AGRICULTURAL GENETICS

James L. Brewbaker

FOUNDATIONS OF MODERN *Genetics* SERIES

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To a devoted plant breeder and
his understanding wife: my parents

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Foundations of Modern Genetics

Genetic research is alive with excitement and revolutionary advances. Important to the development of science and to the evolution of social structure, genetic thought is widening its impact on many areas: immunology, protein chemistry, cellular physiology, developmental biology, medicine, agriculture, and industry.

So many partnerships and such rapidly expanding methodology demand a fresh approach to genetic training —an approach attempted in this series.

The basic principles of genetics are few and simple. We present them with enough description of accessory scientific areas to allow comprehension not only of the principles themselves but also of the types of experiments from which the concepts have evolved. Such an approach compels the reader to ask: What is the *evidence* for this concept? What are its *limitations?* What are its *applications?*

The Prentice-Hall Foundations of Modern Genetics Series presents the evidence upon which *current* genetic thought is based. It is neither a history nor a survey of all genetic knowledge. The short volumes make possible a stimulating, selective treatment of the various aspects of genetics at the intermediate level, and sectional divisions allow free choice of emphasis in differently oriented college genetics courses.

The references cited in each volume and the current research literature are the immediate sequels to this series, but the true sequel remains in the hands of the alert reader. He will find here the seed of more than one enigma, the solution of which he, himself, may help bring into man's comprehension sometime in the future.

SIGMUND R. SUSKIND
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Preface

Genetics assumes its most important role in relation to agriculture. Perhaps this will not be true in another century, as geneticists discover new applications for their knowledge in the fields of medicine and industry. So long as two-thirds of the world's people are undernourished, however, a fitting and challenging task for genetic research is that of discovering new ways to increase agricultural productivity and to improve the nutrition of man.

Some years ago, there existed a popular misimpression that anyone with full command of the genetics of a corn plant or a fruit fly could solve the problems of organisms such as bacteria, molds, and viruses by simple extrapolation. Today, the misimpression more often exists in reverse. In reality, however, genetic advance in agriculture rests almost entirely on genetic facts obtained from studies of cultigens, agriculturally important animals and plants. Most cultigens are complex higher organisms living in a complex environment. They hardly satisfy a scientist's yearning for "model systems."

The practical obstacles of space and finance lead the agricultural geneticist to make a judicious choice of genetic traits for his study. Only too often, these traits are governed by many genes, are greatly influenced by environment, and are difficult to measure—we may reflect, for example, on the problems of a geneticist studying prime rib production in beef cattle. The role of statistics in genetics is thus an integral one, and the biometrical material covered here should provide a solid background for advanced training in quantitative genetics.

Aspects of genetics that are particularly important in relation to agriculture include polygenic inheritance, genotype-environment interactions, hybrid vigor, host-parasite relationships, polyploidy, genetic lethals, genomic reconstruction, and the regulation of breeding systems. These areas will be explored thoroughly in the pages that follow, together with other aspects of genetic inquiry that provide a basis for advanced study into the creative arts of animal and plant breeding.

J.L.B.

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One

Biological Variation

Hard cash paid down, over and over again, is an excellent test of inherited superiority.[1]

Putting inherited superiority to work is a major objective of agricultural research. Well over half the people on our procreative earth have too little to eat, and even the most profound knowledge of the gene provides little comfort to empty stomachs until it is translated into calories. Genetics has paid its way in calories in the past by demonstrating that inherited superiority can be located, transferred, and used in many cultivated plants and domesticated animals. Among perhaps thirty thousand animals and plants that enter the world's commerce, however, comparatively few species have received the benefit of controlled genetic advances. Challenging frontiers for agricultural genetic research are provided by new species, as well as by new environments for crops and animals, new pests and diseases, new uses in biochemistry, and a spiraling world population.

Cultivated plants and domesticated animals are known as cultigens. With increasing precision, man is controlling both the genetics and environments of these cultigens. Agricultural genetics is defined by its relationship to them, just as medical genetics is defined by a relationship

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[1] Charles Darwin, *Animals and Plants under Domestication* (Appleton, 1897), vol. I, p. 447.

to man. The most economically important cultigens are vertebrate animals and flowering plants, to which most of the illustrations and discussions that follow are related. Of course, the basic principles of genetics are the same for a cultigen as they are for a weed. As a matter of fact agricultural genetics often attains its objectives more rapidly through studies of viruses and weeds than it does through studies of cabbages or cows.

The genetics of cultigens is not the same as the breeding of cultigens. Animal and plant breeding involve many arts and sciences relating to cultigens, and genetics may be considered the most important of these. There are, of course, successful breeders who have little or no knowledge of the science of genetics. However, today's breeder has come to rely on some pretty sophisticated genetic methods, a fact that should become apparent in the pages that follow.

Describing biological variation

The description of biological variation is a starting point for any biological inquiry. The geneticist must distinguish the genetic from the nongenetic components of the variation if he is to discern the mode of inheritance of a trait being studied. It is to this partitioning of variability that much of our agricultural genetic inquiry must be directed. To this end, the science of genetics has come to use more and more complicated tools of the statistician. Nowhere is this more evident than in studies of the economically important characters of cultigens.

Two facts underlie the importance of statistics to agricultural genetics. In the first place, many economic traits are governed by many genes, and are continuous rather than discrete in their variation. Second, it is often necessary in agricultural research to derive genetic information with maximum efficiency from small populations. In studies of milk production or fruit color, for example, considerations of economy and time dictate that we get the most information out of the fewest possible cows or apple trees. No attempt will be made here to describe in detail the methodology of statistical or quantitative genetics, but the understanding of results derived from the statistical genetic approach will require the clear understanding of several basic constants and statistical concepts.

The statistics used to describe biological variation include measures of average, dispersion, and relationships. Among those most often used are:

Measures of average: Mean
Measures of dispersion: Variance, Range, Standard deviation
Measures of relationship: Correlation, Covariance

The two most important measures are mean and variance. The mean, symbolized by $\bar{x}$, describes the average or central tendency of a population; it is calculated by summing (Σ) the observations (X) and dividing by the number (n) of observations summed.

$$\bar{x} = \frac{\Sigma X}{n}$$

The dispersion of a population can be indicated most simply by its range, or extreme values. In many instances, a population's dispersion is as important as its mean. Consider, for example, two basketball teams:

Team A: 6′1″, 6′2″, 6′3″, 6′4″, 6′5″ Mean = 6′3″
Team B: 5′5″, 5′6″, 6′3″, 7′0″, 7′1″ Mean = 6′3″

Although these two teams have identical mean heights, the range of team B is five times that of team A. Given his choice of teams, then, a newcomer would probably elect to play with team B, with its towering seven-footers.

Of greater precision than the range in describing the dispersion of a population is the variance (V, or σ^2), the average of the squared deviations (d^2) of individual observations from the mean:

$$\sigma^2 = \frac{\Sigma d^2}{n - 1}$$

Note that we divide by $n - 1$ rather than by n; this is to adjust the variance of a sample of observations for their mean. We say that a single degree of freedom has been lost from n by this adjustment. For ease in machine calculations, variance is calculated directly from original measurements by use of the formula

$$\sigma^2 = \frac{\Sigma X^2 - (\Sigma X)^2/n}{n - 1}$$

The variance is the measure most frequently used in statistical genetics, since it is the most valuable of the statistics that describe the variation of a biological trait.

The square root of variance is the standard deviation (σ), which expresses dispersion in the same units of measurement as does the mean. When it is related directly to the mean in per cent, it forms a useful coefficient of variation.

$$\text{Coefficient of variation} = \frac{\sigma}{\bar{x}}$$

Coefficients of variation can be used to compare different experiments, since they are independent of units of measure. Coefficients of variation smaller than 10 per cent are uncommon in biological data.

For the basketball teams A and B, for example, variance values are

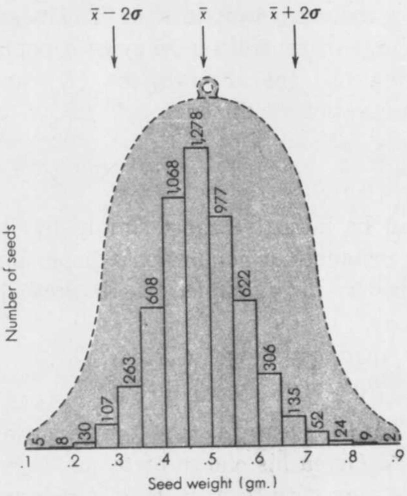

Fig. 1.1. Normal probability distribution of 5,494 kidney bean seeds, grouped according to seed weight. Based on experiments of Wilhelm Johannsen.

2.5 for team A and 90.5 for team B; standard deviations are 1.6 for team A and 9.4 for team B; and coefficients of variation are 2 per cent for team A and 13 per cent for team B. Each of these sets of values indicates the fact that the dispersion is much greater in team B than it is in team A.

The distribution of values about the mean for most biological characters assumes a characteristic bell-shaped pattern. This is illustrated in Fig. 1.1, which shows the weights of 5,494 kidney beans recorded by the great Danish geneticist Wilhelm Johannsen. The bell-shaped distribution can be duplicated by anyone willing to make 5,494 measurements of almost any biological trait. This type of distribution follows certain laws of probability and is known as the normal probability distribution. A normal distribution is symmetrical about the mean as midpoint, and 95 per cent of the population falls within the range from $\bar{x} - 2\sigma$ to $\bar{x} + 2\sigma$. In other words, values in a normal probability distribution exceed a deviation of 2σ, twice the standard deviation, less than 5 per cent of the time. The ratio of 95 per cent to 5 per cent, or of 19 : 1, is taken as safe betting-odds for much bioagricultural research. Thus, when values exceed a deviation of 2σ from the mean, the deviations are considered large enough to be significant, and the biologist may wisely seek a cause other than chance for the deviation. The normal probability distribution may be calculated empirically by expanding the binomial $(p + q)^n$, where n is infinitely large and $p = q$.

Measures of relationship include correlation and covariance. Each of these measures describes the change in one variable character as another one changes. Correlation is a measure of direct proportion. Thus, we say that height and weight of a growing animal are corre-

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