PRINCIPLES OF MENDELIAN GENETICS APPLICABLE IN FORESTRY

by Erich Steiner 1/

It is well known that the variation exhibited by living things has two components, one hereditary, the other environmental. One objective of any crop improvement program is to organize hereditary variability into combinations of maximum economic value. To attain this objective, it is first necessary to understand how the hereditary traits of an organism are determined and how these traits are transmitted from generation to generation.

Our knowledge of the principles of heredity has come largely from a relatively small number of organisms, which, because of their short generation time, ease of culture, and extensive variability, are ideally adapted for genetic studies. Among these are representatives of widely different groups which, nevertheless, have been shown to possess the same basic hereditary mechanism. The universality of the fundamental principles of heredity stands as one of the major unifying concepts of biology. We have every reason to believe, therefore, that in its basic features the hereditary mechanism of forest trees conforms to that of organisms whose genetics have been much more intensively studied.

The Particulate Theory of Heredity

Insight into the hereditary mechanism can be gained by crossing two strains that show contrasting forms of a particular hereditary trait and following this trait through several generations. Let us assume that we have two strains of a tree species that differ appreciably in the height attained by the mature individuals. Each of these strains breeds true. When the tall and short strains are crossed, all of the offspring prove to be tall. If the trees of the first or F1 generation are crossed, the next generation (F2) is composed of both tall and short individuals in the proportion of approximately 3 tall to 1 short. The kind and frequency of offspring in such a series of crosses can be explained if we assume the following:

(1) The height character in this species is controlled by a particle or unit. Such a hereditary determiner is called a gene.

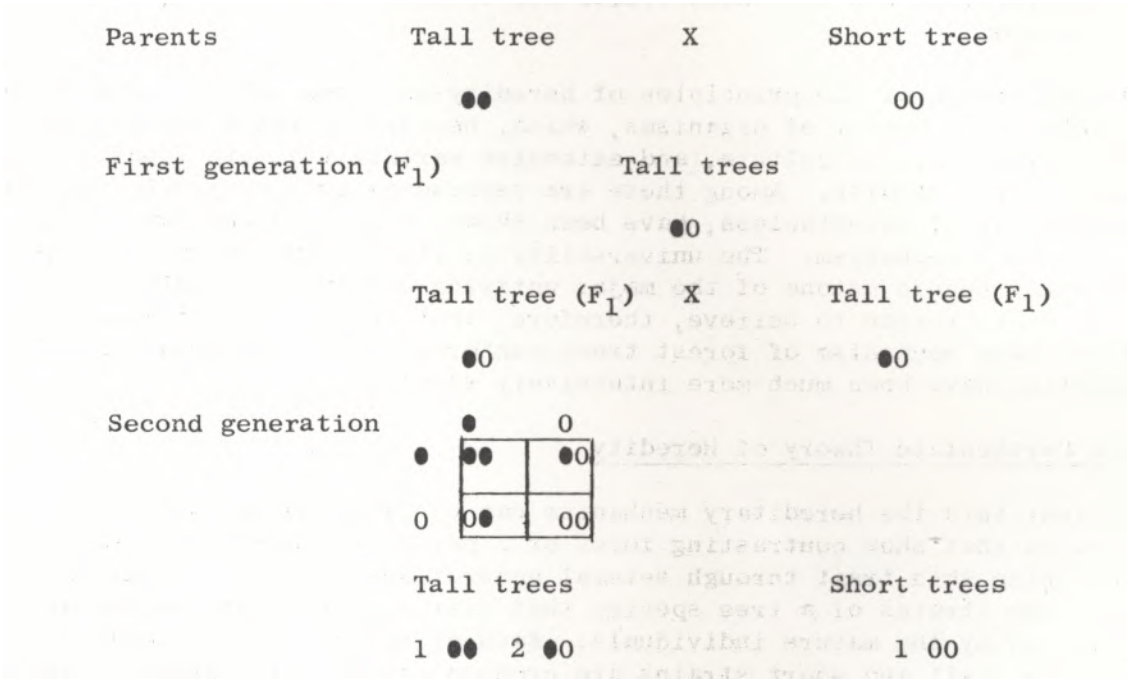
(2) A particular kind of gene--for example, that controlling height--may exist in one or more alternative states, called alleles. Each allele produces a different form of the trait that the gene controls; thus in the above cross one allele of the height gene produces a tall tree, while the other produces a short one.

1/ Associate Professor, Department of Botany, University of Michigan, Ann Arbor, Mich.

(3) Each individual carries two representatives of each kind of gene. Although only one of these is passed on to a particular offspring, each of the two has an equal chance of being transmitted.

(4) The reappearance of the short trees among the progeny of the second generation is evidence that the short form is not lost in the first generation, but merely masked. Short is thus recessive to tail, which is the dominant character.

These assumptions are diagrammed below:



If this scheme is correct, the breeding behavior of each of the individuals in the second generation should be predictable. One-third of the tall trees will breed pure, while two-thirds will breed like the F_1 offspring. The short individuals will all breed true. When such tests are carried out, the predictions are confirmed and the validity of the hypothesis is supported. The concept that the hereditary traits of an organism are determined by particles (genes) which are transmitted from generation to generation without loss of integrity was first developed by Mendel and is known as the Mendelian or particulate theory of heredity.

With respect to the crosses which we have used to derive the concept of a particulate hereditary determiner, two additional points are worthy of emphasis. Although dominance of one allele over another may often occur, it is not by any means always complete nor a universal phenomenon. When two alleles are brought together in an individual, whether dominance will occur or whether each allele will express its own effect cannot be predicted. A second point to be noted is that the first-

generation offspring are uniform in their hereditary constitution. This provides a basis for the generalization that the first-generation offspring between two pure breeding strains are composed of a single hereditary type.

The Chromosome Theory of Heredity

If these units, called genes, exist, where in the organism are they located? What is their physical basis? An understanding of the details of reproduction in an organism helps to answer this question. The link between one generation and the next is found in the gametes, sperm and egg, which fuse to form the zygote from which the new generation develops. In the seed plants the sperm are brought to the egg by the pollen tube. Frequently the male contribution to the zygote consists of only a sperm nucleus with little or no cytoplasm, the cytoplasm Of the zygote being derived from the maternal parent. Yet it is clearly apparent from breeding experiments that with few exceptions the male contributes as much as the female to the heredity of the offspring. Thus it follows that the genes must be carried in the nucleus and not by the cytoplasm of the cell.

The primary constituents of the nucleus are the chromosomes; when a nucleus divides, the chromosomes are duplicated and precisely apportioned in kind and number to the daughter nuclei. The heredity of an organism is remarkably stable within limits. This stability must be related to the precision in chromosome duplication and distribution when new cells identical in heredity are formed from old, and suggests that the genes are carried by the chromosomes.

A study of the chromosomes through the reproductive cycle reveals a direct parallel between chromosome and gene behavior. Each parent possesses two sets of chromosomes; when the spores are formed which give rise to the gametes, a reduction division or meiosis occurs so that each spore, and therefore, each gamete, receives only one set. Meiosis allows the equal distribution of the chromosomes to the spores (gametes), one of each kind of chromosome occurring in each gamete. When the sperm and egg fuse, two sets of chromosomes are brought together in the zygote. If one assumes that the gene is located on a chromosome, the transmission of the hereditary unit can be accounted for in terms of the transmission of the chromosome.

Independent Assortment

In studying the heredity of an organism we must inevitably deal with more than a single hereditary character at a time, Let us assume that another pair of contrasting forms of a trait is determined by a pair of alleles residing on a second pair of chromosomes. If we follow the alleles as well as the chromosomes through the reduction division, we find that the particular combination of genes which a gamete receives

will depend upon the orientation of each pair of chromosomes during meiosis, as shown in Figure 1. Since each pair of chromosomes assumes independently and purely as a matter of chance one or the other of the two possible orientations, each of the combinations of the chromosomes and their alleles occur with equal frequency. For a particular pair of alleles, A and a, the probability of a specific allele occurring in a certain gamete is 1/2. The same probability holds for another pair of alleles on a different chromosome pair. Since each pair of chromosomes becomes oriented independently of the others, when we consider two pairs of alleles simultaneously, the probability of obtaining a particular combination in a gamete, e.g. AB, is 1/2A x 1/2B or 1/4AB. It follows that the general formula, $(1)^n$, will determine the probability of a particular combination of alleles occurring in a gamete, where n represents the number of allelic pairs. Since gametes of different allelic constitution come together to form zygotes purely by chance, the probability of obtaining a specific gametic combination in the zygote becomes $(1/2)^n$ x $(1/2)^n$ or $(1/4)^n$, if each allelic pair is located on a different chromosome pair.

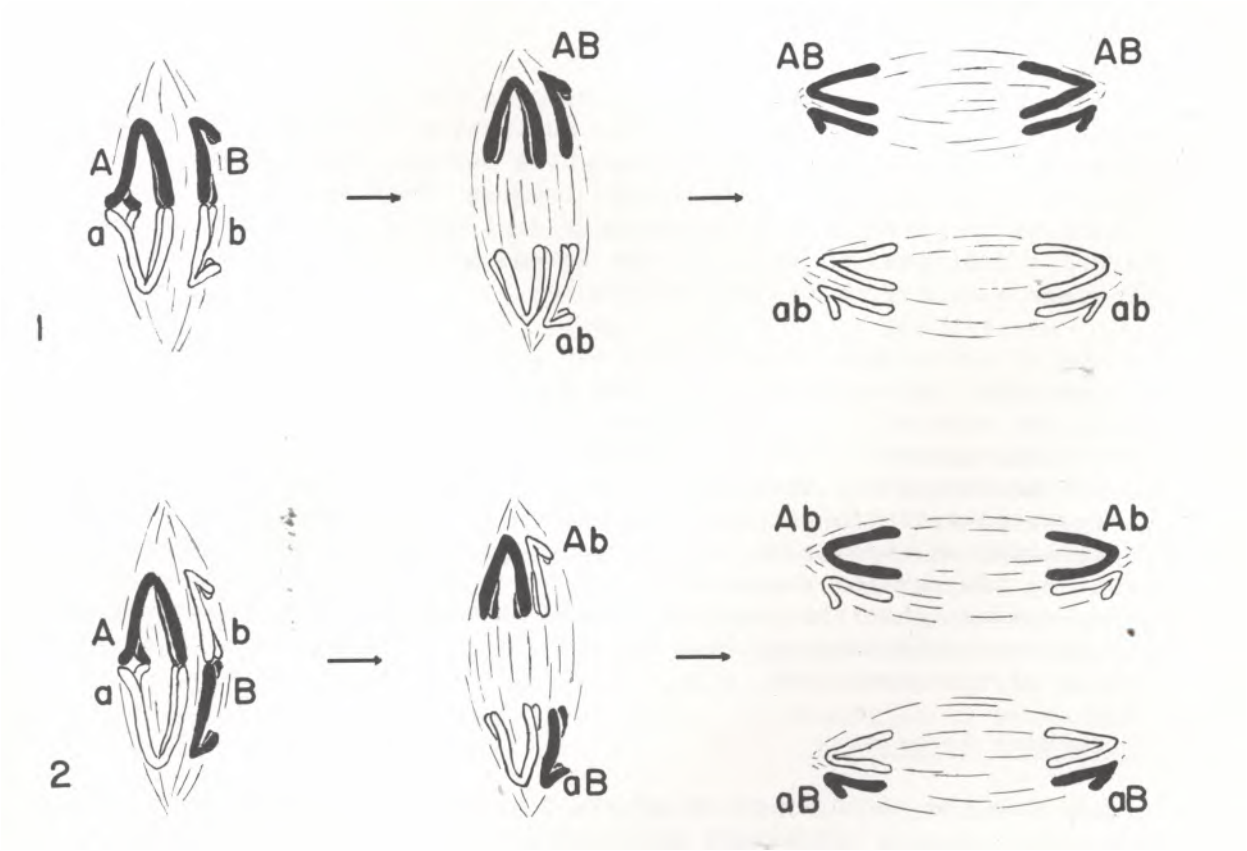


Figure 1.--Chromosome behavior at meiosis; the independent assortment of the allelic pairs, Aa and Bb, depends upon the orientation of the chromosome pairs.

The random recombination that occurs between genes located on different pairs of chromosomes is known as independent assortment. It is obvious that the larger the number of allelic pairs which control a particular combination of characters, the lower the probability of finding such a combination among the progeny of a hybrid. The search for a particular combination of desirable hereditary traits in a plant improvement program must, therefore, take into account independent assortment.

Linkage and Crossing-Over

Although chromosome numbers in different organisms vary over a wide range from as few as 2 to as many as 250 in a set, many species possess a relatively small number. For example, all species of pine show a chromosome number of 12 per set. An organism is composed of thousands of single hereditary traits; if each of these is determined by a single gene, then each chromosome must carry a considerable number of genes. It should follow, therefore, that the genes carried on a particular chromosome are transmitted together; in other words, intact blocks of hereditary characters would appear to be passed from generation to generation. The different genes located on a particular chromosome are thus said to be linked.

Breeding experiments show, however, that linkage of genes is usually not complete and that recombination of genes located on the same chromosome does occur. This phenomenon, known as "crossing-over," becomes clear when chromosome behavior during the early stages of meiosis is observed. When two chromosomes pair, each strand duplicates; as a result four strands are associated. Two of these may exchange segments so that the alleles of different genes that were previously associated are now in a new relationship, as shown in Figure 2. This exchange of segments is a regular feature of meiosis. If two genes are closely associated on a chromosome the chance of a break and exchange of segments between them is less than if two genes are far apart on the chromosome. Linkage tends to hold combinations of genes that are favorable to the organism together, while crossing-over allows greater variability than that provided by independent assortment alone. Since every plant improvement program has as its ultimate goal the development of particular combinations of hereditary characters, linkage and crossing-over must be taken into consideration in obtaining these.

Polygenic Inheritance

Our discussion has dealt only with hereditary variation that is discontinuous, i.e. where the offspring can be classified into distinct types that can be identified, at least within the limitations of dominance, as specific gene combinations. The geneticist is confronted with another type of variation, known as quantitative or continuous variation. For example, if a fast growing strain is crossed with a slow growing strain, the first-generation offspring may show an intermediate growth rate, while the F_2 progeny may show a range of types that vary from fast growers

through every type of intermediate to some that have a slow growth rate. The offspring fall into a normal distribution curve with respect to growth rate.

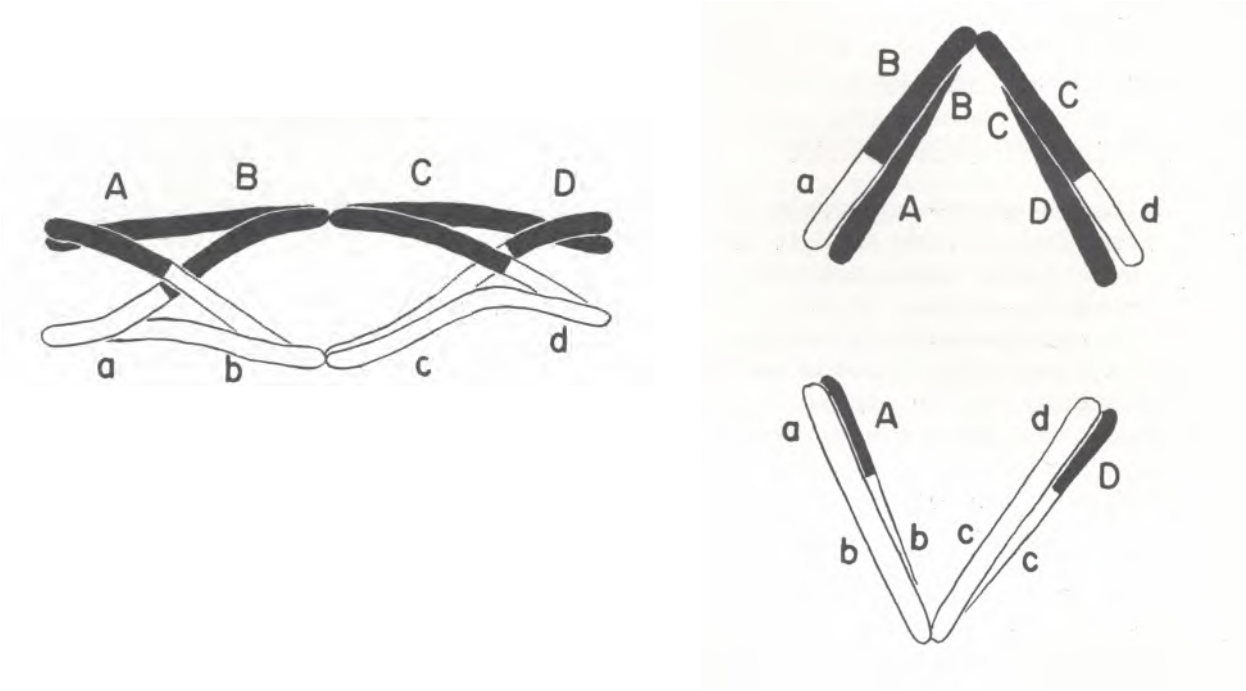


Figure 2.--Crossing-over. An exchange of segments between two of the strands results in recombination of the genes a, d with B, C, and A, D with b, c.

This pattern of inheritance can be reconciled with the concepts previously reviewed, if we make the following assumptions:

(1) The so-called quantitative characters of an organism are under the control of a number of genes, called multiple factors or polygenes.

(2) Each polygene produces a small effect which is, however, equal and additive to the effects of the other polygenes controlling a particular quantitative character.

According to this scheme, the crosses described above can be represented as follows:

Fast growth rate	X	Slow growth rate
AABBCCDDEE		aabbccddee
F_1	intermediate AaBbCcDdEe	

F2 A range of types showing continuous variation from fast growth rate to slow growth rate. These are represented by all the combinations of alleles between the two extremes,

AABBCCDDEE ⟶ aabbccddee

This pattern of inheritance and the methods necessary for its analysis are of major importance in any plant or animal improvement program, since a great many of the hereditary traits of economic significance show continuous variation.

These are the general principles that in most organisms govern the transmission of the hereditary characteristics from one generation to the next. It is within this framework that the tree improvement specialist must work in order to obtain particular combinations of genes which possess the greatest economic value.

Group Discussion 2/

Questions were asked concerning linkage. It was brought out that there are no known methods or techniques for determining linkage without going through the F1 and F2 generations. Such determination might be possible, however, where we have good knowledge of certain individual pedigrees.

Another query was "Can we make observations in natural stands for some characteristics in terms of occurrence of certain characters together?" The answer was that this might be a case of linkage, but that we also have to recognize that single genes may have multiple phenotypic effects.

2/ The report on discussion for this and succeeding articles is based on notes made by Waldemar Albertin, graduate student at the University of Michigan.