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Inheritance of Quantitative Traits



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Introduction

Introduction

Many of the traits that plant breeders strive to improve are quantitatively inherited. For example, breeding efforts targeting quantitative traits have allowed major increases in crop yield during the past 80 years or so. A quantitatively inherited trait is controlled by many genes at different loci, with each gene – known as a **polygene** – contributing a small effect to the expression of the character. Polygenes are also known **quantitative trait loci (QTL)**. QTLs involved in expression of a quantitative character act cumulatively to determine the phenotype of the trait. Their mode of inheritance is called quantitative genetics. Quantitative genetics to show how phenotypic selection of complex characters changes allele frequencies.

Quantitative genetics focuses on the nature of genetic differences, seeks to determine the relative importance of genetic vs. environmental factors, and examines how phenotypic variation relates to evolutionary change. Typically, quantitative genetic analysis is executed on traits showing a continuous range of values. Analysis of quantitative traits is based on statistical predictions of population response. Examples of quantitatively inherited traits include yield, vigor, rate of photosynthesis, protein content, and drought tolerance.

Key Concepts

Central to the mathematical modeling of quantitative genetics is the concept of recognition of family resemblance. If genes influence variation in a trait (and sources of environmental variation are minimized or controlled), related individuals would be expected to resemble one another **more than** unrelated ones. Siblings should resemble each other **more than** distantly related relatives. A comparison of plant individuals with different degrees of relatedness provides information about how much genes influence the character.

Several factors influence the likelihood of progress when breeding for quantitatively inherited traits, including:

- Interaction of the multiple genes contributing to the phenotype;
- Gene actions of the respective genes involved; and
- Frequencies of those genes.

Various models are used to distinguish genetic, environmental, and genetic x environmental interaction effects on phenotype and to improve breeding efficiency of quantitative traits.

Objectives

- Distinguish environmental and hereditary variation and be aware of why detecting the interaction of genetic and environmental factors is important.
- Understand the attributes of quantitative inheritance.
- Be familiar with statistical methods applied to quantitative inheritance.
- Study the types of gene actions and interactions affecting quantitative traits.
- Examine the genetic advance from selection formula and be able to explain how each of its components influences the improvement of the selected characteristic.
- Learn the types of heritability estimates and their importance in plant breeding.

Heritable vs. Environmental Variation

Heritable vs. Environmental Variation

The **<u>phenotype</u>** of a plant or group of plants is modeled as a function of its **<u>genotype</u>** as modified by the environment.

Phenotype = Genotype + Environment + (Genotype x Environment)

 $P = G + E + (G \times E)$

Some characters are **more responsive or sensitive to growing conditions than others**. Qualitative traits such as flower color are not strongly influenced by the environment. On the other hand, quantitative traits such as grain yield or abiotic stress tolerance are influenced markedly by the environment. The degree of sensitivity or the range of potential responses to the environment is determined by the genetic composition of the individual plant or population of plants.

Genetic variation is essential in order to make progress in cultivar improvement. However, sources of variation include:

- Environmental variation
- Genetic variation and
- Interaction of genetic and environmental variation

Plant breeders must distinguish among these sources of variation for the character of interest in order to effectively select and transmit the desired character or assemblage of characters to subsequent generations.

GxE Interaction Example

A classic example of genotype × environment interaction (GxE) involves studies conducted in the 1930s and 1940s by the ecologists Clausen, Keck, and Hiesey (1940, 1948). They collected plants from natural wild populations – principally yarrow (Achillea millefolia) and sticky cinquefoil (Potentilla glandulosa) – that grew along an east-west elevational transect in California, running from near sea level at the Pacific Ocean to more than 3000 m elevation in the Sierra Nevada mountains.





Both species exhibited a vast amount of variation in native populations with respect to growth form and other traits, including such attributes as plant height, winter survival, and number of stems produced. Through a series of reciprocal transplant experiments using cuttings or clonal material from wild populations, they tested the contribution of genetic and environmental variation to observed phenotypic variation among plants established in three main "common gardens" or transplant plots: Stanford, Mather, and Timberline (Fig. 1).

Conclusions

They concluded each species had differentiated into genetically distinct subspecies – which they called ecotypes – that are best suited to their specific environments. In the transplant gardens, no single ecotype performed best at all altitudes. For example, genotypes that produced the tallest plants at the mid altitude garden site grew poorly at the low and high sites. Conversely genotypes that grew the best at the low or high sites sometimes performed poorly at the mid altitude site. Although within a species, all populations were found to be completely interfertile, ecotypes adapted to low or mid altitude died when transplanted to the high altitude garden, while ecotypes from high elevations along the transect survived through the winter when locally grown in the test plots. GxE interaction was observed for height, among other characters.

	Stanford (30m)	Mather (1400m)	Timberline (3050m)
subspecies glandulosa	NATIVE		No winter survival
subspecies reflexa		NATIVE	No winter survival
subspecies hanseni		NATIVE	-
subspecies nevadensis	- Alexandre		NATIVE

Fig. 2 Response of plant ecotypes (Potentilla subspecies) to low, mid-, and high elevation transplant sites. Data from Clausen, Keck, and Hiesey, 1940, in Rauscher, 2005.

Significance Illustration

Figure 3 shows variation in phenotype between two cultivars of watermelon with regard to a quantitatively inherited trait (yield in this case) in response to variation in an environmental factor (soil salinity in this case) and illustrates the significance of genotype x environmental interaction.



Fig. 3 Hypothetical comparisons of genetic x environment interactions (GxE) in yield of two watermelon cultivars in response to increasing levels of soil salinity.

Characteristics of Quantitative Traits

Characteristics of Quantitative Traits

Inheritance of quantitative traits involves two or more nonallelic genes (multiple genes or polygenes); the combined action of these genes, as influenced by the environment, produces the phenotype. The effect of individual genes on the trait is not apparent. However early in the 1900s, it was discovered that the inheritance of the individual genes contributing to the phenotype of quantitative traits do indeed follow the same Mendelian inheritance principles as simply-inherited genes.



Fig. 4 The diameter of Gaillardia pulchella flowers is a quantitative trait. Photo by DanielCD; licensed under CC-SA 3.0 via Wikimedia Commons.

Inheritance of Quantitative Traits

In 1909, Herman Nilsson-Ehle, a Swedish geneticist and wheat breeder, conducted some of the classic studies on quantitatively inherited traits in wheat. He developed what is known as the "Multiple Factor" or multi-factorial theory of genetic transmission. A key observation made by Nilsson-Ehle was that although a spectrum of continuous variation in kernel color (a quantitatively inherited trait influenced by environmental factors) could be observed in segregating generations, he was able to determine that segregation for these genes fit a model that each separate contributing gene followed a pattern of **Mendelian inheritance**.





Inheritance of Quantitative Traits



Fig. 6 Wheat kernels. Photo by zandland; licensed under CC-SA 3.0 via Wikimedia Commons.

Bread wheat is a hexaploid – allopolyploid that contains three slightly different, but similar ancestral genomes (referred to as A, B, and D) in its genome (AABBDD). Depending on the cultivars that Nilsson-Ehle studied, each genome had a single gene that affected kernel color, and each of these loci has a red allele (**R**) and a white allele (**r**). Alleles at each locus varied slightly in their effect on kernel color, and will be designated in this example by different superscripts, e.g., \mathbf{R}^1 or \mathbf{r}^3 .

He crossed two cultivars of wheat that varied in kernel color, one with dark red seeds (homozygous dominant genotype $\mathbf{R^1 R^1 R^2 R^2 R^3 R^3}$, based on the symbols designating the ancestral genomes) and another with white kernels (homozygous recessive $\mathbf{r^1 r^1 r^2 r^2 r^3 r^3}$). He noted that the F₁ of a cross between these parents (heterozygote $\mathbf{R^1 r^1 R^2 r^2 R^3 r^3}$) was intermediate in color (light red), but the F₂ generation could be grouped into seven classes, ranging in color from dark red to white. He explained the distribution on the basis of three pairs of genes segregating independently, with each dominant allele contributing to the intensity of the red color.



Fig. 7

Table 1 Kernel color in F_2 progenies from a wheat cross.

F ₂ genotypes			Color	Number of dominant alleles	Number of plants out of 64
	R ¹ R ¹ R ² R ² R ³ R ³		dark red	6	1
R ¹ R ¹ R ² R ² R ³ r ³	R ¹ r ¹ R ² R ² R ³ R ³	$R^1R^1R^2r^2R^3R^3$	moderately dark red	5	6
R ¹ R ¹ R ² R ² r ³ r ³ r ¹ r ¹ R ² R ² R ³ R ³	R ¹ R ¹ r ² r ² R ³ R ³ R ¹ r ¹ R ² r ² R ³ R ³	R ¹ r ¹ R ² R ² R ³ r ³ R ¹ R ¹ R ² r ² R ³ r ³	red	4	15
R ¹ R ¹ R ² r ² r ³ r ³ R ¹ R ¹ r ² r ² R ³ r ³	R ¹ r ¹ R ² r ² R ³ r ³ R ¹ r ¹ R ² R ² r ³ r ³ R ¹ r ¹ r ² r ² R ³ R ³	r ¹ r ¹ R ² R ² R ³ r ³ r ¹ r ¹ R ² r ² R ³ R ³	light red	3	20
<mark>R¹R¹r²r²r³r³ r¹r¹R²R²r³r³</mark>	r ¹ r ¹ r ² r ² R ³ R ³ R ¹ r ¹ R ² r ² r ³ r ³	R ¹ r ¹ r ² r ² R ³ r ³ r ¹ r ¹ R ² r ² R ³ r ³	pink	2	15
R ¹ r ¹ r ² r ² r ³ r ³	r ¹ r ¹ R ² r ² r ³ r ³	r ¹ r ¹ r ² r ² R ³ r ³	light pink	1	6
	r ¹ r ¹ r ² r ² r ³ r ³		white	0	1

With three independent pairs of genes segregating, each with two alleles, as well as environmental effects acting on kernel color, the F_2 progeny would contain 63 plants with varying shades of red kernels and one with white kernels. Linkage among the genes restricts independent assortment, so that the required size of the F_2 population becomes larger.



Fig. 8 Range of wheat kernel color in an F_2 generation. (a) Kernel color depicted by seven discrete classes modeled on segregation of three contributing genes, each exhibiting partial dominance. (b) Kernel color depicted by continuous variation in all seven color classes.

Characteristics Indicative of Quantitative Inheritance (1)

Phenotypic values for the specific trait, resulting from simultaneous segregation of multiple genes, exhibit continuous variation, rather than distinct classes. In general, the distribution of values of quantitatively inherited traits in a population follows a **normal distribution** (also called a Gaussian distribution or bell curve). These curves are generally characterized by two parameters, the **mean** and the **variance** or **standard deviation**. In the figure below, the mean of the random sample is depicted by the symbol \overline{x} and the standard deviation by the symbol **s**. If the reference is made to a population instead of a sample from a population, the population mean is usually symbolized by **µ** and the population standard deviation by **σ**.



Fig. 9 Based on random sample from a genetically mixed population, the distribution of a quantitative trait's expression approximates a normal or bell curve.

Characteristics Indicative of Quantitative Inheritance (2)

There are three general types of traits that are quantitatively inherited: continuous, meristic, and threshold. An example of the first type, a continuous trait, is fruit width of pineapple. The second type, a meristic character, is a countable trait that can take on integer values only, e.g., number of tillers of maize or branches of a rose bush. The third type of quantitative trait is known as a <u>threshold character</u> or "all-or-none" trait. Such traits are typically ranked simply as presence or absence, e.g., Downy Mildew disease in soybean.

Environment has a large influence on the trait's phenotype. That is, for the particular trait, the relative responses of plants change when grown under different environmental conditions.

Distinct segregation ratios of individual nonallelic genes are not observed. Recombination and segregation patterns are based on the **combined** effect of the polygenes on the trait. The more loci controlling the character, the greater the complexity.

Characteristics Indicative of Quantitative Inheritance (3)

Genes may differ in their individual gene action, but their effect on the trait is cumulative. Types of gene action include additive, dominance, overdominance and epistasis. Effects of gene action using the concepts of <u>genotypic and breeding values</u> are discussed in Appendix A.

Table 2 Summary of interactions among alleles (within or between loci) defining different types of gene action.

	Interaction among alleles		
	No interaction	Interaction	
Within a locus	Additive	Dominance	
Between loci	Additive	Epistasis	

Transgressive segregation may occur. These individuals exhibit phenotypes outside the range of those expressed by the parents. Transgressive segregation occurs when progeny contain new combinations of multiple genes with more positive effects or more negative effects for the quantitative trait than found in either parent. One challenge is that strong environmental effects would make it difficult to assess the mean performance in parental plants vs. progeny in order to detect for the presence of any transgressive segregants.

Measurement of Continuous Variation

Measurement of Continuous Variation

Analysis of inheritance of qualitative traits is generally concerned with individual matings and their progeny and is made by counts and ratios. In contrast, analysis of quantitative traits is concerned with populations of organisms that consist of many possible kinds of matings; analysis of such traits is made by use of statistics. Statistical methods provide a tool for describing and evaluating quantitatively inherited characters. Since it is impractical to examine an entire population, plant breeders sample the population(s) of interest. The sample must be representative of the population — the sample must be:

- large enough to include the entire range of variability of the trait that occurs in the population, and
- random to avoid introducing any bias.

Thus, the greater the variability within the population, the larger the sample size that is required to accurately describe that population. (Throughout this and subsequent modules, you can generally assume that we're referring to a representative sample, rather than a population.)

Statistics may be descriptive or analytical. [See Appendix B to briefly review some statistical terms and <u>concepts</u>].

QTLs and Mapping

The relative importance of genetic and environmental factors for a given trait can be estimated by the phenotypic resemblance between relatives. Until recently, quantitative genetics focused on phenotypic information, but increasingly molecular biology tools are being applied in an effort to locate where **quantitative trait loci (QTLs)** occur in plant and animal genomes. Various genetic markers have been identified and mapped, allowing **identification of QTLs by linkage analysis**.

A common method for mapping QTLs is to cross two homozygous lines that have different alleles at many loci. The F₁ progeny are then backcrossed and intercrossed to allow genes to recombine through independent assortment and crossing over. Offspring in segregating generations are examined for correlations between inheritance of marker alleles and phenotypes that are quantitatively inherited. QTL mapping will be covered in more detail in later courses on **Molecular Genetics and Biotechnology** and **Molecular Plant Breeding**.

Multiple Genes and Gene Action

Multiple Genes and Gene Action (1)

The general types of gene action for quantitative characters (additive, full and partial dominance, and overdominance) do not differ from those for qualitative traits. However, the genes contributing to the phenotype of a quantitative character may or may not differ in their individual gene action, and their relative effects on the trait's expression may differ. Some may have major influence and others may have only minor effects on the phenotype. The genes controlling a quantitative trait may also interact. The table below gives examples of types of gene action at two loci. For quantitative traits this would be expanded to multiple loci.

Table 3

Gene Action or Interaction	Explanation	Example		
Additive Effects	Genes affecting a genetic trait in a manner that each enhances the expression of the trait.	aabb = 0	Aabb = 1	aaBb = 1
		AAbb = 2	AaBb = 2	aaBB = 2
		AABb = 3	AaBB = 3	AABB = 4
Dominance Effects	Deviations from additivity so the heterozygote is more like one parent than the other. With complete dominance, the heterozygote and the homozygote have equal effects	aabb = 0	Aabb = 2	aaBb = 2
		AAbb = 2	AaBb = 4	aaBB = 2
		AABb = 4	AaBB = 4	AABB = 4
Interaction of Epistasis Effects	Two nonallelic genes (e.g., genes at different loci) may have no effect	aabb = 0	Aabb = 0	aaBb = 0
	individually, yet have an effect when combined	AAbb = 0	AaBb = 4	aaBB = 0
		AABb = 4	AaBB = 4	AABB = 4

Gene Action or Interaction	Explanation	Example		
Overdominance Effects	erdominance Each allele contributes a separate effect and the combined alleles contribute an effect greater than that of either allele separately	aabb = 0	Aabb = 2	aaBb = 2
		AAbb = 1	AaBb = 4	aaBB = 1
		AABb = 3	AaBB = 3	AABB = 2

Multiple Genes and Gene Action (2)

In the preceding examples, A and B are assumed to have equal effects. However, this often may not be true because genes at different loci may affect the expression of the trait in different ways. Some QTLs may be genes with major effect, while others may contribute only a minor effect. Penetrance or expressivity (refer to Deviations from Expected Phenotypes in the "Gene Segregation and Genetic Recombination" module) may influence trait expression. Likewise, pleiotropic effects (refer to Gene Interactions in the "Gene Segregation and Genetic Recombination" module) may be present, affecting different traits in different ways.



Fig. 10 Albinism, such as that exhibited by this deer, is one common effect of pleiotropic mutation. Photo by Paulo Brandao; licensed under CC-SA 2.0 via Wikimedia Commons.

Heritability

Conceptual Basis

Conceptual Basis for Understanding Heritability

Heritability estimates the relative contribution of genetic factors to the phenotypic variability observed in a population. What causes variance among plants and among lines or varieties? Phenotypic variation observed among plants or varieties is due to differences in

- their genetic makeup,
- environmental influences on each plant or genotype, and
- interaction of the genotype and environment.

The effectiveness with which selection can be expected to take advantage of variability depends on how much of that variability results from genetic differences. Why? Only genetic effects can be transmitted to progeny. Heritability estimates

- the degree of similarity between parent and progeny for a particular trait, and
- the effectiveness with which selection can be expected to take advantage of genetic variability.

Family Resemblance

As mentioned in the introduction of this lesson, central to the understanding of quantitatively inherited traits is the recognition of family resemblance. Two relatives, such as a parent and its offspring, two full or half-siblings, or identical twins, would be expected to be phenotypically more similar to each other than either is to a random individual from a population. Although close relatives may share not only genes (they may also share similar environments for traits that have a large genetic component), resemblance between relatives is expected to increase as closer pairs of relatives are examined because they share more and more genes in common. In this conceptual framework, heritability can be understood as a measure of the extent to which genetic differences in individuals contribute to differences in observed traits.



Fig. 11 Individuals that are related genetically would be expected to be more phenotypically similar to each other than to other individuals from a population.

Statistical Basis Statistical Basis for Understanding Heritability

For plant breeders, heritability can also be understood in a statistical framework by defining it as the proportion of the phenotypic variance that is explained by genetic variance. Heritability indicates the proportion of the total phenotypic variance attributable to genetic effects, the portion of the variance that is transmittable to offspring. A general formula for calculating heritability is

$$Heritability = \frac{V_G}{V_P} = \frac{V_G}{V_G + V_E + V_{GE}}$$
$$= \frac{\sigma_g^2}{\sigma_{ph}^2} = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_c^2 + \sigma_{ge}^2}$$

where:

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

$$\sigma_{ph}^2 = \sigma_g^2 + \sigma_e^2 + \sigma_{ge}^2$$

and

 $V_P = \sigma_{ph}^2$ = phenotypic variance (total variance of the population) $V_G = \sigma_g^2$ = genotypic variance (variance due to genetic factors) $V_E = \sigma_e^2$ = environmental variance (variance due to environmental factors) $V_{GE} = \sigma_{ge=}^2$ genotype x environmental variance (variance due to interactions between genotypes and environmental factors)

Uses of Heritability Estimates

Heritability serves as a guide for making breeding decisions. It is generally used to

- determine the relative importance of genetic effects which could be transferred from parent to offspring
- determine which selection method would be most likely to improve the character
- predict genetic advance from selection

A key point to understand is that heritability is a **population** concept – application of heritability estimates is restricted to the <u>population on which the estimate was based</u> and to the <u>environment in which the population</u> <u>was grown</u>. However, some characters exhibit fairly consistent estimates (either high or low) among populations (within species) and environments. When considering characters that have high heritability, what we expect to observe for each genotype is that its phenotype will be quite predictable over a range of environments (growing conditions). In other words, for characters with high heritability, genotype fairly accurately predicts phenotype. This is not so for characters with low heritability.

Characters

Heritability depends on the range of typical environments experienced by the population under study (if the environment is fairly uniform, then heritability can be high, but if the range of environmental differences is high, then heritability may be low. Even when heritability is high, environmental factors may influence a characteristic. Heritability does not indicate anything about the degree to which genes determine a trait; instead it indicates the degree to which genes determine variation in a trait.

Characters having low heritabilities are usually highly sensitive to the environment, presenting greater breeding challenges – low heritability traits often require larger populations and more test environments than do characters having high heritabilities for selection and improvement.

Table 4 Average heritability estimates (h²) of maize characters. Data from Hallauer and Miranda, 1988, p. 118. Average estimates are derived from estimates reported in the literature. The magnitude of these estimates reflects both the complexity of the trait and the number of estimates reported in the literature.

Heritability Estimate	Maize Characters
h ² < .70	Percent OilNumber of tillers
.50 < h ² < .70	 Plant height Ear height Kernel-row number Dates to flowering Grain moisture
.30 < h ² < .50	 Number of ears Ear length Ear diameter Kernel weight Cob diameter
h ² < .30	YieldKernel depth

Broad-Sense Heritability

Types of Heritability

There are two types of heritability: broad-sense and narrow-sense heritability.

Broad-Sense Heritability

Broad sense heritability, H², estimates heritability on the basis of all genetic effects.

$$H^2 = \frac{V_G}{V_P} \times 100$$

$$= \frac{\sigma^2 g}{\sigma_{ph}^2} \times 100$$

It expresses total genetic variance as a percentage, and does not separate the components of genetic variance such as additive, dominance, and epistatic effects.

Table 5

Genetic variance	=	Additive variance	+	Dominance variance	+	Epistatic variance
V _G	=	V _A	+	V _D	+	VI
σ_e^2	=	σ_A^2	+	σ_D^2	+	σ_I^2

Generally, broad-sense heritability is a relatively poor predictor of potential genetic gain or breeding progress. Its usefulness depends on the particular population. Broad-sense heritability is

- more commonly used with asexually propagated crops than with sexually propagated agronomic crops
- applied to early generations of self-pollinated crops

Narrow-Sense Heritability

Narrow-sense heritability, h^2 , in contrast, expresses the percentage of genetic variance that is caused by additive gene action, V_A .

$$h^2 = \frac{V_A}{V_P} \times 100$$

$$=\frac{\sigma_A^2}{\sigma_{ph}^2} \times 100$$

Narrow-sense heritability is always less than or equal to broad-sense heritability because narrow-sense heritability includes only additive effects, whereas broad-sense heritability is based on all genetic effects.

The usefulness of broad- vs. narrow-sense heritability depends on the generation and reproductive system of the particular population. In general, narrow-sense heritability is more useful than broad-sense heritability since only additive gene action can normally be transmitted to progeny. This is, because in systems with sexual reproduction, only gametes (alleles) but not genotypes are transmitted to offspring. In contrast, in case of asexual reproduction, genotypes are transmitted to offspring.

Table 6 Comparison of broad- and narrow-sense heritability.

	Broad-sense heritability	Narrow-sense heritability
Symbols used	H ² , H, h _b ² , or h _B ²	h^2 , h_n^2 , or h_N^2
Predictor of Gain	Poor	Better
Genetic Variance	Additive, dominance, and epistatic	Additive only
Generation	Early	Later
Reproductive System	Self-pollinated or cloned population	Cross-pollinated

Estimating Heritability

As the formulas presented above indicate, heritability is calculated from estimates of the components of

phenotypic variation: genetic, environmental, and genetic x environmental interactions. Two main approaches are described here to help estimate the contribution of different G, E, and GxE components and for calculating heritability. One approach focuses on eliminating one or more variance component, while the other focuses on comparing the resemblance of parents and offspring. These estimates can be determined from an analysis of variance or regression analysis of the character performance of a population grown in <u>several</u> <u>environments</u> (multiple locations and/or years).

Estimation Using Analysis of Variance (ANOVA)

Estimating heritability from an **analysis of variance** provides a way to measure the relative contributions of two or more sources of variability.

Estimation using Parent-Offspring Regression

Heritability can also be estimated by evaluating the similarities between progeny and parent performance using **regression analysis**. This analysis is based on several assumptions.

- The particular character has diploid, Mendelian inheritance.
- There is no linkage among loci controlling the character of interest, or the population is in <u>linkage</u> <u>equilibrium</u>.
- The population is random mated.
- Parents are not inbred.
- There is no environmental correlation between the performance of parents and progeny (to avoid violating this last assumption, randomize parents and progeny within replications; i.e., do not test them in the same plot).

The linear regression model is:

 $Y_i = a + bX_i + e_i$

where:

 Y_i = phenotypic value of progeny of the ith parent

a = mean phenotypic value of all parents tested

b = regression coefficient (slope of the line)

 x_i = phenotypic value of the ith parent

ei = experimental error in the measurement of Xi

Alternative Formula

An alternative formula for calculating the regression coefficient, b, is

$$b = \frac{\sum (X - \bar{X})(Y - \bar{Y})}{\sum (X - \bar{X})^2)}$$

where: b = regression coefficient X = parent values Y = progeny values

The performance of the progeny is a function of the genetic factors inherited from the parents. (Assume that "parent" means either a random plant or line from a population.) Thus, X, the parent value, is the independent variable, and Y, the progeny value, is the response or dependent variable.

Regression Coefficient

What does the regression coefficient, b, tell us?

If b = 1, then

- gene action is completely additive,
- negligible environmental effect,
- and negligible experimental error.

The smaller the value of b, the less closely the progeny resemble their parent(s), indicating

- greater environmental influence on the character,
- greater dominance and/or epistatic effects, and/or
- greater experimental error.

An analysis of variance will provide estimates of the relative influence of genetics, environment, and experimental error.

The type of heritability and the specific formula used to estimate it depends on the type of progeny evaluated.

Types of Progeny

The population's reproductive mode and mating design determine the type of heritability and the formula used to calculate the estimate.

Selfed progeny

- 1. F_2 plants are self-pollinated to obtain the F_3 . All the alleles in the F_3 come from the F_2 parent. Evaluate the character performance of the F_3
- 2. Regress the performance of the F_3 on the performance of their F_2 parents.
- 3. The regression coefficient, b, is equal to H², broad-sense heritability because its genetic variance includes dominance, additive, and epistatic effects.

 $H^2 = b \times 100$

4. Since it is difficult to obtain information about gene action (dominance, epistasis, additive) in selfpollinated populations, narrow-sense heritability is a poor predictor of genetic gain and rarely used in these populations. Inbreeding causes an upward bias in the heritability estimate.

Full-sib progeny

- 1. Two random F₂ plants are mated. Half of the alleles in the F3 come from one parent and half from the other. Evaluate the character performance of the F3.
- 2. Determine the **mid-parent value** of the two parents. Mid-parent value, $X = (x_1 + x_2)/2$
- 3. Regress the progeny on the mid-parent value. The regression of progeny on the mid-parent value is

$$\frac{\frac{1}{2}V_{A}}{\frac{1}{2}V_{P}} = \frac{\frac{1}{2}\sigma_{A}^{2}}{\frac{1}{2}\sigma_{ph}} = \frac{\sigma_{A}^{2}}{\sigma_{ph}^{2}}$$

Since the progeny have both parents in common, only additive variance is included, so the regression coefficient, b, is equal to narrow-sense heritability

 $h^2 = b \times 100$

Half-sib progeny

 Open-pollinate F₂ plants. Seed will be harvested from each F₂ individual separately. Progenies from the same F₂ plant have the maternal parent (the respective F₂ plant) in common, while the paternal parent is pollen from the whole F₂ population. Thus all offspring from an F₂ plant after open pollination are "halfsibs". 2. Regress the performance of the half-sib progenies on their parents.

$$b = \frac{\sigma^{xy}}{\sigma_x^2}$$

where:

 σ^{xy} = covariance between parents, x, and their progeny, y

 σ_x^2 = phenotypic variation among parents

- 3. The covariance between parents and progeny includes additive variance and some forms of additive epistasis (usually negligible), but no dominance variance. Thus, narrow-sense heritability can be estimated. The regression coefficient, b, is equal to half the heritability value.
- 4. Multiply the regression coefficient by 2 to obtain narrow-sense heritability.

$$h^2 = 2b \times 100$$



Fig. 12 Half-sib progeny.

Heritability Influences

Heritability is not an intrinsic property of a trait or a population. As we've seen, it is influenced by:

- population generation, reproductive system, and mating design
- environment locations and/or years
- experimental design experimental unit (plant, plot, etc.), replication, cultural practices, techniques for data gathering.

Heritability can be manipulated by increasing the number of replicates and number of environments sampled (in space and/or time). Genetic variance can be increased by using diverse parents and by increasing the selection intensity. Heritability is only an indicator to guide the breeder in making selections and is not a substitute for other considerations, such as breeding objectives and resource availability.

Genetic Advance from Selection

Evolution

Estimating Response to Selection

Evolution can be defined as genetic change in one or more inherited trait that takes place over time within a population or group of organisms. Plant breeders can use quantitative genetics to predict the rate and magnitude of genetic change. The amount and type of genetic variation affects how fast evolution can occur if selection is imposed on a phenotype.

The amount that a phenotype changes in one generation is called the selection response, **R**. The selection response is dependent on two factors—the narrow-sense heritability and the selection differential, **S**. The selection differential is a measure of the average superiority of individuals selected to be parents of the next generation.

 $R=h^2S$

The above equation is often called the "breeder's equation". It shows the key point that **response to selection** increases when either the **heritability** of the trait or the **strength of the selection** increases.

Realized Heritability

In an experiment, the observed response to selection allows the calculation of an estimate of the narrow-sense heritability, often called the realized heritability. A low h^2 (<0.01) occurs when offspring of the selected parents differ very little from the original population, even though there may be a large difference between the population as a whole and the selected parents. Conversely, a high h^2 (> 0.6) occurs when progeny of the selected parents differ from the original population almost as much as the selected parents.

In the figure in the next screen, it can be seen that the selection differential (S) in each generation is the difference between the mean of the entire original population and the mean of group of individuals selected to form the next generation. In contrast, the response to selection (R) indicates the differences in population means across generations. The value of R is the difference between the mean of the offspring from the selected parents and the mean of the entire original population:

$$S = \overline{T}_S - \overline{T}$$
$$R = \overline{T}_O - \overline{T}$$

where:

T = mean of the entire original population T_S = mean of selected parents T_0 = mean of the offspring of the selected parents

Adaptive Value

The proportionate contribution of offspring of an individual to the next generation is referred to as fitness of the individual. Fitness is also sometimes called the adaptive value or selective value. Note in the figure that the non-selected members of the population do not contribute to the next generation and that selection over time reduced the variance of the population.



Fig. 13 How population means shift as a result of selection.

Types of Selection

Artificial selection refers to selective breeding of plants and animals by humans to produce populations with more desirable traits. Artificial selection is typically directional selection because it is applied to individuals at one extreme of the range of variation for the phenotype selected. This type of selection process is also called truncation selection because there is a threshold phenotypic value above which the individuals contribute and below which they do not. In contrast, under natural selection in non-managed populations, other types of selection may occur.

Three main types of selection are generally recognized. All three operate under natural selection in natural populations, whereas under artificial selection via selective breeding by humans only directional selection is common.

Directional selection acts on one extreme of the range of variation for a particular characteristic.



Stabilizing selection works against the extremes in the distribution of the phenotype in the population. An example of this type of selection is human birth weight. Infants of intermediate weight have much higher survival rate than infants who are either too large or too small.





Disruptive selection favors the extremes and disfavors the middle of the range of the phenotype in the population.



Fig. 16 Disruptive selection.

Genetic Advance from Selection

One of the most famous longest-term selection experiments is a study conducted by University of Illinois geneticists who have been selecting maize continuously for over 100 generations since 1896. They have been changing oil and protein content in separate experiments, selecting for either high or low content. In some cases after multiple generations, they have shifted selection from high to low or vice versa.



Fig. 17 Responses to 100 generations for high and low oil concentration in maize kernels. Data from Department of Crop Science, University of Illinois at Urbana-Champaign, 2007.

Expected Gain From Selection

Because resources are limited, the breeder's objective is to carry forward as few plants or lines as possible without omitting desirable ones. How does the breeder decide how many and which plants or lines within a population to carry forward to the next generation? The breeder can use heritability estimates to predict the probability that selecting a given percentage of the population or selection intensity, i, will result in progress. The expected progress or gain can be calculated using this formula:

$$G_C = (k)(\sqrt{V_P})(h^2) = k\sigma_{ph}h^2$$

where:

 G_c = expected gain or predicted genetic advance from selection per cycle k = selection intensity – a constant based on the percent selected and obtained from statistical tables (note that some people use hte i symbol instead of k for selection intensity $\sqrt{V_p}$ or σ_{ph} = square root of phenotypic variance (equivalent to standard deviation) h^2 = narrow - sense heritability in decimal form (narrow - sense is used for sexually reproduced populations whenever possible, and broad sense heritability, H², is used for self - pollinating and asexually reproduce populations)

Caution: The phenotypic values must exhibit a normal, or bell-curve, distribution for Gc to be valid

Reflection

The Module Reflection appears as the last "task" in each module. The purpose of the Reflection is to enhance your learning and information retention. The questions are designed to help you reflect on the module and obtain instructor feedback on your learning. Submit your answers to the following questions to your instructor.

- 1. In your own words, write a short summary (< 150 words) for this module.
- 2. What is the most valuable concept that you learned from the module? Why is this concept valuable to you?
- 3. What concepts in the module are still unclear/the least clear to you?

References

- Barbour, M.G, J.H. Burk, F.S. Gilliam, W.D. Pitts and M.W. Schwartz. 1999. Terrestrial Plant Ecology. 3rd edition. Benjamin Cummings, San Francisco, CA.
- Clausen, J., D.D. Keck, and W. Hiesey. 1940. Experimental studies on the nature of species. I. Effects of varied environments on western North American plants. Carnegie Inst. Wash. Publ. 520.
- Clausen, J., D. D. Keck, and W. M. Hiesey. 1948. Experimental studies on the nature of species. III. environmental responses of climactic races of Achillea. Carnegie Inst. Wash. Publi. 581.
- Conner, J.K. and D.L. Hartl. 2004. A Primer of Ecological Genetics. Sinauer Associates, Sunderland, MA.
- Falconer, D.S., and T.F.C. Mackay. 1996. Introduction to Quantitative Genetics. 4th edition. Longman Publ. Group, San Francisco, CA.
- Hallauer, A. R. and J. B. Miranda. 1988. Quantitative Genetics in Maize Breeding. 2nd Edition. Iowa State University Press, Ames, IA.
- Hill, W.G. 2005. A century of corn selection. Science 307: 683-684.
- Pierce, B. A. 2008. Genetics: A Conceptual Approach. 3rd edition. W.H. Freeman, New York.
- Rausher, M.D.. 2005. Example of Clausen, Keck, and Hiesey Experiment, Lecture 1-Lineages, Populations, and Genetic Variation. Online lecture notes from course on Principles of Evolution.
- Department of Crop Science, University of Illinois at Urbana-Champaign. Values obtained for protein in the strains selected for oil and the values for oil obtained for the strains selected for protein each generation (1896-2004). 2007.

For Your Information

Genotypic Value

The genotypic value is equal to

G=A+D+I

G = genotypic value of all loci considered together

A = sum of all additive effects (i.e. breeding values) for seperate loci

D = sum of all dominance deviations (i.e., interaction between alleles at a locus or so-called intralocus interactions)

I = interaction of alleles among loci (also referred to as the deviation or epistatic deviation)

For an individual, the breeding value is calculated by the summation of the average effects of its genes (also referred to as the additive effect of genes). The average effect of an allele is approximately the average deviation of the mean phenotypic value from the population mean if the allele at a particular locus is substituted by another allele (Falconer and Mackay 1996).

Performance

As will be explained in the next section, a key statistic used to describe populations is the <u>mean performance</u> of the population of genotypes. The mean performance of a population can be described by a combination of values for performance of both homozygous and heterozygous genotypes, as well as the relative frequency of alleles.

For illustration using a locus with two alleles, A_1 and A_2 , the genotypic value of the homozygotes is designated as A_1A_1 =+a and A_2A_2 = -a, while the heterozygous genotype is A_1A_2 = d.

The value of a is the performance of a homozygous genotype minus the average performance of the two homozygous genotypes.

$$+a = A_1A_1 - \frac{(A_1A_1 + A_2A_2)}{2} \quad -a = A_2A_2 - \frac{(A_1A_1 = A_2A_2)}{2}$$

The value of d measures the degree of dominance between alleles, and is the difference between the value of the heterozygote and the mean of the homozygotes.

$$d = A_1 A_2 - \frac{(A_1 A_1 + A_2 A_2)}{2}$$

Degrees of Dominance

Examples of relative genotypic values are given here in depictions showing a and d under different types of gene action.

Gene Action	Degree of Dominance	Relative Genotypic Values
Additive	0	$\begin{array}{c cccc} A_2A_2 & A_1A_2 & A_1A_1 \\ \hline -a & 0 & +a \\ \hline d \end{array}$
Complete dominance	1	$\begin{array}{c} A_1A_1\\ A_2A_2\\ \hline -a & 0 \\ d \end{array}$
Partial dominance	3/4	$\begin{array}{ccc} A_2A_2 & A_1A_2A_1A_1 \\ -a & 0 & d + a \end{array}$
Partial dominance	1/2	$\begin{array}{c c} A_2A_2 & A_1A_2 & A_1A_1 \\ \hline -a & 0 & d & +a \end{array}$
Overdominance	2	$\begin{array}{c c} A_2A_2 & A_1A_1 & A_1A_2 \\ \hline -a & 0 & +a & d \end{array}$

Gene action depicted using a and d in relation to genotypic values. Adapted from Conner and Harti, 2004.

The difference between the depictions of partial dominance show an example of how the effect of an allele can vary depending on whether the locus is a major gene or minor. Remember, additivity of genetic effects for

quantitative traits does not mean that there are equal effects of all alleles at a locus or all loci affecting the trait.

The study of quantitative traits is sometimes referred to as "statistical genetics" because of its reliance on statistical methods. In order to understand the inheritance of quantitative characters and the methods applied to these characters, it is essential that you become familiar with fundamental statistics. A basic review is provided here.

When using symbols to represent these population parameters, it is important to distinguish between information about the population and that concerning a sample representing the population.

Similar Statistical Symbols

As a shorthand, statistics commonly use symbols to convey concepts. Often there are several symbols that relate to very similar, but slightly differing concepts. Here's a list of symbols related to means, variance, and standard deviation that you will encounter in this lesson. The latter two parameters describe the variability or dispersion about the mean of the population or sample derived from a population.

Although the differences between these are important from a statistical perspective, they are commonly used synonymously.

Parameter	For a population	For a fixed or selected sample of a population
Mean	μ or M	\bar{X}
Variance	V or δ^2	s ²
Standard deviation	δ	S

Several Environments

Testing a character's performance in multiple environments (e.g., more than one location and/or years) is essential to get an accurate estimate of the environmental effects on the character. Test environments should be either random or representative of the target environment—the type of environment for which the cultivar under development is intended. Heritability is based on variance, the average of the squared deviations about the mean—a statistical measure of how values vary from the mean. Testing in a single environment provides no measure of variance. The greater the number of environments used in the character's evaluation, the better is the reliability of the variance estimate, as well as the heritability estimate. Without adequate testing in multiple environments, heritability estimates may be misleading.

When evaluating different genotypes for a specific character, if the genotypes vary widely in response to differing environments, environmental variance will be relatively high and heritability for the character low. Conversely, if the different genotypes perform in a similar manner across environments, e.g., certain genotypes are always among the best and others always the poorest regardless of environment, environmental variance will be low and heritability high.

Analytical Tools

Several analytical procedures are commonly used to sort out the sources of variation in the sample, to determine the relationship among factors contributing to the variability, and to estimate the heritability of the character.

Analysis of Variance – this procedure identifies the relative contribution of the sources of observed variation in the sample. Sources of variation may include environment, replication, or genotypic effects. The portion of variation that cannot be attributed to known causes is called "error."

Analysis of Variance table.

Source of Variation	Expected Mean Squares
Genotypes	$\sigma_e^2 + r \sigma_g^2$
Error	σ_e^2

In this example, phenotypic variance is explained by differences in genetic composition, as well as to unknown factors. r stands for the number of replications.

$$\sigma_{ph}^2 = \sigma^2 + r\sigma_g^2$$

The particular steps involved in this procedure and the analysis of variance table that results depend on the design of the experiment. Analysis of variance procedures and interpretation are discussed in the Quantitative Methods course.

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Regression – this procedure examines the strength of the relationship between factors or the influence one factor has on another. The linear regression procedure fits a straight line to a scatterplot of data points. The general equation for the regression line is:

y = a + bx

where:

- y = response or dependent variable
- x = predictor or independent variable
- a = y-intercept of the line
- b = regression coefficient, the slope of the line



The regression line always passes through the point (\bar{x}, \bar{y}) . Relative to the total spread of the data, if most of the datapoints lie on or very near the line, there is a strong relationship between the predictor and response variables—x has a strong influence on y. In contrast, the fewer the points that fall on or near the line, the less influence x has on y. A cautionary note: although the x variable may have strong influence on the y variable, x may not be the cause of the y response, nor the sole factor influencing y.

Regression can be used to assess the relative effect of environment on phenotypic value or to obtain information about gene action. The relative scatter about the regression line of a plot of genotype (the predictor variable, x) against phenotypic value (the response variable, y), provides information about gene action. For example, regression analysis of the following two examples suggests that the gene action in example 1 (left

panel) is additive (no dominance), whereas there is a complete dominance (by the A₂ allele) in the case of example 2 (right panel) (Fehr, 1987).

When the heterozygous genotype has a value midway between the two homozygotes and thus all three genotypic values fall on the linear regression line the only gene action contributing to the phenotype is additive.

Regression analysis of phenotypic values of progeny (y) against parents (x) provides useful information about the degree of similarity of progeny to the parents.



Regression analysis may indicate the type of gene action.

Statistical Terms

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Descriptive Statistics

Range – the lowest and highest phenotypic values in the population or sample for the character.

Mean (μ or **M** for population; \bar{X} for sample) – describes the average performance of a random sample from a population for a trait. The mean is a measure of central tendency – it does **not** tell anything about the distribution of individual observations. Mean equals the sum of the trait values of each individual divided by the number of samples (n):

$$\bar{x} = \frac{\sum x}{n}$$

Variance (**V** or σ^2 for population; s^2 for sample) – a measure of the scatter or dispersion of phenotypic values. The greater the variability among individuals, the greater the variance. Two populations with the same mean for the same character could differ greatly in their respective variance for that character.

Average the squared deviations from the mean, $(X - X)^2$:

$$V = \sigma^2 = \frac{\sum [(x - \bar{x})^2]}{n - 1}$$

Standard deviation (σ for population; **s** for sample) – also a measure of dispersion around the mean. Standard deviation expresses the dispersion in the same unit as the mean.

Standard deviation is the square root of the variance.

$$\sigma = \sqrt{V} \operatorname{or} \sqrt{\sigma^2}$$

A small variance and a small standard deviation tell us that the phenotypic values are near the mean value. In contrast, a large variance and standard deviation indicate that the trait values have a wide range.



Samples in which the observations are clustered closely around the mean (red) have a smaller variance and standard deviation than observations dispersed widely (blue).

Coefficient of variation (CV) – the standard deviation as a percentage of the mean. Because the units cancel out, CV is a unitless measure.

Divide the standard deviation by the mean and multiply by 100:

$$CV = \frac{\sigma}{\bar{X}} \times 100$$

A CV of about 10% or less is desirable in assessing biological systems. When the CV is greater than 10%, the variability in the sample or the population may be too great to sort out the factors contributing to that variability.

The **mean** and the **variance** are used to describe an <u>individual</u> characteristic, but plant breeders are frequently interested in <u>more than one trait simultaneously</u>. Two or more characteristics can vary together, and are thus not independent of one another.

Covariance provides measure of the strength of the **correlation** or dependent relationship between two or more sets of variables. When two traits are correlated, a change in one trait is likely to be associated with a change in the other trait. **Variance** is a special case of covariance that is the covariance of a variable with itself. Correlations between characteristics are measured by a **correlation coefficient** (**r**).

Covariance – the mean value of the product of the deviations of two random variables from their respective means. For example, the covariance of two random variables, x and y is expressed as:



Covariance of variables x and y.

Correlation coefficient (r) – measures the interdependence of two or more variables and is obtained by dividing the covariance of x and y by the product of the standard deviations of x and y. The correlation coefficient can range from -1 to +1.

$$r = \frac{Cov_{x,y}}{S_x S_y}$$

Correlation is a "scaled" version of covariance and the two parameters always have the same sign—positive, negative, or zero (0). When the sign is positive, the variables are positively correlated; when it's negative, they are said to be negatively correlated, and when it's zero, the variable are described as being uncorrelated. But it is important to note that a correlation between variables indicates that they are associated, but it does not imply a cause-and-effect relationship.

Threshold Traits

Although they have only two phenotypes, threshold traits are considered to be quantitatively inherited because their expression depends on a liability (such as disease susceptibility or tolerance of nicotine levels) that varies continuously. Heritability of these traits is a function of the incidence of the trait in the population, so it is difficult to determine the importance of genetic factors in different environments or in different populations that differ in incidence. Threshold traits are assumed to be represented by an underlying normally distributed "liability trait" that is the sum of the independent genetic and environmental components of the distribution. A disease would have to be present before you could determine if certain genotypes were susceptible or not. For example, plants might be able to tolerate low to moderate levels of nicotine in their tissues until a threshold was crossed, above which the high level of nicotine present would be lethal.

Threshold characters exhibit only two phenotypes – the trait is either present or absent – but the susceptibility to the trait varies continuously and environmental components of the distribution. A disease would have to be present before you could determine if certain genotypes were susceptible or not. For example, plants might be able to tolerate low to moderate levels of nicotine in their tissues until a threshold was crossed, above which the high level of nicotine present would be lethal.



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Several Environments

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Selection Intensity Table

As long as the distribution of phenotypic values is normally distributed, selection intensity values (symbolized by k or sometimes i) can be found in statistical tables. The intensity of selection practiced by plant or animal breeders depends just on the proportion of the population in the selected group. The selection intensity is a standardized selection differential and is a measure of the superiority of the individuals selected as parents for breeding relative to the population from which they were selected. Representative values of k are the following.

Representative selection intensity (k) values.

%	k
1	2.67
2	2.42
5	2.06
10	1.76
20	1.40
50	0.80
90	0.20
100	0

Genotypic and Breeding Values

Populations can be characterized by the amount and type of genetic variability contained within them. Genetic improvement of a quantitative character is based on effective selection among individuals that differ in what is known as the genotypic value. Variation among the genotypic values represents the genotypic variance of a population.

The genotypic value is the phenotype exhibited by a given genotype averaged across environments. A related concept is the breeding value, which is the portion of the genotypic value that determines the performance of the offspring. **Genotypic value** is property of the genotype and therefore is a concept that describes the value of genes to the <u>individual</u>, whereas **breeding value** describes the value of genes to <u>progeny</u> and therefore helps us understand how a trait is inherited and transmitted from parents to offspring. Remember that only additive genetic effects can be passed on to progeny. Non-additive genetic effects and environmental effects cannot be inherited by offspring.

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