

Modern plant breeding began when the emerging science of genetics was in its infancy.

Until the twentieth century various lines of genetic investigation (cytology – cytogenetics, evolution, inheritance of characteristics) were usually separate, because so little was known about both transmitted characters and transmitted substances.

Scientists at the turn of the century knew nothing about the genetic structure of populations and Darwin's theory had failed to give any explanation for the rudiments of hereditary transmission. When Mendel's work was rediscovered at the turn of the century some viewed it as antagonistic to, rather than complementary to the role of natural selection. Reconciliation of Darwinian thought with Mendelian genetics was a challenge for some of the foremost geneticists of the day. As the early 20th century progressed, Darwin's ideas were gradually joined with the realizations made by Mendel i.e. particulate or physical inheritance of traits from the respective parents. Researchers soon showed the relationship between the genotype and the phenotype in the inheritance of traits.

After Darwin described his initial theories of evolution he identified a fifth major premise: Selection is the principal agent of change. He acknowledged early plant and animal breeders in identifying selection as the chief directing agent in bringing about evolutionary change.

Many, but not all, plant and animal breeders acknowledged Darwin's principles. It is not difficult to imagine how breeders could relate to concepts such as natural selection and adaptation when they themselves were engaged primarily in effecting selection pressure to develop better adapted strains of plants and animals.

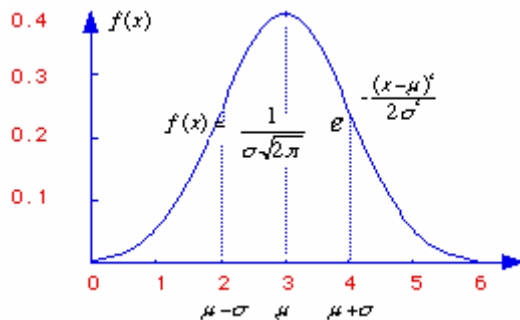
The current scientific phase of plant breeding:

- The process started in the late nineteenth and early twentieth century.
- Darwinian and Mendelian principles became established as the framework within which evolutionary changes in living organisms occur.

The term Neo-Darwinism was adopted.

Formerly separate areas of research came together around the turn of the 20th century and gave rise to a general understanding of how species differentiated and became adapted to different environments. The mechanics of just how genes fit into Darwin's evolutionary scheme were not readily apparent. It had never been clear just what gave rise to the variations that provided the raw material for the evolutionary process. There was also a dilemma in that most wild species are out-crossing -- so how could variation be maintained in a population or a species? If populations were progressively diluted by outcrossing – how could they give rise to new species? This problem was referred to as the “swamping” effect of crossing. The solution lay in Mendel's research: character differences are not blended but persist. During the early 20th century the concept of “blending” inheritance did not rest easily and the early “Mendelists” had a difficult time convincing others that the collective action of individual factors could be responsible for the observed patterns of continuous variation.

Experiments by Johannsen helped to distinguish between the effects of the genotype and the environment in the expression of continuously varying traits. His experiments contributed toward the understanding that continuously varying traits might result from the presence of multiple genetic factors, each responsible for some measurable degree of expression of the quantitative trait. Johannsen found that with a general population of a self-fertilizing plant (*Phaseolus* beans) selection for a trait was effective in shifting the average of the population in the direction of selection.



See also: http://www.dur.ac.uk/stat.web/chart_main.htm

But when selection was similarly applied to the offspring derived from self-fertilization of a single plant, it was ineffective in changing the average value of the character. In short, a population consisted of pure lines, or -- selfing populations eventually wind up as a mixture of distinct homozygous families. Selection applied to a mixed population sorts out pure lines, small, large and intermediate, but within a homogenous line, there is no more genetic variation (which can respond to selection). He showed that the phenotypic differences between pure lines (assignable to a class) were heritable, not that different genes controlled them per se. He postulated that the differences were due to Mendelizing factors that he termed genes.

(To make conclusions about the inheritance of genes it is necessary to make a cross between parental genotypes displaying contrasting alleles, and generate a segregating population e.g. F_2 or progenies e.g. F_3 .)

The problem with attributing small differences in phenotypes to individual genes is that it is difficult to clearly and consistently score small differences in quantitative traits. Johannsen's methodology and the fact that he chose a seed lot that was indeed comprised of many "pure – lines" was paramount to the success of the study. It provided a wealth of "circumstantial evidence."

His market sample probably consisted of a bulk sample of local varieties all called the same thing by different farmers. What might happen if the experiment were conducted today?

Here are the experimental procedures (courtesy of <http://www.stat.berkeley.edu/users/terry/Classes/s260.1998/Week4/week4/node2.html>)

Here is what Johannsen did. He experimented with beans, specifically Princess beans, *Phaseolus vulgaris nana*. Recall that, like peas, beans are naturally self-fertilizing. He began his series of experiments in 1900 by planting a number of bean seeds from an 8 kg lot, always permitting self-fertilization. In 1901 he harvested 287 plants from selected seeds of very different sizes and known weights.

In 1902 he planted 524 seeds from his 1901 crop, and harvested 5,494 seeds. Each of the 524 seeds originated from one of a set of 19 single beans (which he designated A, B, ..., T). He kept

track of the weight (in mg) of the mother and the grandmother beans (being Princesses, all these beans are being viewed as female!).

Finally, he selected the smallest and largest beans (seeds) in each generation, and planted these (1902-1907).

For nice graphics and the data from the experiments, see:

<http://www.biologie.uni-hamburg.de/b-online/e13/13.html>.

As Mendel's principles were aligned with Darwin's theory and applied to populations, and the source of variation (mutation) and the maintenance of variation (allele frequency) became both explainable and demonstrable. Mutations and recombination were accepted as the sources of variation and gradual evolutionary changes in populations as a result of changes in gene frequency seemed quite logical. It is also noteworthy that at the turn of the century transmission of genes on chromosomes was established (Sutton and Boveri, 1903-04).

The Mendelian basis of continuous variation was recognized by researchers such as R.A. Fisher, and a mathematical treatment of natural selection began. The union of population genetics with natural selection generated a new view of the evolutionary process, called Neo-Darwinism. By the end of the 1940s, neo-Darwinian ideas were almost universally accepted and some authors cited the development of a "Modern Synthesis" of evolution.

The leading features of modern evolutionary theory as stated by Simmonds and Smartt (1999) are as follows:

- Natural selection acts upon genetic variation and plant species are differentiated into sub-species, ecotypes, clines, etc. these populations often become separated geographically.
- Variability is maintained by heterozygosity supplemented by gene-flow between populations.
- Heterozygosity (polymorphic loci) is adjusted upward or downwards by various cytological or genetical mechanisms. (A polymorphic locus is any locus that has more than one allele present within a population.)
- Reproductive isolation between populations leads to speciation (which generally develops gradually).
- Speciation is a continuous process. It is not an endpoint or a dis-continuous process.
- Adaptation is procured by successive gene substitutions in evolving populations, leading to local differentiation and speciation. (I prefer the use of terms allele substitutions and allele frequency.)

Different hereditary **elements** or **factors** – **genes**

Alternative members of the elements -- **alleles**