8

Introduction to quantitative genetics

Purpose and expected outcomes

Most of the traits that plant breeders are interested in are quantitatively inherited. It is important to understand the genetics that underlie the behavior of these traits in order to develop effective approaches for manipulating them. After studying this chapter, the student should be able to:

1. Define quantitative genetics and distinguish it from population genetics.
2. Distinguish between qualitative traits and quantitative traits.
3. Discuss polygenic inheritance.
4. Discuss gene action.
5. Discuss the variance components of quantitative traits.
6. Discuss the concept of heritability of traits.
7. Discuss selection and define the breeders' equation.
8. Discuss the concept of general worth of a plant.
9. Discuss the concept of combining ability.

What is quantitative genetics?

Genetics has several branches, including population genetics, quantitative genetics, biometric genetics, and molecular genetics. Population genetics is an extension of Mendelian genetics applied at the population level. Population genetics does not assign a genotypic or numerical value to each of the individuals (genotypes) in the population (except in the case of coefficients of selection). **Quantitative genetics**, on the other hand, is a branch of genetics in which individual genotypes are unidentified, and the traits of individuals are measured. Genotypic values are assigned to genotypes in the population. Quantitative genetics emphasizes the role of selection in controlled populations of known ancestry. Some topics of population genetics are often discussed in quantitative genetics books, partly because population genetics is basic to quantitative genetics.

A quantitative geneticist observes the phenotype, a product of the genotype and the environment. The genotypic array depends on mating systems and genetic linkage relationships, as well as on allelic frequencies, which in turn are impacted by mutation, migration, random drift, and selection (see Chapter 7). To make effective observations about phenotypes, the quantitative geneticist has to make assumptions about the mating system, allelic frequency altering forces, and the environment.

Common assumptions of quantitative genetic analysis are as follow:

1. **Reference population defined**. Allelic and genotypic frequencies can only be defined with respect to a specified population. The researcher should define a base reference population. All inferences made about the estimates should depend upon the composition of this reference population.

2 **Absence of linkage**. It is assumed that the trait (phenotype) observed is not affected by autosomal linkage genes.
3 **Presence of diploid Mendelian inheritance**. The plants are assumed to be diploid in which genes segregate and assort independently. Analysis of polyploids is possible, but is involved and handled differently.
4 **Absence of selection during the formation of inbred lines**. In order for the estimates of genetic variances to pertain to the base reference population, it is required that no selection occur when inbred lines are crossed.
5 **No breeding of the reference population**. It is assumed that the inbreeding coefficient of the reference population is zero. The analysis becomes more complex when inbreeding is coupled with more than two loci and includes the presence of epistasis.

Quantitative traits

The topic of quantitative traits was first discussed in Chapter 5. Most traits encountered in plant breeding are quantitatively inherited. Many genes control such traits, each contributing a small effect to the overall phenotypic expression of a trait. Variation in quantitative trait expression is without natural discontinuities (i.e., the variation is continuous). The traits that exhibit continuous variations are also called **metric traits**. Any attempt to classify such traits into distinct groups is only arbitrary. For example, height is a quantitative trait. If plants are grouped into tall versus short plants, one could find relatively tall plants in the short group and, similarly, short plants in the tall group.

Qualitative genetics versus quantitative genetics

The major ways in which qualitative genetics and quantitative genetics differ may be summarized as:

1 **Nature of traits**. Qualitative genetics is concerned with traits that have Mendelian inheritance and can be described according to kind and, as previously discussed, can be unambiguously categorized. Quantitative genetics traits are described in terms of the degree of expression of the trait, rather than the kind.
2 **Scale of variability**. Qualitative genetic traits provide discrete (discontinuous) phenotypic variation, whereas quantitative genetic traits produce phenotypic variation that spans the full spectrum (continuous).
3 **Number of genes**. In qualitative genetics, the effects of single genes are readily detectable, while in quantitative genetics, single gene effects are not discernible. Rather, traits are under polygenic control (genes with small indistinguishable effects).
4 **Mating pattern**. Qualitative genetics is concerned with individual matings and their progenies. Quantitative genetics is concerned with a population of individuals that may comprise a diversity of mating kinds.
5 **Statistical analysis**. Qualitative genetic analysis is quite straightforward, and is based on counts and ratios. On the other hand, quantitative analysis provides estimates of population parameters (attributes of the population from which the sample was obtained).

The environment and quantitative variation

All genes are expressed in an environment (phenotype = genotype + environmental effect). However, quantitative traits tend to be influenced to a greater degree than qualitative traits. It should be pointed out that, under significantly large environmental effects, qualitative traits (controlled by one or a few major genes) can exhibit a quantitative trait inheritance pattern (Figure 8.1). A strong environmental influence causes the otherwise distinct classes to overlap.

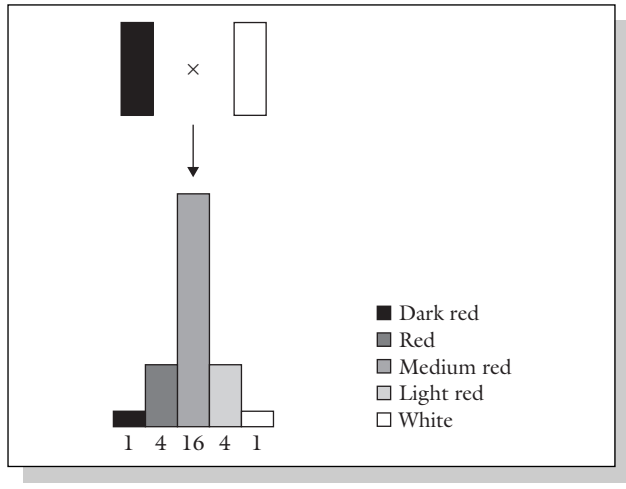


Figure 8.1 Nilsson-Ehle's classic work involving wheat color provided the first formal evidence of genes with cumulative effect.

Polygenes and polygenic inheritance

Quantitative traits are controlled by multiple genes or polygenes.

What are polygenes?

Polygenes are genes with effects that are too small to be individually distinguished. They are sometimes called **minor genes**. In polygenic inheritance, segregation occurs at a large number of loci affecting a trait. The phenotypic expression of polygenic traits is susceptible to significant modification by the variation in environmental factors to which plants in the population are subjected. Polygenic variation cannot be classified into discrete groups (i.e., variation is continuous). This is because of the large number of segregating loci, each with effects so small that it is not possible to identify individual gene effects in the segregating population or to meaningfully describe individual genotypes. Instead, biometrics is used to describe the population in terms of means and variances. Continuous variation is caused by environmental variation and genetic variation due to the simultaneous segregation of many genes affecting the trait. These effects convert the intrinsically discrete variation to a continuous one. Biometric genetics is used to distinguish between the two factors that cause continuous variability to occur.

Another aspect of polygenic inheritance is that different combinations of polygenes can produce a particular phenotypic expression. Furthermore, it is difficult to measure the role of the environment on trait expression because it is very difficult to measure the environmental effect on the plant basis. Consequently, a breeder attempting to breed a polygenic trait should evaluate the cultivar in an environment that is similar to that prevailing in the production region. It is beneficial to plant breeding if a tight linkage of polygenes (called **polygenic block** or **linkage block**) that has favorable effects on traits of interest to the breeder is discovered.

In 1910, a Swedish geneticist, Nilsson-Ehle provided a classic demonstration of polygenic inheritance and in the process helped to bridge the gap between our understanding of the essence of quantitative and qualitative traits. Polygenic inheritance may be explained by making three basic assumptions:

1. Many genes determine the quantitative trait.
2. These genes lack dominance.
3. The action of the genes are additive.

Table 8.1 Transgressive segregation.

P_1	$R_1R_1R_2R_2$ (dark red)	×	$r_1r_1r_2r_2$ (white)
F_1	$R_1r_1R_2r_2$		
F_2	1/16	=	$R_1R_1R_2R_2$
	4/16	=	$R_1R_1R_2r_2$, $R_1r_1R_2R_2$
	6/16	=	$R_1R_1r_2r_2$, $R_1r_1R_2r_2$, $r_1r_1R_2R_2$
	4/16	=	$R_1r_1r_2r_2$, $r_1r_1R_2r_2$
	1/16	=	$r_1r_1r_2r_2$

Nilsson-Ehle crossed two varieties of wheat, one with deep red grain of genotype $R_1R_1R_2R_2$, and the other white grain of genotype $r_1r_1r_2r_2$. The results are summarized in Table 8.1. He observed that all the seed of the F_1 was medium red. The F_2 showed about 1/16 dark red and 1/16 white seed, the remainder being intermediate. The intermediates could be classified into 6/16 medium red (like the F_1), 4/16 red, and 4/16 light red. The F_2 distribution of phenotypes may be obtained as an expansion of the bionomial $(a + b)^4$, where $a = b = \frac{1}{2}$.

His interpretation was that the two genes each had a pair of alleles that exhibited cumulative effects. In other words, the genes lacked dominance and their action was additive. Each R_1 or R_2 allele added some red to the phenotype so that the genotypes of white contained neither of these alleles, while the dark red genotype contained only R_1 and R_2. The phenotypic frequency ratio resulting from the F_2 was 1 : 4 : 6 : 4 : 1 (i.e., 16 genotypes and five classes) (see Figure 8.1).

The study involved only two loci. However, most polygenic traits are conditioned by genes at many loci. The number of genotypes that may be observed in the F_2 is calculated as 3^n, where n is the number of loci (each with two alleles). Hence, for three loci, the number of genotypes is 27, and for 10 loci, it will be $3^{10} = 59{,}049$. Many different genotypes can have the same phenotype, consequently, there is no strict one-to-one relationship between genotypes (Table 8.2). For n genes, there are 3^n genotypes and $2n + 1$ phenotypes. Many complex traits such as yield may have dozens and conceivably even hundreds of loci.

Other difficulties associated with studying the genetics of quantitative traits are dominance, environmental variation, and epistasis. Not only can dominance obscure the true genotype, but both the amount and direction can vary from one gene to another. For example, allele A may be dominant to a, but b may be

Table 8.2 As the number of genes controlling a trait increases, the phenotypic classes become increasingly indistinguishable. Given n genes, the number of possible phenotypes in the F_2 is given by $2n + 1$.

Number of gene loci	1	2	3.....n
Ratio of F_2 individuals expressing either extreme phenotype (parental)	1/4	1/16	1/64.....$(1/4)^n$

dominant to *B*. It has previously been mentioned that environmental effects can significantly obscure genetic effects. Non-allelic interaction is a clear possibility when many genes are acting together.

Number of genes controlling a quantitative trait

Polygenic inheritance is characterized by segregation at a large number of loci affecting a trait as previously discussed. Biometric procedures have been proposed to estimate the number of genes involved in a quantitative trait expression. However, such estimates, apart from not being reliable, have limited practical use. Genes may differ in the magnitude of their effects on traits, not to mention the possibility of modifying gene effects on certain genes.

Modifying genes

One gene may have a major effect on one trait, and a minor effect on another. There are many genes in plants without any known effects besides the fact that they modify the expression of a major gene by either enhancing or diminishing it. The effect of modifier genes may be subtle, such as slight variations in traits like the shape and shades of color of flowers, or, in fruits, variation in aroma and taste. Those trait modifications are of concern to plant breeders as they conduct breeding programs to improve quantitative traits involving many major traits of interest.

Decision-making in breeding based on biometric genetics

Biometric genetics is concerned with the inheritance of quantitative traits. As previously stated, most of the genes of interest to plant breeders are controlled by many genes. In order to effectively manipulate quantitative traits, the breeder needs to understand the nature and extent of their genetic and environmental control. M. J. Kearsey summarized the salient questions that need to be answered by a breeder who is focusing on improving quantitative (and also qualitative) traits, into four:

1. Is the character inherited?
2. How much variation in the germplasm is genetic?
3. What is the nature of the genetic variation?
4. How is the genetic variation organized?

By having answers to these basic genetic questions, the breeder will be in a position to apply the knowledge to address certain fundamental questions in plant breeding.

What is the best cultivar to breed?

As will be discussed later in the book, there are several distinct types of cultivars that plant breeders develop – pure lines, hybrids, synthetics, multilines, composites, etc. The type of cultivar is closely related to the breeding system of the species (self- or cross-pollinated), but more importantly on the genetic control of the traits targeted for manipulation. As breeders have more understanding of and control over plant reproduction, the traditional grouping between types of cultivars to breed and the methods used along the lines of the breeding system have diminished. The fact is that the breeding system can be artificially altered (e.g., self-pollinated species can be forced to outbreed, and vice versa). However, the genetic control of the trait of interest cannot be changed. The action and interaction of polygenes are difficult to alter. As Kearsey notes, breeders should make decisions about the type of cultivar to breed based on the genetic architecture of the trait, especially the nature and extent of dominance and gene interaction, more so than the breeding system of the species.

Generally, where additive variance and additive × additive interaction predominate, pure lines and inbred cultivars are appropriate to develop. However, where dominance variance and dominance × dominance interaction suggest overdominance predominates, hybrids would be successful cultivars. Open-pollinated cultivars are suitable where a mixture of the above genetic architectures occur.

What selection method would be most effective for improvement of the trait?

The kinds of selection methods used in plant breeding are discussed in Chapters 16 and 17. The genetic control

of the trait of interest determines the most effective selection method to use. The breeder should pay attention to the relative contribution of the components of genetic variance (additive, dominance, epistasis) and environmental variance in choosing the best selection method. Additive genetic variance can be exploited for long-term genetic gains by concentrating desirable genes in the homozygous state in a genotype. The breeder can make rapid progress where heritability is high by using selection methods that are dependent solely on phenotype (e.g., mass selection). However, where heritability is low, the method of selection based on families and progeny testing are more effective and efficient. When overdominance predominates, the breeder can exploit short-term genetic gain very quickly by developing hybrid cultivars for the crop.

It should be pointed out that as self-fertilizing species attain homozygosity following a cross, they become less responsive to selection. However, additive genetic variance can be exploited for a longer time in open-pollinated populations because relatively more genetic variation is regularly being generated through the ongoing intermating.

Should selection be on single traits or multiple traits?

Plant breeders are often interested in more than one trait in a breeding program, which they seek to improve simultaneously. The breeder is not interested in achieving disease resistance only, but in addition, high yield and other agronomic traits. The problem with simultaneous trait selection is that the traits could be correlated such that modifying one affects the other. The concept of correlated traits is discussed next. Biometric procedures have been developed to provide a statistical tool for the breeder to use. These tools are also discussed in this section.

Gene action

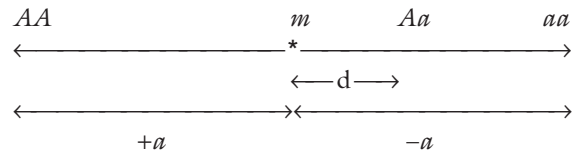
There are four types of gene action: **additive**, **dominance**, **epistatic**, and **overdominance**. Because gene effects do not always fall into clear-cut categories, and quantitative traits are governed by genes with small individual effects, they are often described by their gene action rather than by the number of genes by which they are encoded. It should be pointed out that gene action is conceptually the same for major genes as well as minor genes, the essential difference being that the action of a minor gene is small and significantly influenced by the environment.

Additive gene action

The effect of a gene is said to be additive when each additional gene enhances the expression of the trait by equal increments. Consequently, if one gene adds one unit to a trait, the effect of $aabb = 0$, $Aabb = 1$, $AABb = 3$, and $AABB = 4$. For a single locus (A, a) the heterozygote would be exactly intermediate between the parents (i.e., $AA = 2$, $Aa = 1$, $aa = 0$). That is, the performance of an allele is the same irrespective of other alleles at the same locus. This means that the phenotype reflects the genotype in additive action, assuming the absence of environmental effect. Additive effects apply to the allelic relationship at the same locus. Furthermore, a superior phenotype will breed true in the next generation, making selection for the trait more effective to conduct. Selection is most effective for additive variance; it can be fixed in plant breeding (i.e., develop a cultivar that is homozygous).

Additive effect

Consider a gene with two alleles (A, a). Whenever A replaces a, it adds a constant value to the genotype:



Replacing a by A in the genotype aa causes a change of a units. When both aa are replaced, the genotype is $2a$ units away from aa. The midparent value (the average score) between the two homozygous parents is given by m (representing a combined effect of both genes for which the parents have similar alleles and environmental factors). This also serves as the reference point for measuring deviations of genotypes. Consequently, $AA = m + a_A$, $aa = m - a$, and $Aa = m + d_A$, where a_A is the **additive effect** of allele A, and d is the dominance effect. This effect remains the same regardless of the allele with which it is combined.

Average effect

In a random mating population, the term **average effect** of alleles is used because there are no homozygous lines. Instead, alleles of one plant combine with alleles from

pollen from a random mating source in the population through hybridization to generate progenies. In effect the allele of interest replaces its alternative form in a number of randomly selected individuals in the population. The change in the population as a result of this replacement constitutes the average effect of the allele. In other words, the average effect of a gene is the mean deviation from the population mean of individuals that received a gene from one parent, the gene from the other parent having come at random from the population.

Breeding value

The average effects of genes of the parents determine the mean genotypic value of the progeny. Further, the value of an individual judged by the mean value of its progeny is called the **breeding value** of the individual. This is the value that is transferred from an individual to its progeny. This is a measurable effect, unlike the average effect of a gene. However, the breeding value must always be with reference to the population to which an individual is to be mated. From a practical breeding point of view, the additive gene effect is of most interest to breeders because its exploitation is predictable, producing improvements that increase linearly with the number of favorable alleles in the population.

Dominance gene action

Dominance action describes the relationship of alleles at the same locus. Dominance variance has two components – variance due to homozygous alleles (which is additive) and variance due to heterozygous genotypic values. Dominance effects are deviations from additivity that make the heterozygote resemble one parent more than the other. When dominance is complete, the heterozygote is equal to the homozygote in effects (i.e., $Aa = AA$). The breeding implication is that the breeder cannot distinguish between the heterozygous and homozygous phenotypes. Consequently, both kinds of plants will be selected, the homozygotes breeding true while the heterozygotes will not breed true in the next generation (i.e., fixing superior genes will be less effective with dominance gene action).

Dominance effect

Using the previous figure for additive effect, the extent of dominance (d_A) is calculated as the deviation of the heterozygote, Aa, from the mean of the two homozygotes (AA, aa). Also, $d_A = 0$ when there is no dominance while d is positive if A is dominant, and negative if a_A is dominant. Further, if dominance is complete $d_A = a_A$, whereas $d_A < a_A$ for incomplete (partial) dominance, and $d_A > a_A$ for overdominace. For a single locus, $m = \frac{1}{2}(AA + aa)$ and $a_A = \frac{1}{2}(AA - aa)$, while $d_A = Aa - \frac{1}{2}(AA + aa)$.

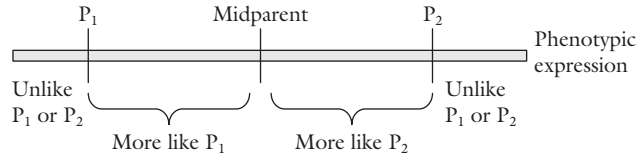


Figure 8.2 An illustration of overdominance gene action. The heterozygote, *Aa*, is more valuable than either homozygote.

Overdominance gene action

Overdominance gene action exists when each allele at a locus produces a separate effect on the phenotype, and their combined effect exceeds the independent effect of the alleles (i.e., $aa = 1$, $AA = 1$, $Aa = 2$) (Figure 8.2). From the breeding standpoint, the breeder can fix overdominance effects only in the first generation (i.e., F_1 hybrid cultivars) through apomixis, or through chromosome doubling of the product of a wide cross.

Epistasic gene action

Epistatic effects in qualitative traits are often described as the masking of the expression of a gene by one at another locus. In quantitative inheritance, **epistasis** is described as non-allelic gene interaction. When two genes interact, an effect can be produced where there was none (e.g., $Aabb = 0$, $aaBB = 0$, but $A–B– = 4$).

The estimation of gene action or genetic variance requires the use of large populations and a mating design. The effect of the environment on polygenes makes estimations more challenging. As N. W. Simmonds observed, at the end of the day, what qualitative genetic analysis allows the breeder to conclude from partitioning variance in an experiment is to say that a portion of the variance behaves *as though* it could be attributed to additive gene action or dominance effect, and so forth.

Variance components of a quantitative trait

The genetics of a quantitative trait centers on the study of its variation. As D. S. Falconer stated, it is in terms of

variation that the primary genetic questions are formulated. Further, the researcher is interested in partitioning variance into its components that are attributed to different causes or sources. The genetic properties of a population are determined by the relative magnitudes of the components of variance. In addition, by knowing the components of variance, one may estimate the relative importance of the various determinants of phenotype.

K. Mather expressed the phenotypic value of quantitative traits in this commonly used expression:

$$P(\text{phenotype}) = G(\text{genotype}) + E(\text{environment})$$

Individuals differ in phenotypic value. When the phenotypes of a quantitative trait are measured, the observed value represents the phenotypic value of the individual. The phenotypic value is variable because it depends on genetic differences among individuals, as well as environmental factors and the interaction between genotypes and the environment (called $G \times E$ interaction).

Total variance of a quantitative trait may be mathematically expressed as follows:

$$V_P = V_G + V_E + V_{GE}$$

where V_P = total **phenotypic variance** of the segregating population, V_G = **genetic variance**, V_E = environmental variance, and V_{GE} = variance associated with the genetic and environmental interaction.

The genetic component of variance may be further partitioned into three components as follows:

$$V_G = V_A + V_D + V_I$$

where V_A = **additive variance** (variance from additive gene effects), V_D = **dominance variance** (variance from dominance gene action), and V_I = **interaction** (variance from interaction between genes). Additive genetic variance (or simply additive variance) is the variance of breeding values and is the primary cause of resemblance between relatives. Hence V_A is the primary determinant of the observable genetic properties of the population, and of the response of the population to selection. Further, V_A is the only component that the researcher can most readily estimate from observations made on the population. Consequently, it is common to partition genetic variance into two – additive versus all other kinds of variance. This ratio, V_A/V_P, gives what is called the **heritability** of a trait, an estimate that is of practical importance in plant breeding (see next).

The total phenotypic variance may then be rewritten as:

$$V_P = V_A + V_D + V_I + V_E + V_{GE}$$

To estimate these variance components, the researcher uses carefully designed experiments and analytical methods. To obtain environmental variance, individuals from the same genotype are used.

An inbred line (essentially homozygous) consists of individuals with the same genotype. An F_1 generation from a cross of two inbred lines will be heterozygous but genetically uniform. The variance from the parents and the F_1 may be used as a measure of environmental variance (V_E). K. Mather provided procedures for obtaining genotypic variance from F_2 and backcross data. In sum, variances from additive, dominant, and environmental effects may be obtained as follows:

$$V_{P1} = E;\ V_{P2} = E;\ V_{F1} = E$$
$$V_{F2} = \tfrac{1}{2}A + \tfrac{1}{4}D + E$$
$$V_{B1} = \tfrac{1}{4}A + \tfrac{1}{4}D + E$$
$$V_{B2} = \tfrac{1}{4}A + \tfrac{1}{4}D + E$$
$$V_{B1} + V_{B2} = \tfrac{1}{2}A + \tfrac{1}{2}D + 2E$$

This represents the most basic procedure for obtaining components of genetic variance since it omits the variances due to epistasis, which are common with quantitative traits. More rigorous biometric procedures are needed to consider the effects of interlocular interaction.

It should be pointed out that additive variance and dominance variance are statistical abstractions rather than genetic estimates of these effects. Consequently, the concept of additive variance does not connote perfect additivity of dominance or epistasis. To exclude the presence of dominance or epistasis, all the genotypic variance must be additive.

Concept of heritability

Genes are not expressed in a vacuum but in an environment. A phenotype observed is an interaction between the genes that encode it and the environment in which the genes are being expressed. Plant breeders typically select plants based on the phenotype of the desired trait, according to the breeding objective. Sometimes, a genetically inferior plant may appear superior to other plants only because it is located in a more favorable region of the soil. This may mislead the breeder. In other words, the selected phenotype will not give rise to the same progeny. If the genetic variance is high and the

environmental variance is low, the progeny will be like the selected phenotype. The converse is also true. If such a plant is selected for advancing the breeding program, the expected genetic gain will not materialize. Quantitative traits are more difficult to select in a breeding program because they are influenced to a greater degree by the environment than are qualitative traits. If two plants are selected randomly from a mixed population, the observed difference in a specific trait may be due to the average effects of genes (hereditary differences), or differences in the environments in which the plants grew up, or both. The average effects of genes is what determines the degree of resemblance between relatives (parents and offspring), and hence is what is transmitted to the progenies of the selected plants.

Definition

The concept of the reliability of the phenotypic value of a plant as a guide to the breeding value (additive genotype) is called the **heritability** of the metric trait. As previously indicated, plant breeders are able to measure phenotypic values directly, but it is the breeding value of individuals that determines their influence on the progeny. Heritability is the proportion of the observed variation in a progeny that is inherited. The bottom line is that if a plant breeder selects plants on the basis of phenotypic values to be used as parents in a cross, the success of such an action in changing the characteristics in a desired direction is predictable only by knowing the degree of correspondence (genetic determination) between phenotypic values and breeding values. Heritability measures this degree of correspondence. It does not measure genetic control, but rather how this control can vary.

Genetic determination is a matter of what causes a characteristic or trait; heritability, by contrast, is a scientific concept of what causes differences in a characteristic or trait. Heritability is, therefore, defined as a fraction: it is **the ratio of genetically caused variation to total variation** (including both environmental and genetic variation). Genetic determination, by contrast, is an informal and intuitive notion. It lacks quantitative definition, and depends on the idea of a normal environment. A trait may be described as genetically determined if it is coded in and caused by the genes, and bound to develop in a normal environment. It makes sense to talk about genetic determination in a single individual, but heritability makes sense only relative to a population in which individuals differ from one another.

Types of heritability

Heritability is a property of the trait, the population, and the environment. Changing any of these factors will result in a different estimate of heritability. There are two different estimates of heritability.

1 **Broad sense heritability**. Heritability estimated using the total genetic variance (V_G) is called broad sense heritability. It is expressed mathematically as:

$$H = V_G / V_P$$

It tends to yield a high value (Table 8.3). Some use the symbol H^2 instead of H.

2 **Narrow sense heritability**. Because the additive component of genetic variance determines the response to selection, the narrow sense heritability estimate is more useful to plant breeders than the broad sense estimate. It is estimated as:

$$h^2 = V_A / V_P$$

However, when breeding clonally propagated species (e.g., sugarcane, banana), in which both additive and non-additive gene actions are fixed and transferred from parent to offspring, broad sense heritability is also useful. The magnitude of narrow sense heritability cannot exceed, and is usually less than, the corresponding broad sense heritability estimate.

Heritabilities are seldom precise estimates because of large standard errors. Characters that are closely related to reproductive fitness tend to have low heritability estimates. The estimates are expressed as a fraction, but

Table 8.3 Heritability estimates of some plant architectural traits in dry bean.

Trait	Heritability
Plant height	45
Hypocotyl diameter	38
Number of branches/plant	56
Nodes in lower third	36
Nodes in mid section	45
Nodes in upper third	46
Pods in lower third	62
Pods in mid section	85
Pods in upper third	80
Pod width	81
Pod length	67
Seed number per pod	30
100 seed weight	77

may also be reported as a percentage by multiplying by 100. A heritability estimate may be unity (1) or less.

Factors affecting heritability estimates

The magnitude of heritability estimates depends on the genetic population used, the sample size, and the method of estimation.

Genetic population

When heritability is defined as $h^2 = V_A/V_P$ (i.e., in the narrow sense), the variances are those of individuals in the population. However, in plant breeding, certain traits such as yield are usually measured on a plot basis (not on individual plants). The amount of genotypic variance present for a trait in a population influences estimates of heritability. Parents are responsible for the genetic structure of the populations they produce. More divergent parents yield a population that is more genetically variable. Inbreeding tends to increase the magnitude of genetic variance among individuals in the population. This means that estimates derived from F_2 will differ from, say, those from F_6.

Sample size

Because it is impractical to measure all individuals in a large population, heritabilities are estimated from sample data. To obtain the true genetic variance for a valid estimate of the true heritability of the trait, the sampling should be random. A weakness in heritability estimates stems from bias and lack of statistical precision.

Method of computation

Heritabilities are estimated by several methods that use different genetic populations and produce estimates that may vary. Common methods include the **variance component method** and **parent–offspring regression**. Mating schemes are carefully designed to enable the total genetic variance to be partitioned.

Methods of computation

The different methods of estimating heritabilities have both strengths and weaknesses.

Variance component method

The variance component method of estimating heritability uses the statistical procedure of **analysis of variance** (ANOVA, see Chapter 9). Variance estimates depend on the types of populations in the experiment. Estimating genetic components suffers from certain statistical weaknesses. Variances are less accurately estimated than means. Also, variances are unrobost and sensitive to departure from normality. An example of a heritability estimate using F_2 and backcross populations is as follows:

$$V_{F2} = V_A + V_D + V_E$$
$$V_{B1} + V_{B2} = V_A + 2V_D + 2V_E$$
$$V_E = V_{P1} + V_{P2} + V_{F1}$$
$$H = (V_A + V_D)/(V_A + V_D + V_E) = V_G/V_P$$
$$h^2 = (V_A)/(V_A + V_D + V_E) = V_A/V_P$$

Example For example, using the data in the table below:

	P_1	P_2	F_1	F_2	BC_1	BC_2
Mean	20.5	40.2	28.9	32.1	25.2	35.4
Variance	10.1	13.2	7.0	52.3	35.1	56.5

$$V_E = [V_{P1} + V_{P2} + V_{F1}]/3$$
$$= [10.1 + 13.2 + 7]/3$$
$$= 30.3/3$$
$$= 10.1$$

$$V_A = 2V_{F2} - (V_{B1} + V_{B2})$$
$$= 2(52.3) - (35.1 + 56.5)$$
$$= 104.6 - 91.6$$
$$= 13.0$$

$$V_D = [(V_{B1} + V_{B2}) - F_2 - (V_{P1} + V_{P2} + F_1)]/3$$
$$= [(35.1 + 56.5) - 52.3 - (10.1 + 13.2 + 7.0)]/3$$
$$= [91.6 - 52.3 - 30.3]/3$$
$$= 3.0$$

Broad sense heritability

$$H = [13.0 + 3.0]/[13.0 + 3.0 + 10.1]$$
$$= 16/26.1$$
$$= 0.6130$$
$$= 61.30\%$$

Narrow sense heritability

$$h^2 = 13.0[13.0 + 3.0 + 10.1]$$
$$= 13.0/26.1$$
$$= 0.4980$$
$$= 49.80\%$$

Other methods of estimation

$$H = [V_{F2} - \tfrac{1}{2}(V_{P1} + V_{P2})]/F_2$$
$$= [52.3 - \tfrac{1}{2}(10.1 + 13.2)]/52.3$$
$$= 40.65/52.3$$
$$= 0.7772$$
$$= 77.72\%$$

This estimate is fairly close to that obtained by using the previous formula.

Parent–offspring regression

The type of offspring determines if the estimate would be broad sense or narrow sense. This method is based on several assumptions: the trait of interest has diploid Mendelian inheritance; the population from which the parents originated is randomly mated; the population is in linkage equilibrium (or no linkage among loci controlling the trait); parents are non-inbred; and there is no environmental correlation between the performance of parents and offspring.

The parent–offspring method of heritability is relatively straightforward. First, the parent and offspring means are obtained. Cross products of the paired values are used to compute the covariance. A regression of offspring on midparent value is then calculated. Heritability in the narrow sense is obtained as follows:

$$h^2 = b_{op} = V_A/V_P$$

where b_{op} is the regression of offspring on midparent value, and V_A and V_P are the additive variance and phenotypic variance, respectively.

However, if only one parent is known or relevant (e.g., a polycross):

$$b = {}^1\!/_2(V_A/V_P)$$

and

$$h^2 = 2b_{op}$$

Applications of heritability

Heritability estimates are useful for breeding quantitative traits. The major applications of heritability are:

1. To determine whether a trait would benefit from breeding. If, in particular, the narrow sense heritability for a trait is high, it indicates that the use of plant breeding methods will likely be successful in improving the trait of interest.
2. To determine the most effective selection strategy to use in a breeding program. Breeding methods that use selection based on phenotype are effective when heritability is high for the trait of interest.
3. To predict gain from selection. Response to selection depends on heritability. A high heritability would likely result in high response to selection to advance the population in the desired direction of change.

Evaluating parental germplasm

A useful application of heritability is in evaluating the germplasm assembled for a breeding project to determine if there is sufficient genetic variation for successful improvement to be pursued. A replicated trial of the available germplasm is conducted and analyzed by ANOVA as follows:

Source	Degrees of freedom (df)	Error mean sum of squares (EMS)
Replication	$r-1$	
Genotypes	$g-1$	$\sigma^2 + r\sigma^2_g$
Error	$(r-1)(g-1)$	σ^2

From the analysis, heritability may be calculated as:

$$H/h^2 = [\sigma^2_g]/[\sigma^2_g + \sigma^2_e]$$

It should be pointed out that whether the estimate is heritability in the narrow or broad sense depends on the nature of the genotypes. Pure lines or inbred lines would yield additive type of variance, making the estimate narrow sense. Segregating population would make the estimate broad sense.

Response to selection in breeding

Selection was discussed in Chapter 7. The focus of this section is on the **response to selection** (**genetic gain** or **genetic advance**). After generating variability, the next task for the breeder is the critical one of advancing the population through selection.

Selection, in essence, entails discriminating among genetic variation (heterogeneous population) to identify and choose a number of individuals to establish the next generation. The consequence of this is differential reproduction of genotypes in the population such that gene frequencies are altered, and, subsequently, the genotypic and phenotypic values of the targeted traits. Even though artificial selection is essentially directional, the concept of "complete" or "pure" artificial selection is an abstraction because, invariably, before the breeder gets a chance to select plants of interest, some amount of natural selection has already been imposed.

The breeder hopes, by selecting from a mixed population, that superior individuals (with high genetic potential)

will be advanced, and will consequently change the population mean of the trait in a positive way in the next generation. The breeder needs to have a clear objective. The trait to be improved needs to be clearly defined. Characters controlled by major genes are usually easy to select. However, polygenic characters, being genetically and biologically complex, present a considerable challenge to the breeder.

The response to selection (***R***) is the difference between the mean phenotypic value of the offspring of the selected parents and the whole of the parental generation before selection. The response to selection is simply the change of population mean between generations following selection. Similarly, the **selection differential** (***S***) is the mean phenotypic value of the individuals selected as parents expressed as a deviation from the population mean (i.e., from the mean phenotypic value of all the individuals in the parental generation before selection). Response to selection is related to heritability by the following equation:

$$R = h^2 S$$

Prediction of response in one generation: genetic advance due to selection

The genetic advance achieved through selection depends on three factors:

1. The total variation (phenotypic) in the population in which selection will be conducted.
2. Heritability of the target character.
3. The selection pressure to be imposed by the plant breeder (i.e., the proportion of the population that is selected for the next generation).

A large phenotypic variance would provide the breeder with a wide range of variability from which to select. Even when the heritability of the trait of interest is very high, genetic advance would be small without a large amount of phenotypic variation (Figure 8.3). When the heritability is high, selecting and advancing only the top few performers is likely to produce a greater genetic advance than selecting many moderate performers. However, such a high selection pressure would occur at the expense of a rapid loss in variation. When heritability is low, the breeder should impose a lower selection pressure in order to advance as many high-potential genotypes as possible.

In principle, the prediction of response is valid for only one generation of selection. This is so because a response to selection depends on the heritability of the trait estimated in the generation from which parents are selected. To predict the response in subsequent generations, heritabilities must be determined in each generation. Heritabilities are expected to change from one generation to the next because, if there is a response, it must be accompanied by a change in gene frequencies on which heritability depends. Also, selection of parents reduces the variance and the heritability, especially in the early generations. It should be pointed out that heritability changes are not usually large.

If heritability is unity ($V_A = V_P$; no environmental variance), progress in a breeding program would be perfect, and the mean of the offspring would equal the mean of the selected parents. On the other hand, if heritability is zero, there would be no progress at all ($R = 0$).

The response in one generation may be mathematically expressed as:

$$\bar{X}_o - \bar{X}_p = R = ih^2\sigma \text{ (or } \Delta G = ih^2\sigma_p)$$

where $\bar{X}_o$ = mean phenotype of the offspring of selected parents, $\bar{X}_p$ = mean phenotype of the whole parental generation, R = advance in one generation of selection, h^2 = heritability, σ_p = phenotypic standard deviation of the parental population, i = intensity of selection, and ΔG = genetic gain or genetic advance.

This equation has been suggested by some to be one of the fundamental equations of plant breeding, which must be understood by all breeders, and hence is called the **breeders' equation**. The equation is graphically illustrated in Figure 8.4. The factor "i", the intensity of selection, is a statistical factor that depends on the fraction of the current population retained to be used as parents for the next generation. The breeder may consult statistical tables for specific values (e.g., at 1% i = 2.668; at 5% i = 2.06; at 10% i = 1.755). The breeder must decide the selection intensity to achieve a desired objective. The selection differential can be predicted if the phenotypic values of the trait of interest are normally distributed, and the selection is by truncation (i.e., the individuals are selected solely in order of merit according to their phenotypic value – no individual being selected is less good than any of those rejected).

The response equation is effective in predicting response to selection, provided the heritability estimate (h^2) is fairly accurate. In terms of practical breeding, the parameters for the response equation are seldom available and hence not widely used. Over the long haul, repeated selection tends to fix favorable genes, resulting

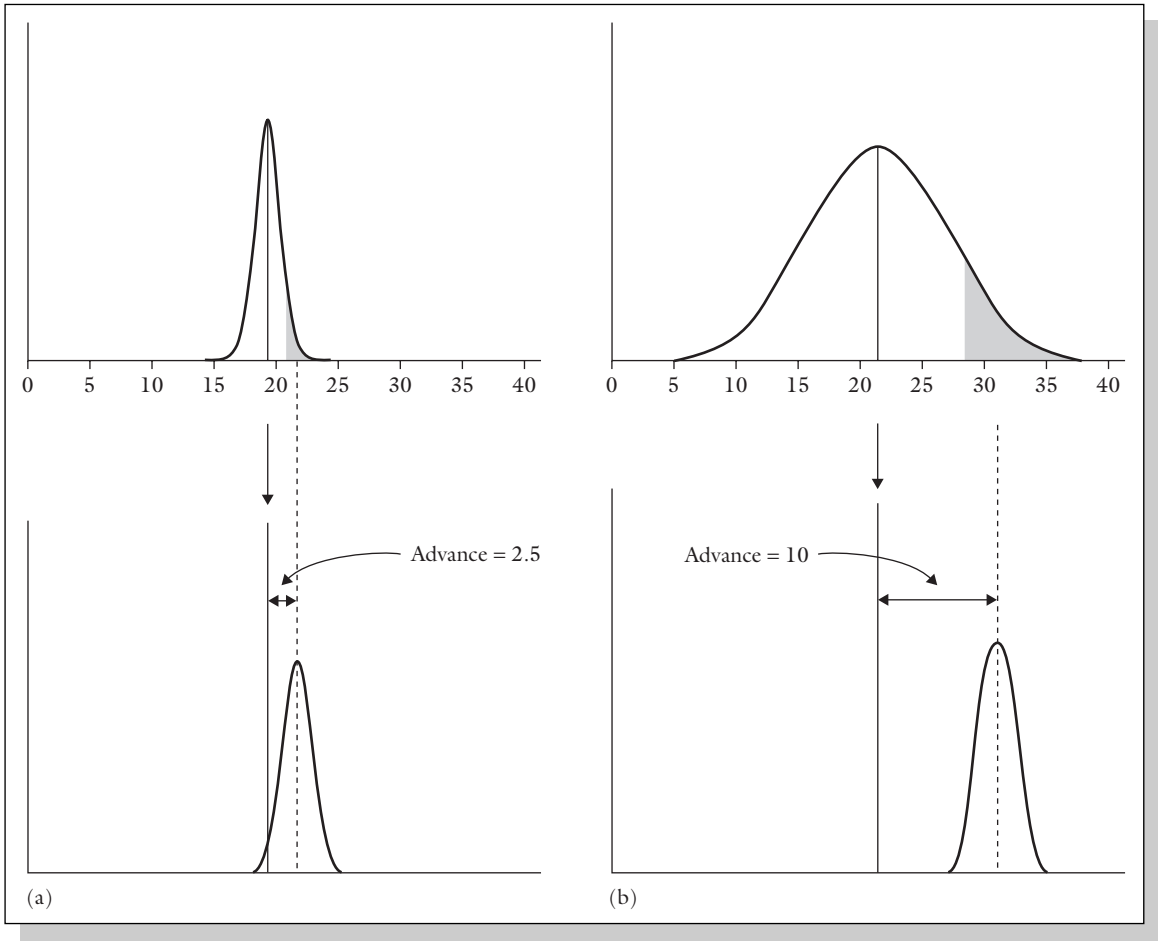


Figure 8.3 The effect of phenotypic variance on genetic advance. (a) If the phenotypic variance is too small, the genetic variability from which to select will be limited, resulting in a smaller genetic gain. (b) The reverse is true when the phenotypic variance is large.

in a decline in both heritability and phenotypic standard deviation. Once genes have been fixed, there will be no further response to selection.

Example For example:

	X	σ_P	V_P	V_A	V_E
Parents	15	2	6	4	3
Offspring	20.2	15	4.3	2.5	3

$R = ih^2\sigma_p$

Parents

$h^2 = V_A/V_P$
$= 4/6$
$= 0.67$

for i at $P = 10\% = 1.755$ (read from tables and assuming a very large population).

$R = 1.755 \times 0.67 \times 2$
$= 2.35$

Offspring

$h^2 = V_A/V_P$
$= 2.5/4.3$
$= 0.58$
$R = 1.755 \times 0.58 \times 1.5$
$= 1.53$

Generally, as selection advances to higher generations, genetic variance and heritability decline. Similarly, the advance from one generation to the next declines, while the mean value of the trait being improved increases.

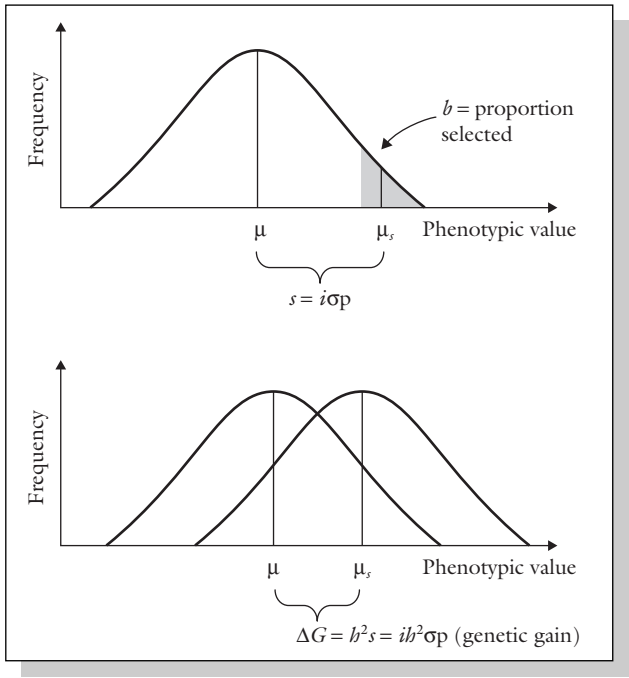


Figure 8.4 Genetic gain or genetic advance from selection indicates the progress plant breeders make from one generation to another based on the selection decisions they make.

Concept of correlated response

Correlation is a measure of the degree of association between traits as previously discussed. This association may be on the basis of genetics or may be non-genetic. In terms of response to selection, genetic correlation is what is useful. When it exists, selection for one trait will cause a corresponding change in other traits that are correlated. This response to change by genetic association is called **correlated response**. Correlated response may be caused by pleotropism or linkage disequilibrium. Pleotropism is the multiple effect of a single gene (i.e., a single gene simultaneously affects several physiological pathways). In a random mating population, the role of linkage disequilibrium in correlated response is only important if the traits of interest are closely linked.

In calculating correlated response, genetic correlations should be used. However, the breeder often has access to phenotypic correlation and can use them if they were estimated from values averaged over several environments. Such data tend to be in agreement with genetic correlation. In a breeding program the breeder, even while selecting simultaneously for multiple traits, has a primary trait of interest and secondary traits. The correlated response (CRy) to selection in the primary trait (y) for a secondary trait (x) is given by:

$$CRy = i_x h_x h_y \rho_g \sqrt{V_{Py}}$$

where h_x and h_y are square roots of the heritabilities of the two respective traits, and ρ_g is the genetic correlation between traits. This relationship may be reduced to:

$$CRy = i_x \rho_g h_x \sqrt{V_{Gy}}$$

since $h_y = \sqrt{(V_{Gy}/V_{Py})}$

It is clear that the effectiveness of indirect selection depends on the magnitude of genetic correlation and the heritability of the secondary traits being selected. Further, given the same selection intensity and a high genetic correlation between the traits, indirect selection for the primary trait will be more effective than directional selection, if heritability of the secondary trait is high ($\rho_g h_x > h_y$). Such a scenario would occur when the secondary trait is less sensitive to environmental change (or can be measured under controlled conditions). Also, when the secondary trait is easier and more economic to measure, the breeder may apply a higher selection pressure to it.

Correlated response has wider breeding application in homozygous, self-fertilizing species and apomicts. Additive genetic correlation is important in selection in plant breeding. As previously discussed, the additive breeding value is what is transferred to offspring and can be changed by selection. Hence, where traits are additively genetically correlated, selection for one trait will produce a correlated response in another.

Selection for multiple traits

Plant breeders may use one of three basic strategies to simultaneously select multiple traits: **tandem selection**, **independent curling**, and **selection index**. Plant breeders often handle very large numbers of plants in a segregating population using limited resources (time, space, labor, money, etc.). Along with the large number of individuals are the many breeding characters often considered in a breeding program. The sooner they can reduce the numbers of plants to the barest minimum, but more importantly, to the most desirable and promising individuals, the better. Highly heritable and readily scorable traits are easier to select for in the initial stages of a breeding program.

Tandem selection

In this mode of selection, the breeder focuses on one trait at a time (serial improvement). One trait is selected for several generations, then another trait is focused on for the next period. The question of how long each trait is selected for before a switch and at what selection intensity, are major considerations for the breeder. It is effective when genetic correlation does not exist between the traits of interest, or when the relative importance of each trait changes throughout the years.

Independent curling

Also called truncation selection, independent curling entails selecting for multiple traits in one generation. For example, for three traits, A, B, and C, the breeder may select 50% plants per family for A on phenotypic basis, and from that group select 40% plants per family based on trait B; finally, from that subset, 50% plants per family are selected for trait C, giving a total of 10% selection intensity ($0.5 \times 0.4 \times 0.5$).

Selection index

A breeder has a specific objective for conducting a breeding project. However, selection is seldom made on the basis of one trait alone. For example, if the breeding project is for disease resistance, the objective will be to select a genotype that combines disease resistance with the qualities of the elite adapted cultivar. Invariably, breeders usually practice selection on several traits, simultaneously. The problem with this approach is that as more traits are selected for, the less the selection pressure that can be exerted on any one trait. Therefore, the breeder should select on the basis of two or three traits of the highest economic value. It is conceivable that a trait of high merit may be associated with other traits of less economic value. Hence, using the concept of selection on total merit, the breeder would make certain compromises, selecting individuals that may not have been selected if the choice was based on a single trait.

In selecting on a multivariate phenotype, the breeder explicitly or implicitly assigns a weighting scheme to each trait, resulting in the creation of a univariate trait (an **index**) that is then selected. The index is the best linear prediction of an individual's breeding value. It takes the form of a multiple regression of breeding values on all the sources of information available for the population.

The methods used for constructing an index usually include heritability estimates, the relative economic importance of each trait, and genetic and phenotypic correlation between the traits. The most common index is a linear combination that is mathematically expressed as follows:

$$I = \sum_{i=1}^{m} b_j z_j = b^{I} z$$

where z = vector of phenotypic values in an individual, and b = vector of weights. For three traits, the form may be:

$$I = aA^1 + bB^1 + cC^1$$

where a, b, and c are coefficients correcting for relative heritability and the relative economic importance of traits A, B, and C, respectively, and A^1, B^1, and C^1 are the numerical values of traits A, B, and C expressed in standardized form. A standardized variable (X^1) is calculated as:

$$X^1 = (X - \bar{X})/\sigma_x$$

where X = record of performance made by an individual, $\bar{X}$ = average performance of the population, and σ_x = standard deviation of the trait.

The classic selection index has the following form:

$$I = b_1x_1 + b_2x_2 + b_3x_3 + \ldots + b_mx_n$$

where x_1, x_2, x_3, to x_n are the phenotypic performance of the traits of interest, and b_1, b_2, and b_3 are the relative weights attached to the respective traits. The weights could be simply the respective relative economic importance of each trait, with the resulting index called the **basic index**, and may be used in cultivar assessment in official registration trials.

An index by itself is meaningless, unless it is used in comparing several individuals on a relative basis. Further, in comparing different traits, the breeder is faced with the fact that the mean and variability of each trait is different, and frequently, the traits are measured in different units. Standardization of variables resolves this problem.

Concept of intuitive index

Plant breeding was described in Chapter 2 as both a science and an art. Experience (with the crop, the methods of breeding, breeding issues concerning the crop) is advantageous in having success in solving plant breeding problems. Plant breeders, as previously indicated, often

Industry highlights

Recurrent selection with soybean

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Selection using a restricted index

Two commodities, protein meal and oil, are produced from soybean (*Glycine max* (L.) Merr.) and give the crop its value. Soybean seeds are crushed, oil is extracted, and protein meal is what remains. On a dry weight basis, soybeans are approximately 20% oil and 40% protein. Concentration of protein in the meal is dependant on protein concentration in soybean seeds. Protein meal is traded either as 44% protein or 48% protein. The 48% protein meal is more valuable, so increasing or maintaining protein concentration in soybean seeds has been a breeding objective. Protein is negatively associated with oil in seeds and in many breeding populations it is negatively associated with seed yield (Brim & Burton 1979).

The negative association between yield and protein could be due to genetic linkage as well as physiological processes (Carter et al. 1982). Thus a breeding strategy is needed that permits simultaneous selection of both protein and yield. Increased genetic recombination should also be helpful in breaking unfavorable linkages between genes that contribute to the negative yield and protein relation. We devised a recurrent S_1 family selection program to satisfy the second objective and applied a restricted index to family performance to achieve the first objective.

Selection procedure

A population designated RS4 was developed using both high-yielding and high protein parents. The high-yielding parents were the cultivars, "Bragg", "Ransom", and "Davis". The high protein parents were 10 F_3 lines from cycle 7 of another recurrent selection population designated IA (Brim & Burton 1979). In that population, selection had been solely for protein. Average protein concentration of the 10 parental F_3 lines was 48.0%. The base or C_0 population was developed by making seven or eight matings between each high protein line and the three cultivars, resulting in 234 hybrids (Figure 1). The S_0 generation was advanced at the US Department of Agriculture (USDA) winter soybean nursery in Puerto Rico resulting in 234 S_1 families. These were tested in two replications at two locations. Both seed yield and protein concentration were determined for each family. Average protein concentration of the initial population was 45.6%. As this was an acceptable increase in protein, a restricted selection index was applied aimed at increasing yield and holding protein constant. This index was:

$$I = \text{yield} - (\sigma_{Gyp}/\sigma^2_{Gp}) \times \text{protein}$$

where σ_{Gyp} = estimated genetic covariance between yield and protein, and σ^2_{Gp} = estimated genetic variance of protein (Holbrook et al. 1989). Using this index, 29 families were selected.

The following summer, these 29 families (now in the S_2 generation) were randomly intermated. To do this, we used the following procedure. Each day of the week, flowers for pollen were collected from 24 of the families and used to pollinate the remaining five families. A different set of 24 and five families were used as males and females, respectively, each

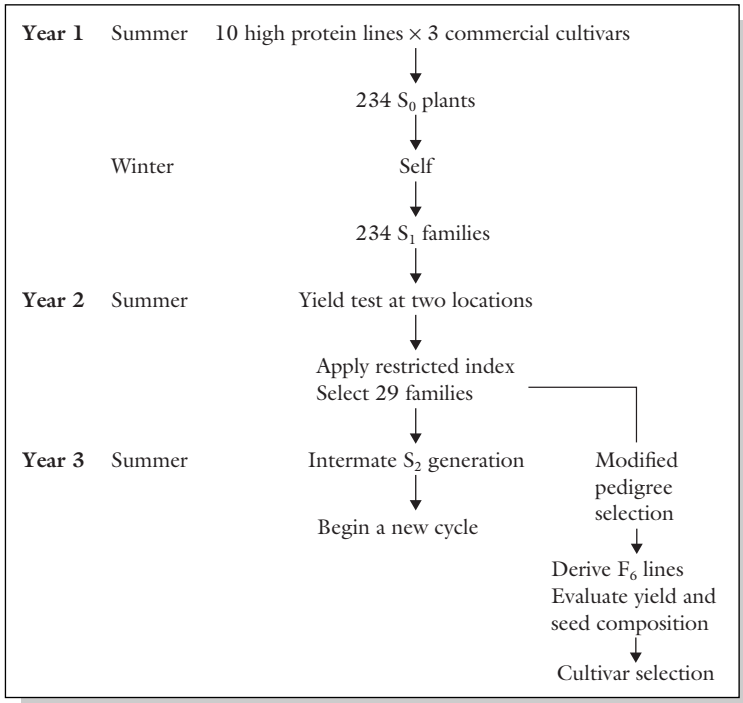

Figure 1 Recurrent S_1 family selection for yield and seed protein concentration using a restricted index.

day. This process was followed until each family had at least seven successful pollinations on seven different plants within each family. These were advanced in the winter nursery to generate the S_1 families for the next cycle of selection.

Development of "Prolina" soybean

Modified pedigree selection was applied to the S_1 families chosen in the first restricted index selection cycle. F_6 lines were tested in replicated yield tests. One of those lines, N87-984, had good yielding ability and 45% seed protein concentration. Because of heterogeneity for plant height within the line, F_9 lines were derived from N87-984 using single-seed descent. These were yield tested in multiple North Carolina locations. The two lines most desirable in terms of uniformity, protein concentration, and seed yield, were bulked for further testing and eventual release as the cultivar "Prolina" (Burton et al. 1999). At its release, "Prolina" had 45% protein compared with 42.7% for the check cultivar, "Centennial", and similar yielding ability.

Recurrent selection using male sterility

In the previous example, intermating the selections was done using hand pollinations. Hand pollination with soybean is time-consuming and difficult. The average success rate in our program during the August pollinating season has been 35%. Thus, a more efficient method for recombination would be helpful in a recurrent selection program that depends on good random mating among selected progeny for genetic recombination and reselection.

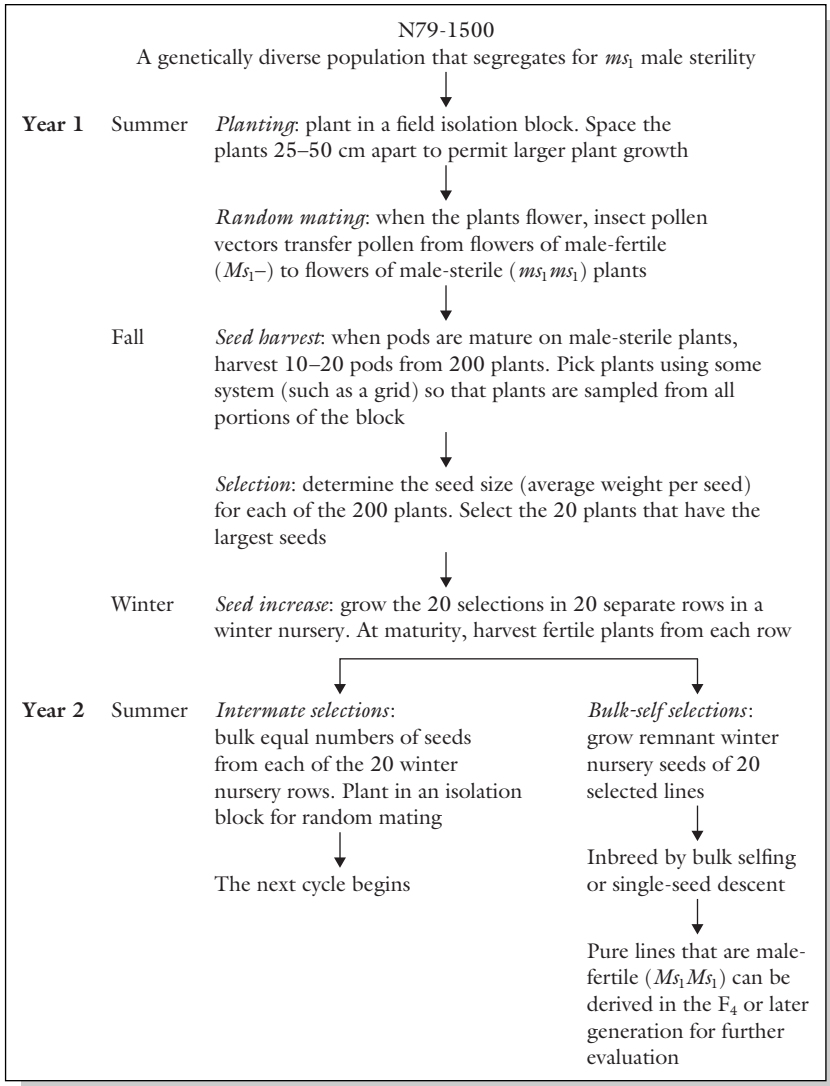

Figure 2 Recurrent mass selection for seed size in soybean using nuclear male sterility to intermate selections.

Genetic (nuclear) male sterility has been used for this purpose. Several nuclear male-sterile alleles have been identified (Palmer et al. 2004). The first male-sterile allele to be discovered (ms_1) is completely recessive (Brim & Young 1971) to the male-fertility allele (Ms_1). Brim and Stuber (1973) described ways that it could be used in recurrent selection programs. Plants that are homozygous for the ms_1 allele are completely male-sterile. All seeds produced on male-sterile plants result from pollen contributed by a male-fertile plant (Ms_1Ms_1 or Ms_1ms_1) via an insect pollen vector. The ms_1ms_1 male-sterile plants are also partially female-sterile, so that seed set on male-sterile plants is low in number, averaging about 35 seeds per plant. In addition, most pods have only one seed and that seed is larger (30–40% larger) than seeds that would develop on a fertile plant with a similar genetic background. The ms_1 allele is maintained in a line that is 50% ms_1ms_1 and 50% Ms_1ms_1. This line is planted in an isolation block. One-half of the pollen from male-fertile plants carries the Ms_1 fertile allele and one-half carries the ms_1 sterile allele. Male-sterile plants are pollinated by insect vectors, usually various bee species. At maturity, only seeds of male-sterile plants are harvested. These occur in the expected genotypic ratio of $^1/_2Ms_1ms_1 : {}^1/_2ms_1ms_1$.

One of the phenotypic consequences of ms_1 male sterility and low seed set is incomplete senescence. At maturity, soybeans normally turn yellow, leaves abscise, and the pods and seeds dry. Seed and pods on male-sterile plants mature and dry normally, but the plants remain green and leaves do not abscise. Thus, they are easily distinguished from male-fertile plants.

To use nuclear male sterility in a recurrent selection experiment, a population is developed for improvement that segregates for one of the recessive male-sterile alleles. This can be accomplished in a number of ways depending on breeding objectives. Usually, a group of parents with desirable genes are mated to male-sterile genotypes. This can be followed by one or more backcrosses. Eventually, an F_2 generation that segregates for male sterility is allowed to randomly intermate. Seeds are harvested from male-sterile plants. Then several different selection units are possible. These include the male-sterile plant itself (Tinius et al. 1991); the seeds (plants) from a single male-sterile plant (a half-sib family) (Burton & Carver 1993); and selfed seeds (plants) of an individual from a male-sterile plant (S_1 family) (Burton et al. 1990). Selection can be among and/or within the families (Carver et al. 1986). If appropriate markers are employed, half-sib selection using a tester is also possible (Feng et al. 2004). As with all recurrent selection schemes, selected individuals are intermated. These can be either remnant seed of the selection unit or progeny of the selection unit. The male-sterile alleles segregate in both because both were derived in some manner from a single male-sterile plant.

Recurrent mass selection for seed size

Because seed set on male-sterile plants is generally low in number, we hypothesized that size of the seed was not limited by source (photosynthate) inputs. Thus selecting male-sterile plants with the largest seeds would be selecting plants with the most genetic potential for producing large seeds. If so, this would mean that male-fertile plants derived from those selections would also produce larger seeds and perhaps have increased potential for overall seed yield.

To test this hypothesis, we conducted recurrent mass selection for seed size (mg/seed) in a population, N80-1500, that segregated for the ms_1 male-sterile allele and had been derived from adapted high-yielding cultivar and breeding lines (Burton & Brim 1981). The population was planted in an isolation block. Intermating between male-sterile and male-fertile plants occurred at random. In North Carolina there are numerous wild insect pollen vectors so introduction of domestic bees was not needed. If needed, bee hives can be placed in or near the isolation block. At maturity, seeds were harvested from approximately 200 male-sterile plants. To make sure that the entire population was sampled, the block was divided into sections, and equal numbers of plants were sampled from each section. Seeds from each plant were counted and weighed. The 20 plants with the largest seeds (greatest mass) were selected. These 20 selections were grown in a winter nursery and bulk-selfed to increase seed numbers. Equal numbers of seeds from the 20 selfed selections were combined and planted in another isolation block the following summer to begin another selection cycle (Figure 2).

With this method, one cycle of selection is completed each year. This is mass selection where only the female parent is selected. Additionally the female parents all have an inbreeding coefficient of 0.5 because of the selfing seed increase during the winter. Thus the expected genetic gain (Δ_G) for this selection scheme is:

$$\Delta_G = S(0.75)\sigma_A^2(\sigma_P^2)^{-1}$$

where S = selection differential, σ_A^2 = additive genetic variance, and σ_P^2 = phenotypic variance. This method was also used to increase oleic acid concentration in seed lipids (Carver et al. 1986).

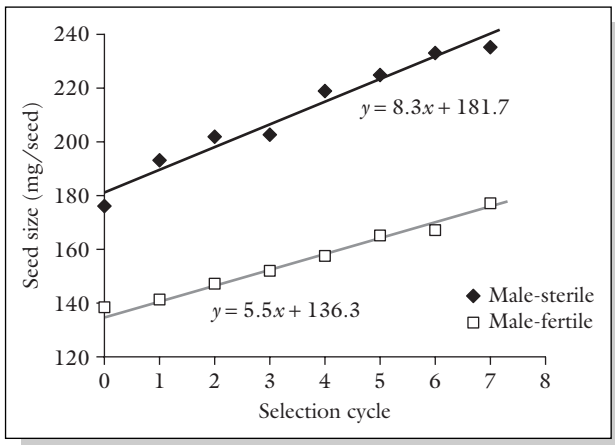

Figure 3 Seed size changes with each selection for male-sterile and male-fertile soybeans.

At the end of cycle 4 and cycle 7, selected materials from each cycle were evaluated in replicated field trials. Results of those trials showed that the method had successfully increased both seed size and yield in the population. In seven cycles of selection, seed size of the male-sterile plants increased linearly from 182 to 235 mg/seed. Male-fertile seed size also increased linearly from 138 to 177 mg/seed (Figure 3). Not only the mass, but the physical size of the seeds increased. The range in seed diameter initially was 4.8 to 7.1 mm. After four cycles of selection, the diameter range had shifted and was 5.2 to 7.5 mm (Figure 4). Yield increased at an average rate of 63.5 kg/ha each cycle (Figure 5) or about 15% overall. There was some indication that after cycle 5 changes in yield were leveling off as yields of selections from cycle 5 and cycle 7 were very similar.

This method is relatively inexpensive. Little field space is required, and only a balance is needed to determine which individual should be selected. The ability to complete one cycle each year also makes it efficient. The largest expense is probably that needed to increase the seeds from selected male-sterile plants in a winter greenhouse or nursery. The

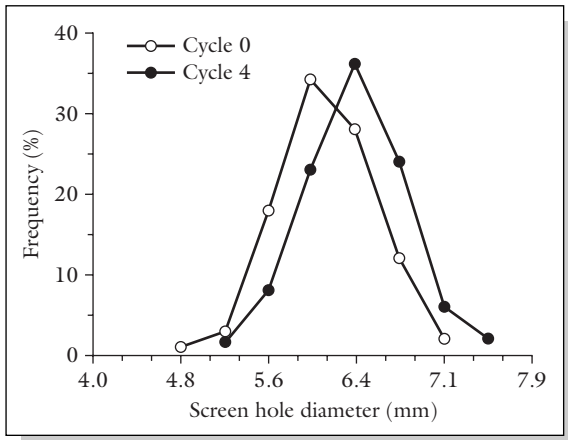

Figure 4 Distribution of seed diameters initially, and after four cycles of selection, for larger seeds.

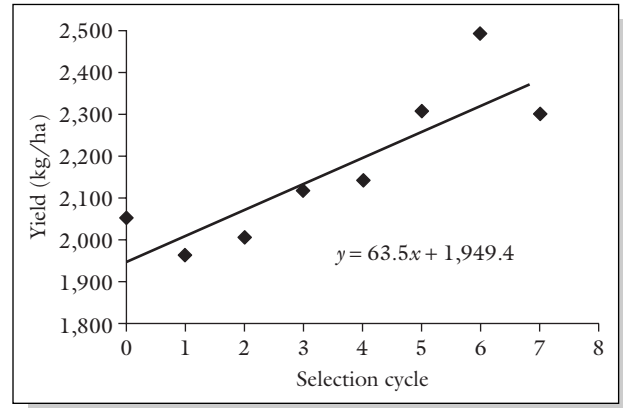

Figure 5 Correlated changes in seed yield with selection for increased seed size.

method may be quite useful for introgressing unadapted germplasm into an adapted breeding population, followed by rapid improvement of productivity. The population could be sampled in any cycle using single-seed descent. Pure lines developed from these populations would be handled exactly as those developed from single crosses in typical modified pedigree selection programs.

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must evaluate many plant characters in a breeding program. Whereas one or a few would be identified as key characters and focused on in a breeding program, breeders are concerned about the overall performance of the cultivar. During selection, breeders formulate a mental picture of the product desired from the project, and balance good qualities against moderate defects as they make final judgments in the selection process.

Explicit indices are laborious, requiring the breeder to commit to extensive record-keeping and statistical analysis. Most breeders use a combination of truncation selection and intuitive selection index in their programs.

Concept of general worth

For each crop, there are a number of characters, which considered together, define the overall desirability of the cultivar from the combined perspectives of the producer and the consumer. These characters may range between about a dozen to several dozens, depending on the crop, and constitute the primary pool of characters that the breeder may target for improvement. These characters differ in importance (economic and agronomic) as well as ease with which they can be manipulated through breeding. Plant breeders typically target one or few of these traits for direct improvement in a breeding program. That is, the breeder draws up a working list of characters to address the needs embodied in the stated objectives. Yield of the economic product is almost universally the top priority in a plant breeding program. Disease resistance is more of a local issue, since what may be economically important in one region may not be important in another area. Even though a plant breeder may focus on one or a few traits at a time, the ultimate objective is the improvement of the totality of the key traits that impact the overall desirability or general worth of the crop. In other words, breeders ultimately have a holistic approach to selection in a breeding program. The final judgments are made on a balanced view of the essential traits of the crop.

Nature of breeding characteristics and their levels of expression

Apart from relative importance, the traits the plant breeder targets vary in other ways. Some are readily evaluated by visual examination (e.g., shape, color, size), whereas others require a laboratory assay (e.g., oil content) or mechanical measurement (e.g., fiber characteristics of cotton). Special provisions (e.g., greenhouse, isolation block) may be required in disease breeding, whereas yield evaluations are most reliable when conducted over seasons and locations in the field.

In addition to choosing the target traits, the breeder will have to decide on the level of expression of each one, below which a plant material would be declared worthless. The acceptability level of expression of a trait may be narrowly defined (stringent selection) or broadly defined (loose selection). In industrial crops (e.g., cotton), the product quality may be strictly defined (e.g., a certain specific gravity, optimum length). In disease-resistance breeding, there may not be a significant advantage of selecting for extreme resistance over selecting for less than complete resistance. On the other hand, in breeding nutritional quality, there may be legal guidelines as to threshold expression for toxic substances.

Early generation testing

Early generation testing is a selection procedure in which the breeder initiates testing of genetically heterogeneous lines or families in an earlier than normal generation. In Chapter 17, recurrent selection with testers was used to evaluate materials in early generations. A major consideration of the breeder in selecting a particular breeding method is to maximize genetic gain per year. Testing early, if effective, helps to identify and select potential cultivars from superior families in the early phase of the breeding program. The early generation selection method has been favorably compared with other methods such as pedigree selection, single-seed descent, and bulk breeding. The question of how early the test is implemented often arises. Should it be in the F_1-, F_2- or F_3-derived families? Factors to consider in deciding on the generation in which selection is done include the trait being improved, and the availability of off-season nurseries to use in producing additional generations per year (in lieu of selecting early).

Concept of combining ability

Over the years, plant breeders have sought ways of facilitating plant breeding through the efficient selection of parents for a cross, effective and efficient selection within a segregating population, and prediction of response to selection, among other needs. Quantitative assessment of the role of genetics in plant breeding entails the use of statistical genetics approaches to estimate variances and to partition them into components, as previously discussed. Because variance estimates are neither robust nor accurate, the direct benefits of statistical genetics to the breeder have been limited.

In 1942, Sprague and Tatum proposed a method of evaluation of inbred lines to be used in corn hybrid production that was free of the genetic assumptions that accompany variance estimates. Called **combining**

ability, the procedure entails the evaluation of a set of crosses among selected parents to ascertain the extent to which variances among crosses are attributable to statistically additive characteristics of the parents, and what could be considered the effect of residual interactions. Crossing each line with several other lines produces an additional measure in the mean performance of each line in all crosses. This mean performance of a line, when expressed as a deviation from the mean of all crosses, gives what Sprague and Tatum called the **general combining ability** (**GCA**) of the lines.

The GCA is calculated as the average of all F_1s having this particular line as one parent, the value being expressed as a deviation from the overall mean of crosses. Each cross has an expected value (the sum of GCAs of its two parental lines). However, each cross may deviate from the expected value to a greater or lesser extent, the deviation being the **specific combining ability** (**SCA**) of the two lines in combination. The differences of GCA are due to the additive and additive × additive interactions in the base population. The differences in SCA are attributable to non-additive genetic variance. Further, the SCA is expected to increase in variance more rapidly as inbreeding in the population reaches high levels. The GCA is the average performance of a plant in a cross with different tester lines, while the SCA measures the performance of a plant in a specific combination in comparison with other cross combinations.

The mathematical representation of this relationship for each cross is:

$$X_{AB} = \bar{X} + G_A + G_B + S_{AB}$$

where $\bar{X}$ is the general mean and G_A and G_B are the general combining ability estimates of the parents, and S_{AB} is the statistically unaccounted for residual or specific combining ability. The types of interactions that can be obtained depend upon the mating scheme used to produce the crosses, the most common being the diallel mating design (full or partial diallel).

Plant breeders may use a variety of methods for estimating combining abilities, including the polycross and topcrossing methods. However, the diallel cross (each line is mated with every other line) developd by B. Griffing in 1956 is perhaps the most commonly used method. The GCA of each line is calculated as follows:

$$Gx = [Tx/(n-2)] - [\sum T/n(n-2)]$$

where x represents a specific line. Using the data in Table 8.4, G_A can be calculated as:

$$\begin{aligned} G_A &= [T_A/(n-2)] - [\sum T/n(n-2)] \\ &= [226/(10-2)] - [2{,}024/10(10-2)] \\ &= 28.25 - 25.3 \\ &= 2.95 \end{aligned}$$

The others may be calculated as for line A. The next step is to calculate the expected value of each cross. Using the cross CD as an example, the expected value is calculated as:

$$E(X_{CD}) = -4.18 + 5.33 + 22.49 = 23.64$$

The SCA is calculated as follows:

$$\begin{aligned} SCA_{CD} &= 26 - 23.64 \\ &= 2.36 \end{aligned}$$

Table 8.4 Calculating general and specific combining abilities.

	B	C	D	E	F	G	H	I	J	Total	GCA
A	26	24	29	28	22	21	27	21	28	226	2.98
B		21	35	30	26	22	29	14	19	222	2.45
C			26	21	10	14	13	17	23	169	–4.18
D				25	31	32	28	21	18	245	5.33
E					13	23	15	15	14	184	–2.3
F						20	31	17	15	185	–2.18
G							32	14	12	190	–1.55
H								35	38	248	5.7
I									17	171	–3.93
J										184	–2.3
										2,024	0

This is done for each combination and a plot of observed values versus expected values plotted. Because the values of SCA are subject to sampling error, the points on the plot do not lie on the diagonal. The distance from each point to the diagonal represents the SCA plus sampling error of the cross. Additional error would occur if the lines used in the cross are not highly inbred (error due to the sampling of genotypes from the lines).

Combining ability calculations are statistically robust, being based on first-degree statistics (totals, means). No genetic assumptions are made about individuals. The concept is applicable to both self-pollinated and cross-pollinated species, for identifying desirable cross combinations of inbred lines to include in a hybrid program or for developing synthetic cultivars. It is used to predict the performance of hybrid populations of cross-pollinated species, usually via a testcross or polycross. It should be pointed out that combining ability calculations are properly applied only in the context in which they were calculated. This is because GCA values are relative and depend upon the mean of the chosen parent materials in the crosses.

A typical ANOVA for combining ability analysis is as follows:

Source	df	Sum of squares (SS)	Mean sum of squares (MS)	EMS
GCA	$p-1$	S_G	M_G	$\sigma^2_E + \sigma^2_{SCA} + \sigma^2_{GCA}$
SCA	$p(p-1)/2$	S_S	M_S	$\sigma^2_E + \sigma^2_{SCA}$
Error	m	S_E	M_E	σ^2_E

The method used for a combining ability analysis depends on the available data:

1. Parents + F_1 or F_2 and reciprocal crosses (i.e., p^2 combinations).
2. Parents + F_1 or F_2, without reciprocals (i.e., $\frac{1}{2}p(p+1)$ combinations).
3. $F_1 + F_2$ + reciprocals, without parents and reciprocals (i.e., $\frac{1}{2}p(p-1)$ combinations).
4. Only F_1 generations, without parents and reciprocals (i.e., $\frac{1}{2}p(p-1)$ combinations).

Mating designs

Artificial crossing or mating is a common activity in plant breeding programs for generating various levels of relatedness among the progenies that are produced. Mating in breeding has two primary purposes:

1. To generate information for the breeder to understand the genetic control or behavior of the trait of interest.
2. To generate a base population to initiate a breeding program.

The breeder influences the outcome of a mating by the choice of parents, the control over the frequency with which each parent is involved in mating, and the number of offspring per mating, among other ways. A mating may be as simple as a cross between two parents, to the more complex diallel mating.

Hybrid crosses

These are reviewed here to give the student a basis for comparison with the random mating schemes to be presented.

1. Single cross $= A \times B \rightarrow F_1\,(AB)$
2. Three-way cross $= (A \times B) \rightarrow F_1 \times C \rightarrow (ABC)$
3. Backcross $= (A \times B) \rightarrow F_1 \times A \rightarrow (BC_1)$
4. Double cross $= (A \times B) \rightarrow F_{AB}; (C \times D) \rightarrow F_{CD}; F_{AB} \times F_{CD} \rightarrow (ABCD)$

These crosses are relatively easy to genetically analyze. The breeder exercises significant control over the mating structure.

Mating designs for random mating populations

The term mating design is usually applied to schemes used by breeders and geneticists to impose random mating for a specific purpose. To use these designs, certain assumptions are made by the breeder:

1. The materials in the population have diploid behavior. However, polyploids that can exhibit disomic inheritance (alloploids) can be studied.
2. The genes controlling the trait of interest are independently distributed among the parents (i.e., uncorrelated gene distribution).
3. The absence of: non-allelic interactions, reciprocal differences, multiple alleles at the loci controlling the trait, and $G \times E$ interactions.

Biparental mating (or paired crosses)

In this design, the breeder selects a large number of plants (n) at random and crosses them in pairs to produce $\frac{1}{2}n$ full-sib families. The biparental (BIP) is the simplest of the mating designs. If r plants per progeny

family are evaluated, the variation within (w) and between (b) families may be analyzed as follows:

Source	df	MS	EMS
Between families	$(\frac{1}{2}n)-1$	MS_1	$\sigma^2 w + r\sigma^2 b$
Within families	$\frac{1}{2}n(r-1)$	MS_2	$\sigma^2 w$

where $\sigma^2 b$ is the covariance of full sibs ($\sigma^2 b = \frac{1}{2}V_A + \frac{1}{4}V_D + V_{EC} = 1/r\,(MS_1 - MS_2)$ and $\sigma^2 w = \frac{1}{2}V_A + \frac{3}{4}V_D + V_{EW} = MS_2$.

The limitation of this otherwise simple to implement design is its inability to provide the needed information to estimate all the parameters required by the model. The progeny from the design comprise full sibs or unrelated individuals. There is no further relatedness among individuals in the progeny. The breeder must make unjustifiable assumptions in order to estimate the genetic and environmental variance.

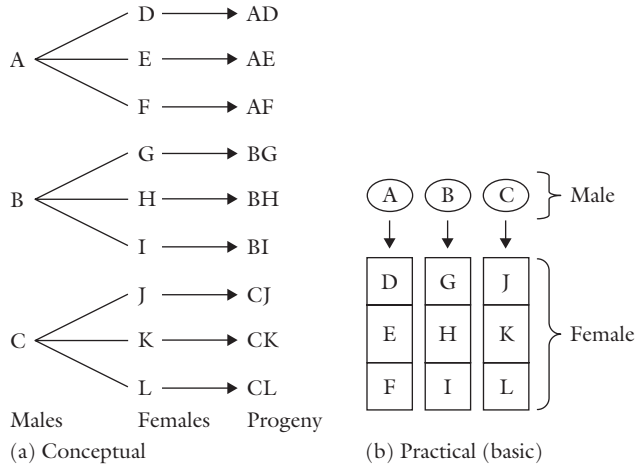

Figure 8.5 North Carolina Design I. (a) This design is a nested arrangement of genotypes for crossing in which no male is involved in more than one cross. (b) A practical layout in the field.

Polycross

This design is for intermating a group of cultivars by natural crossing in an isolated block. It is most suited to species that are obligate cross-pollinaters (e.g., forage grasses and legumes, sugarcane, sweet potato), but especially to those that can be vegetatively propagated. It provides an equal opportunity for each entry to be crossed with every other entry. It is critical that the entries be equally represented and randomly arranged in the crossing block. If 10 or less genotypes are involved, the Latin square design may used. For a large number of entries, the completely randomized block design may be used. In both cases, about 20–30 replications are included in the crossing block. The ideal requirements are hard to meet in practice because of several problems, placing the system in jeopardy of deviating from random mating. If all the entries do not flower together, mating will not be random. To avoid this, the breeder may plant late flowering entries earlier.

Pollen may not be dispersed randomly, resulting in concentrations of common pollen in the crossing block. Half sibs are generated in a polycross because progeny from each entry has a common parent. The design is used in breeding to produce synthetic cultivars, recombining selected entries of families in recurrent selection breeding programs, or for evaluating the GCA of entries.

North Carolina Design I

Design I is a very popular multipurpose design for both theoretical and practical plant breeding applications (Figure 8.5). It is commonly used to estimate additive and dominance variances as well as for the evaluation of full- and half-sib recurrent selection. It requires sufficient seed for replicated evaluation trials, and hence is not of practical application in breeding species that are not capable of producing large amounts of seed. It is applicable to both self- and cross-pollinated species that meet this criterion. As a nested design, each member of a group of parents used as males is mated to a different group of parents. NC Design I is a hierarchical design with non-common parents nested in common parents.

The total variance is partitioned as follows:

Source	df	MS	EMS
Males	$n-1$	MS_1	$\sigma^2 w + r\sigma^2_{mf} + rf\sigma^2_m$
Females	$n_1(n_2-1)$	MS_2	$\sigma^2 w + r\sigma^2_{mf}$
Within progenies	$n_1 n_2(r-1)$	MS_3	$\sigma^2 w$

$$\sigma^2_m = [MS_1 - MS_2]/rn_2 = \tfrac{1}{4}V_A$$
$$r\sigma^2_{mf} = [MS_2 - MS_3]/r = \tfrac{1}{4}V_A + \tfrac{1}{4}V_D$$
$$\sigma^2 w = MS_3 = \tfrac{1}{2}V_A + \tfrac{3}{4}V_D + E$$

This design is most widely used in animal studies. In plants, it has been extensively used in maize breeding for estimating genetic variances.

North Carolina Design II

In this design, each member of a group of parents used as males is mated to each member of another group of

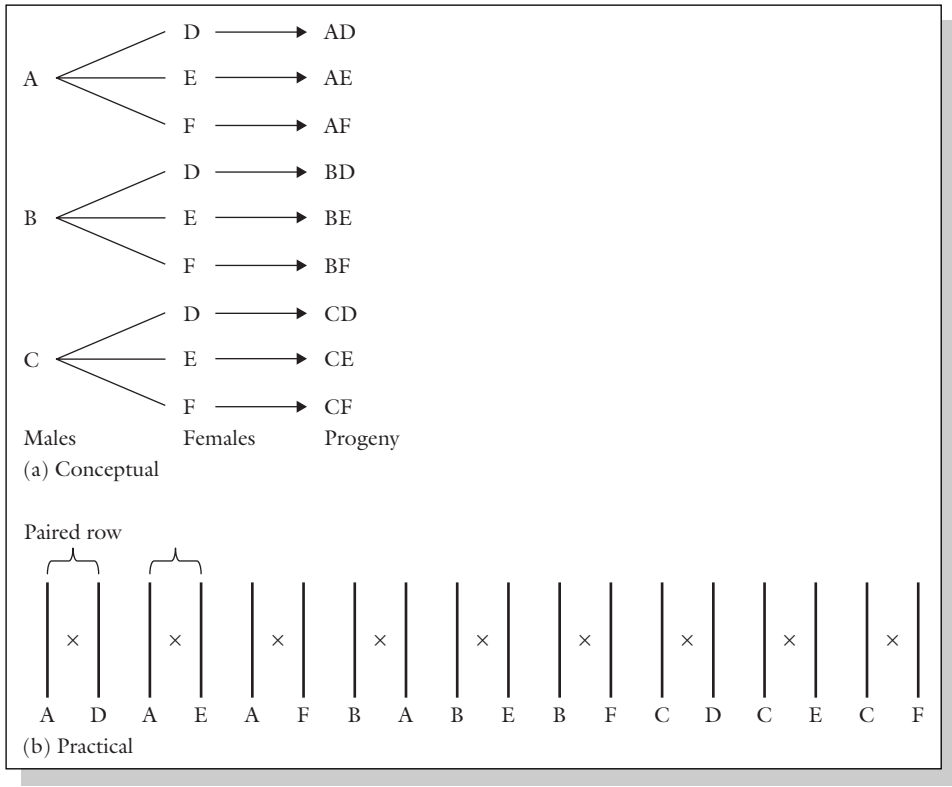

Figure 8.6 North Carolina Design II. (a) This is a factorial design. (b) Paired rows may be used in the nursery for factorial mating of plants.

parents used as females. **Design II** is a factorial mating scheme similar to Design I (Figure 8.6). It is used to evaluate inbred lines for combining ability. The design is most adapted to plants that have multiple flowers so that each plant can be used repeatedly as both male and female. Blocking is used in this design to allow all the mating involving a single group of males to a single group of females to be kept intact as a unit. The design is essentially a two-way ANOVA in which the variation may be partitioned into difference between males (m) and females (f) and their interaction. The ANOVA is as follows:

Source	df	MS	EMS
Males	$n_1 - 1$	MS_1	$\sigma^2 w + r\sigma^2_{mf} + rn\sigma^2_m$
Females	$n_2 - 1$	MS_2	$\sigma^2 w + r\sigma^2_{mf} + rn_1\sigma^2_f$
Males × females	$(n_1 - 1)(n_2 - 1)$	MS_3	$\sigma^2 w + r\sigma^2_{mf}$
Within progenies	$n_1 n_2 (r - 1)$	MS_4	$\sigma^2 w$

$$\sigma^2_m = [MS_1 - MS_3]/rn_2 = \tfrac{1}{4}V_A$$
$$r\sigma^2_f = [MS_2 - MS_3]/rn_1 = \tfrac{1}{4}V_A$$
$$r\sigma^2_{mf} = [MS_3 - MS_4]/r = \tfrac{1}{4}V_D$$
$$\sigma^2 w = MS_4 = \tfrac{1}{2}V_A + \tfrac{3}{4}V_D + E$$

The design also allows the breeder to measure not only GCA but also SCA.

North Carolina Design III

In this design, a random sample of F_2 plants is backcrossed to the two inbred lines from which the F_2 was descended. It is considered the most powerful of all the three NC designs. However, it was made more powerful by the modifications made by Kearsey and Jinks that adds a third tester (not just the two inbreds) (Figure 8.7). The modification is called the **triple testcross** and is capable of testing for non-allelic (epistatic) interactions, which the other designs cannot, and also capable of estimating additive and dominance variance.

Diallel cross

A **complete diallel mating** design is one that allows the parents to be crossed in all possible combinations, including selfs and reciprocals. This is the kind of mating scheme required to achieve Hardy–Weinberg

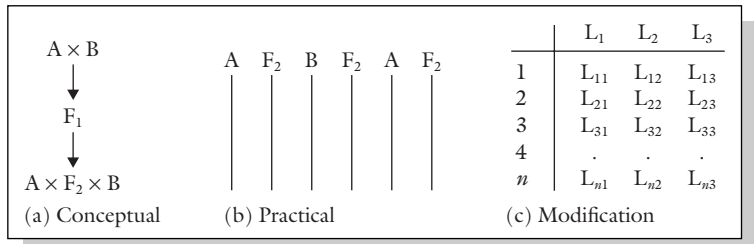

Figure 8.7 North Carolina Design III. The conventional form (a), the practical layout (b), and the modification (c) are shown.

equilibrium (see Chapter 7) in a population. However, in practice, a diallel with selfs and reciprocals is neither practical nor useful for several reasons. Selfing does not contribute to the recombination of genes between parents. Furthermore, recombination is achieved by crossing in one direction making reciprocals unnecessary. Because of the extensive mating patterns, the number of parents that can be mated this way is limited. For p entries, a complete diallel will generate p^2 crosses. Without selfs and reciprocals, the number is $p(p-1)/2$ crosses.

When the number of entries is large, a **partial diallel mating** design, which allows all parents to be mated to some but not all other parents in the set, is used. A diallel design is most commonly used to estimate combining abilities (both general and specific). It is also widely used for developing breeding populations for recurrent selection.

Nursery arrangements for the application of complete and partial diallel are varied. Because a large number of crosses are made, diallel mating takes a large amount of space, seed, labor, and time to conduct. Because all possible pairs are contained in one half of a symmetric Latin square, this design may be used to address some of the space needs.

There are four basic methods developed by Griffing that vary in either the omission of parents or the omission of reciprocals in the crosses. The number of progeny families (pf) for methods 1 through 4 are: pf = n^2, pf = $\frac{1}{2}n(n+1)$, pf = $n(n-1)$, and pf = $\frac{1}{2}n(n-1)$, respectively. The ANOVA for method 4, for example, is as follows:

Source	df	EMS
GCA	$n_1 - 1$	$\sigma^2 e + r\sigma^2_g + r(n-2)\sigma^2$
SCA	$[n(n-3)]/2$	$\sigma^2 e + r\sigma^2_g$
Reps × crosses	$(r-1)\{[n(n-1)/2]-1\}$	$\sigma^2 e$

Comparative evaluation of mating designs

Hill, Becker, and Tigerstedt roughly summarized these mating designs in two ways:

1. In terms of coverage of the population: BIPs > NC I > polycross > NC III > NC II > diallel, in that order of decreasing effectiveness.
2. In terms of amount of information: diallel > NC II > NC III > NC I > BIPs.

The diallel mating design is the most important for GCA and SCA. These researchers emphasized that it is not the mating design *per se*, but rather the breeder who breeds a new cultivar. The implication is that the proper choice and use of a mating design will provide the most valuable information for breeding.

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Outcomes assessment

Part A

Please answer the following questions true or false:

1 Quantitative traits are more influenced by the environment than qualitative traits.
2 Quantitative traits are controlled by polygenes.
3 Heritability is a population phenomenon.
4 The specific combining ability of a trait depends on additive gene action.
5 Polygenes have distinct and distinguishable effects.
6 Quantitative variation deals with discrete phenotypic variation.
7 Quantitative traits are also called metric traits.

Part B

Please answer the following questions:

1 What is quantitative genetics, and how does it differ from qualitative genetics?
2 Give two specific assumptions of quantitative genetic analysis.
3 Describe additive gene action.
4 What is the heritability of a trait?
5 What is the breeders' equation?

Part C

Please write a brief essay on each of the following topics:

1 Discuss the role of the environment in quantitative trait expression.
2 Discuss the concept of general worth of a plant.
3 Discuss the concept of intuitive selection.
4 Discuss the application of combining ability analysis in plant breeding.
5 Discuss a method of estimating heritability of a trait.