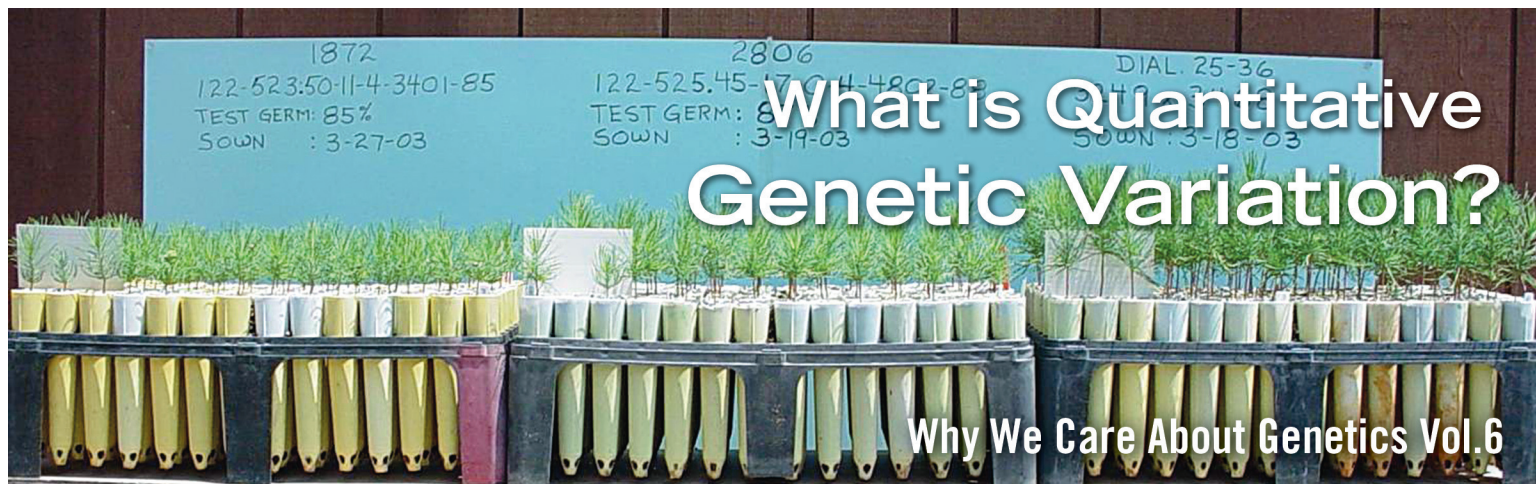




The measurement of genetic diversity — an important part of biological diversity — can take various forms, depending on the objectives of the diversity assessment and the 'type' of genetic diversity of interest (see Table). In Volume 5 (*What is a Genetic Marker*), it was explained that genetic diversity is often categorized on the basis of the type of DNA involved — generally, DNA fragments or genes that may not have any known function or do not seem to be influenced by natural selection (i.e., neutral genetic diversity) are measured with 'genetic

[randomly selected bits
of DNA do not reflect adaptive
genetic variation]

markers' (such as allozymes or microsatellites); more complex genetic interactions that give rise to traits of adaptive significance are often measured through quantitative analysis of the trait itself. These categories are not exclusive but serve as a useful generalization. They reflect the current, but perhaps ephemeral, assumptions that randomly selected bits of DNA do not reflect adaptive genetic variation and that most adaptive traits (or those under selection) are the result of not one or a few, but several to many genes acting in concert.

Quantitative genetic variation refers to the second general category of genetic variation — that based on the combined expression of two or more genes and which results in traits that have a continuous distribution of values or phenotypes. In situations where one gene

controls a trait (e.g., petal color of a flower) there may be a simple expression of that gene when parents with differing petal colors interbreed. In Figure 1A, such a system—with one gene and two alleles—is assumed. Here, a 'blue' is crossed with a 'red' parent, and the resulting progeny (called the 'F1 generation') are expected in a frequency of 1:2:1 of blue, purple, and red flower color, respectively. So working backwards from the colors seen in progeny (as was Mendel's approach), one can deduce there was one gene responsible for this trait. If we now assume that two genes and four alleles are involved in color expression, mating of the two extreme colored parents will now result in nine different colors, with a certain expected frequency (Figure 1B). As more genes are involved, the color categories become more numerous until there is a continuous array of expected colors. Height is another example of such a trait where the values vary continuously rather than in discrete categories, and is governed by many genes.

The range of values that are observed (phenotypic variation) for a continuous trait (e.g., height) is due to both the genetic variation (the genes and alleles involved) and the variation in the environments in which the trait is measured. This relationship is represented as: $P = G + E$ (Phenotype = Genotype plus Environment). Indeed, because the environment may not always have the same effects on each genotype, we add another term to this relationship to reflect the specific 'genotype x environment' interaction. So the expression becomes: $P = G + E + G \times E$. For example, different individuals of the



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ATTRIBUTE	SINGLE LOCUS		MULTIPLE LOCI
	ALLOZYMES	DNA	QUANTITATIVE GENETICS
Sample size needed	Small	Small	Large
Material needed	Various	Various	Measurements
Time	Months	Months-years	Years (typically, several growing seasons or generations)
Data type	Protein variation	DNA sequence or fragment variation	Continuous phenotypic trait variation
Probability of detecting variation	Low	High	Higher
Ability to detect genetic structure	Yes	Yes	Yes (design dependent)
Ability to study adaptation	Often not	Often not	Typically yes

same species may react differently when moved from a cooler to a warmer environment: some may grow more quickly, some more slowly, and some may not be affected.

[the great divide between single- and multi-locus methods for studying genetic diversity is narrowing]

Quantitative analysis of these continuous traits has traditionally involved the use of carefully designed studies (usually field tests) that allow one to tease apart genetic and environmental factors. Replication of the test plants evens out environmental variation; planting test plants on sites that are as uniform as possible reduces environmental variation; using clonal replicates of the plants provides a direct measure of within-site environmental variation; and randomization of the plants disassociates each plant from any particular

microenvironment (i.e., removes bias). Measurements are then taken on all test plants, often over more than one season or year, and appropriate statistical methods are used to analyze the data (e.g., ANOVA — analysis of variance). Results from such tests provide information on whether or not there are genetic differences between the test plants for the traits measured and the relative amount of genetic vs. environmental effects on the traits.

Recently there has been progress towards using marker technology to assist in studying traditionally quantitative traits. One approach is to identify ‘quantitative trait loci’ (QTLs) — genetic loci or chromosomal regions that are statistically related to the genetic portion of the quantitative trait as measured in progeny that result from specific crosses. Several of these QTL mapping studies have been developed for growth and drought tolerance in loblolly pine (*Pinus taeda*). Although sometimes inefficient, this approach can produce information on the number and



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genome location of major genes affecting a quantitative trait. A second more recent approach is that of genetic association mapping: finding statistical associations between molecular markers and particular phenotypes that demonstrate expression of the trait of interest. This approach can be used on natural populations rather than test populations constructed by controlled breeding and generally identifies closer connections (i.e., finer mapping) between phenotypes and molecular markers than standard QTL approaches. More recently, tools of genetic association mapping have been integrated with those of population genomics to produce a powerful approach for studying the genetic basis of adaptive variation in plant species. The great divide between single- and multi-locus methods for studying genetic diversity is narrowing.■

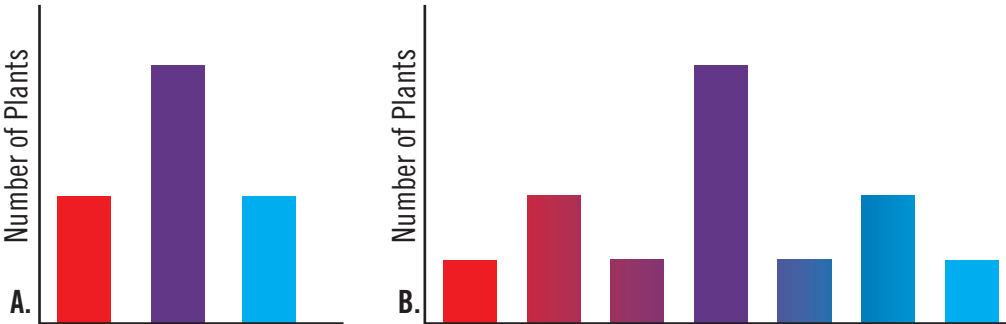


Figure 1. Hypothetical example of progeny (resulting from a cross between two extremes for the trait) expected when there is: A) a single locus controlling petal color; and B) two loci controlling petal color

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