap. 18). The genotype variance, σ^2_g, can only be separated from the three interactions when genotypes are tested in two or more locations and years. If genotypes are evaluated at only one location in one year, σ^2_g cannot be separated from the three interactions and an estimate of heritability is equal to

$$\frac{\sigma^2_g + \sigma^2_{gl} + \sigma^2_{gy} + \sigma^2_{gly}}{\sigma^2_{ph}}$$

A heritability estimate based on data from one location in two or more years would be $(\sigma^2_g + \sigma^2_{gl})/\sigma^2_{ph}$, and an estimate derived from one year of data at two or more locations would be $(\sigma^2_g + \sigma^2_{gy})/\sigma^2_{ph}$. If the interactions with genotypes are important, heritability estimates will be inflated whenever genotypes are evaluated at less than two locations in two years.

Linkage Disequilibrium

Two alleles at each of two loci can be linked in coupling $\frac{AB}{ab}$ or repulsion $\frac{Ab}{aB}$. A population is said to be in linkage disequilibrium when the frequency of

coupling and repulsion phase linkages are not equal. Linkage disequilibrium can influence heritability estimates by causing an upward bias (increase) or downward bias (decrease) in the estimates of additive and dominance genetic variance. An upward bias in the additive variance (σ_A^2) will inflate the heritability, and downward bias will cause the heritability to be lower than if linkage equilibrium were present.

An excessive frequency of coupling phase linkages causes an upward bias in the estimates of additive and dominance variances (Hallauer and Miranda, 1981). When an excess of repulsion phase linkages is responsible for the disequilibrium, there is an upward bias in the dominance variance and a downward bias in the additive variance.

Linkage disequilibrium can be reduced by random-mating of a population. The number of generations of hybridization required to achieve linkage equilibrium depends on the closeness of the linkage (Hanson, 1959).

Conduct of Experiment

The accuracy with which measurements of the character(s) of interest can be made will affect experimental error. The degree of uniformity in the test environment will also influence the experimental error. Any precautions that the breeder can take to reduce experimental error (σ_e^2) will improve the heritability of a character (Table 7–1).

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