VEGETATIVE REPRODUCTION

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All of the important fruit-crop plants in the United States, many of the ornamentals, a few crops like potatoes, and some of the nut and forest trees are multiplied or propagated for commercial production by vegetative means. This means that a new plant is developed from a vegetative portion of a mother plant, such as a cutting or bud, instead of from a seed, as is the case with most of the cereal, forage, and vegetable crops. This fact is extremely important from the standpoint of the principles and methods employed in the improvement of fruit crops by breeding.

As was explained in detail in the article on Heredity Under the Microscope, in the 1936 Yearbook, the seed in the ordinary plant develops from a single cell, the fertilized egg, which has received in the fertilizing process chromosomes from both the female or seed parent and the male or pollen parent. These chromosomes transmit the hereditary factors or genes from both parents, and the offspring that develops from this cell, therefore, inherits the characteristics of both. If the germ cells from the two parents carry genes that are alike for all characteristics, the plants that develop from the seeds will be very similar to these parents. On the other hand, if the parents transmit unlike genes for various characters, many of the offspring will vary widely from either parent because of the effects of dominance, recessiveness, or modifying factors.

In vegetative propagation the new plant also develops from a single original cell. Although the bud or other propagative tissue may consist of thousands of cells, at one stage of its development only a single cell was involved. This cell carries the same genes as the mother tissue from which it was developed, and the genetic characteristics of the new tissue correspond to those of the mother plant, except in the case of vegetative mutations, to be discussed later in this article. From the hereditary standpoint it may be said that the vegetative offspring of a plant is a part of that plant itself rather than a new individual.

The Winesap apple, for example, originated as a seedling about 200 years ago. The original tree has probably been dead for more than a century. Before that tree died, however, buds taken from it were grafted into other apple roots and these buds developed into new individual Winesap trees, the tops of which are genetically a continuation of the parent trees. Many generations of trees have been grown from this original Winesap, yet the characteristics of the Winesap
trees and fruits today are but little, if at all, changed from those of the original tree.

Varieties of European wine grapes exist today that are believed to have originated several hundred years ago. These grapes have come down to the present time practically unchanged in character because vegetative portions of the vines rather than the sexual portions or seeds have been used for propagating them. The Wilson strawberry, originated in 1852, is still grown to some extent in Oregon. It has been propagated by runner plants ever since its origin and after many vegetative generations is today apparently similar in all respects to the parent plant.

**CELL DIVISION IN VEGETATIVE TISSUES**

In many respects the division of a cell to form two daughter cells in vegetative tissue is quite similar to that described in the article on Heredity Under the Microscope for germ cells. Each vegetative cell consists of the cell wall, the cytoplasm, and a nucleus. The nucleus, while the cell is in the resting stage—that is, not in the act of dividing—contains numerous chromatin granules, just as the germ cells do. In the beginning stages of cell division these chromatin granules collect in threadlike bodies, which are the forerunners of the more definitely organized chromosomes. These threadlike bodies are usually more or less separate, though in some cases they appear to be arranged end to end. Later they break up into independent chromosomes.

At this stage one very important step occurs that does not occur in the same way in the germ cell. After the chromosomes are formed in the vegetative cell, each chromosome appears to split longitudinally into two parts, giving twice the original number. Each of these parts appears to function as an independent chromosome. After that, the process is like that in the germ cell. The two halves of each original chromosome migrate, one to each of two poles on opposite sides of the nucleus. These two groups of chromosomes, one at either pole, now reorganize as separate daughter nuclei, each similar to the original one. A cell wall is formed between the two daughter nuclei, and there are two complete cells instead of the original one. Each of these cells, however, has the same number of chromosomes as the original, whereas if they were germ cells they would have half the original number.

Apparently the genes, which are the carriers of hereditary factors in the chromosomes, are also divided in this process of longitudinal splitting of the chromosomes, and this gives each daughter cell exactly the same hereditary factors. If it were possible at this stage to isolate each daughter cell and develop from it a wholly new individual, the new individuals would be exactly alike genetically and both would be exact genetic replicas of the parent plant.

However, it is, of course, never possible to grow two plants and have them exactly alike even though they have exactly the same genetic make-up. The final size and shape of a plant depends upon two factors—its genetic make-up and its environment. It is never possible to have exactly the same environment for two individuals. Variations in nutrition, light exposure, moisture relations, or in other
factors in the environment will always make some difference in the ultimate development of individuals. Genetically, however, plants that develop from these vegetative daughter cells will have the same make-up that was contained in the parent cell from which they were derived.

But, even in the most nearly perfect mechanism there is always the possibility that it may not function exactly the same in every case. Thus in the division of thousands of cells there is the possibility that certain cells may not divide so as to give the daughter cells exactly the same genetic make-up. In the splitting of the chromosomes, for example, it might occasionally happen that certain genes would fail to split, in which case one daughter cell might have a certain gene while the companion daughter cell might lack it.

There is ample evidence in the horticultural field that abnormal cell division occasionally occurs in the vegetative development of the plant. When it does occur, if the cell concerned is one from which major portions of the plant develop, a so-called bud sport branch may arise, showing a different character, and this sport or mutant may be propagated by vegetative means. Thus, in an apple variety a gene for fruit color may be added to or taken from a chromosome in a dividing cell at the tip, giving rise to a "color sport branch."

In certain plants shoots arise, not from the continued division of a single cell at the tip, but rather from the divisions of many cells in a group. In such cases the mutant cell may affect only one portion of the new shoot. This may represent a sector running throughout the length of the shoot, in which case we have what is called a sectorial chimera or variation. Buds taken from that particular section will develop into plants showing the variation throughout.

Also, in certain plants mutations occur involving only the outer ring or rings of cells on the stem. These are termed periclinal chimeras. The thornless sports of blackberries are of this type. They reproduce true to the thornless type from propagations made from stem tissue as tip layers, since in this case the new bark develops as a continuation of the old, but not from root tissues, because in this case all the new tissues originate from deep-seated cells that carry genes for thorniness.

These mutations in the vegetative tissues may involve only one gene or they may involve several. Thus, not only color of fruit might be modified, but shape, texture, season of ripening, or chemical composition might be affected by such mutations. At rare intervals a doubling of some or all of the chromosomes may occur without nuclear division, followed by regular division thereafter. Such a mutation, which produces a permanent increase in the number of chromosomes in each cell, often results in marked variations in vigor, fruit size, quality, and other factors in the mutant tissue. The variations can be reproduced in practically identical form by vegetative propagation.

It is noteworthy, however, that in most plants these vegetative mutations occur very infrequently. Ten thousand buds taken from a grape variety may develop into as many individual vines with hardly an observable variation that can be attributed to a lack of perfectly regular genetic reproduction in the vegetative cells. The remarkable feature is not that occasional irregular cell divisions occur, but rather that the irregularities are so rare.
VEGETATIVE REPRODUCTION

This fact is of tremendous importance from the standpoint of establishing fruit varieties. Once an individual plant is obtained, as a result either of hybridization or of selection, it is possible to reproduce that plant almost exactly by vegetative propagation. With seed-propagated plants, on the other hand, before a new variety can be established it is necessary not only to secure an individual plant that has the characteristics desired but to follow this with selfing or inbreeding until a group of plants is secured of proper genetic purity to come true in large proportion from seed. This long process of breeding to secure varieties that come true from seed is not necessary in the improvement of plants that are vegetatively propagated.

The fact that all fruit varieties are vegetatively propagated, however, is not an unmixed advantage to the breeder of fruit crops. The very fact that individuals can be reproduced by vegetative means has resulted in the selection of varieties without any regard to how nearly they reproduce true to type from seed. Furthermore, up to the present time much less study has been made of the hereditary make-up of our fruits as a group than of many of the seed-propagated crop plants. We can usually judge what characters will be transmitted in inheritance, in the case of seed-propagated varieties of sufficient purity, by the type of parent material. This is not always true of vegetatively propagated plants.

The Northern Spy apple, for example, in its vegetatively propagated form is large-fruited. Seed of this variety, however, produces mostly smaller apples. A particular variety of grape may be black, yet seed planted from this variety may produce white, red, or black grapes. The possibilities of our horticultural varieties as breeding stock can be determined only by trial. In actual experience it has sometimes been found that a variety having very valuable characteristics when vegetatively propagated does not tend to reproduce these characteristics in the seed offspring. On the other hand, certain rather mediocre varieties may prove superior as parents for the development of improved sorts by breeding methods.

Most of our tree fruits and some ornamentals are propagated by budding or grafting the desired variety on the roots of the same or closely related species. With our tree fruits, these roots are mainly developed from seedlings. With grapes and roses, the roots are also propagated vegetatively.

There is much need for investigations in the United States to determine the best rootstock to use with the various fruit and nut varieties. The use of the best rootstocks might greatly improve the vigor and longevity of orchards under certain conditions. For example, peach rootstocks resistant to nematodes in the South and in parts of California should result in longer lived and more vigorous trees. The development of grape rootstocks resistant to phylloxera has saved the vinifera grape industry of southern Europe and in parts of California. The development of apple stocks resistant to woolly aphis would be a great asset to apple growing in many parts of the world. The characters of the rootstock are second only to the characters of the variety in determining successful production of many of our fruit varieties.
DO VEGETATIVELY PROPAGATED VARIETIES "RUN OUT"?

Closely allied to this discussion of the relation of vegetative propagation to breeding is the question of whether or not such vegetatively propagated varieties last indefinitely. It was long held, even by horticultural authorities, that after a few generations of vegetative propagation, varieties gradually lose their superior characters, become less vigorous, and decrease in value until they are abandoned as commercial sorts. Andrew Knight, of England, probably the greatest horticultural authority at the beginning of the nineteenth century, believed that varieties "run out" under vegetative propagation. Potato growers strongly held to this view until recent years, because their varieties appeared to deteriorate rather rapidly. Until recently, most growers of vegetatively propagated plants believed that such propagation is a weakening process and that new varieties propagated from seed must be developed frequently if vigor, quality, and productiveness are to be maintained.

It is true that many vegetatively propagated varieties are popular for a plant generation or two and then pass out of the trade. However, there is no evidence that varieties have become progressively weaker owing to repeated vegetative multiplication. In some cases, varieties develop diseases that may be carried from the mother plant to the daughter through the bud, cutting, or runner plant. This is especially true of the virus group of diseases, and many varieties may have disappeared because of such transmitted infection. A number of virus diseases are known that affect potatoes (fig. 1), strawberries, raspberries, and other vegetatively propagated plants. An under-
Standing of these diseases has come only in very recent years. Prior to a knowledge of these diseases it was natural that the grower would assume that the weakened or malformed plants, resulting from vegetative propagation from infected parent material, were "running out." By keeping the parent material for vegetative propagation free of disease, such deterioration can be prevented.

Other varieties are discarded because of changing preferences on the part of the consumer or because the plant may not be sufficiently

Figure 2.—Winesap apple trees still vigorous, productive, and producing good-quality fruit. The leading commercial apple variety of the United States, this variety has been propagated vegetatively since its origin almost 200 years ago.

hardy, vigorous, or disease-resistant to meet new demands. The Early Crawford peach is an excellent example of this. This variety, which originated about 100 years ago, is still identical with the original in all the characters that made it very popular 50 years ago. Today, however, it is little grown, despite its high quality. Other varieties have developed that are heavier yielders, that can be shipped and held on the market in better condition, and that are somewhat harder.

The Esopus Spitzenburg apple is another example of a very high-quality dessert variety that is disappearing from American orchards because the tree is not hardy and is particularly susceptible to many diseases. Yet there is no reason to believe that this variety as propagated today is in any way inherently different from the parent tree of 150 years ago. It is still a vigorous tree and productive, if protected from low winter temperatures and diseases. In contrast, the most extensively grown apple in the United States today is the Winesap (fig. 2), which is believed to have originated at least 200 years ago.
Occasionally a variety may show a lack of stability under vegetative propagation, which leads to an abundance of vegetative mutations generally of one particular type. For example, in a number of strawberry varieties under vegetative propagation there has been a marked tendency to mutate to a yellow-foliage form (fig. 3). Such wholesale

![Figure 3.—The yellow-plant mutation (center) in the Blakemore strawberry. This mutation occurs very frequently in this variety and will result in the commercial deterioration of the variety unless propagating material is carefully selected to avoid it.](image)

mutation has occurred in the Howard 17, or Premier, variety, and in recent years it has occurred in the Blakemore. Apparently some unstable gene occurs in the make-up of these varieties that develops a very high proportion of mutations. In certain strawberry varieties this has resulted in their passing out of commercial production.

The Washington Navel orange also appears to develop a rather large number of mutations under vegetative propagation. In most cases careful selection of the parent stock will permit the maintenance of such varieties. Perhaps this marked tendency to mutate, which occurs in a very few vegetatively propagated varieties, most nearly represents "running out" in the sense that the term has usually been employed. Even in this case, however, the selection of true-to-type parent material will usually maintain a variety indefinitely.