The Importance of Polyploidy In Modern Apple Breeding

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During the past 25 or 30 years the science of apple breeding has gone through a period of change from the basic orthodox methods of plant hybridization to a new series of techniques which involve not only the genes — the units which control heredity—but also the chromosomes on which these genes are located. When the chromosomes are considered, rather than the genes, the important factor is the number of chromosomes which are contained in the cells of a particular plant. This variation in number may cause a change in the characteristics of the individual, even though there is no alteration in the particular genes which it possesses. These changes may show up as an increase in size, more vigor, large plant parts (including fruit), changes in flowering time and date of fruit ripening, differences in flesh texture and keeping quality and variations in many other, perhaps less obvious ways.

Plants with an increased number of chromosomes are known as polyploids, and the degree of polyploidy is in direct proportion to the number of duplications which have taken place in the sets of chromosomes, one from each parent. In the first degree of polyploidy the individual has three sets, and in the next step, four sets. The normal plants are spoken of as diploids, while these polyploids are known as triploids and tetraploids respectively. There may be even higher degrees of polyploidy, but in most cases these show little change from the tetraploid individuals, and, at least in the case of apples, triploids and tetraploids are the high chromosome number types which are of commercial importance.

The importance of polyploidy was first realized commercially in apple production when the question of apple pollination was shown to be of major importance. In this work it was found that certain varieties were very poor pollinators while other varieties were very successful. A further study showed that most of these poor pollinating varieties were natural triploids, that is, possessed three sets of chromosomes. This stimulated the survey of the important apple varieties to determine their chromosome number—work which has continued to the present time. The normal diploid varieties have been found to possess 34 chromosomes, while the triploids have 51 chromosomes.

A perusal of the list of triploid varieties shows that it includes many of the old varieties which originated in Europe during the 19th century and were brought from there to this continent. Older triploids still cultivated include such varieties as the Gravenstein, Nonpareil, Stark, Stayman, Baldwin, King, Rhode Island Greening, etc. Varieties which have originated more recently have, almost without exception, been found to be diploids. One reason for this is that while the old varieties originated as chance seedlings, many of the recent varieties have been the products of controlled hybridization.

When cross-pollinations are made with triploid varieties it has been found, in addition to the fact that they are poor pollinators, that the seedlings are very weak and stunted. They grow poorly, and many die at an early stage in their development. Less than five percent show vigorous growth, and most of these are poor plants if compared with the seedlings of crosses between two diploids (Cover). To cite an example, in the apple seedling plantings at Kentville, there are at present less than 50 trees surviving from a total of more than 3000 progeny of female triploids after about 18 years of growth. Most of these 50 are worthless from the point of tree type alone.

The reason for this seems to be that these seedlings from triploid varieties possess an unbalanced chromosome number—that is, the number is between 34 and 51—they have more than 2 complete sets of chromosomes but less than 3 sets. This chromosome unbalance results in genetic unbalance, and causes an upset in the functioning of the cells of the plant. The tissues develop abnormally, and in many cases the effect causes death of the individual.

In recent years scientists interested in apple breeding have begun to realize that polyploidy may be of considerable practical importance, rather than just a hinderance. Instead of avoiding triploids in a breeding program, polyploidy may offer something which could be of real practical value. Looking back to the 19th century, we see that many of the varieties which originated and were propagated during that period were found to be natural triploids. Since these proved their worth at that time, it seems reasonable to assume that triploids might prove superior at the present time, if we could produce and study them in quantity.

There are two possible ways of obtaining polyploid apples—one is by natural methods, and the other is by artificial methods. The polyploid condition of either type can only be proven by means of chromosome counts with the aid of a microscope. However, there are a number of indirect characteristics which can sometimes be used to select likely individuals for chromosome counting, and thus avoid a great deal of tedious work. Those who are well acquainted with apple varieties will know the characteristics of typical triploids like a Gravenstein or King—large, vigorous trees with a spreading habit, large leaves and flowers, and large fruit. Several other characters which are less obvious, but actually more reliable, are the large size of the anthers and pollen grains, and an increase in the length of the stomata or breathing pores on the undersides of the leaves.

Many, if not all, of these characteristics are found to apply to tetraploids as well as triploids. For example, the type of general tree habit may be seen in the picture below which shows one of the tetraploid seedlings at Kentville.

The artificial production of polyploidy in apples is a difficult problem. So far, though many have tried, no one has yet succeeded in doubling the chromosome number of a particular apple variety. The attempts made have usually involved the drug colchicine which has been used successfully in similar experiments with other kinds of plants. This drug has a specific action on the dividing cells of plant tissue which results in an increase in the chromosome number, but so far has proved ineffective in the rather woody tissue of apple.

Natural polyploids may occur either as seedlings or as what are known as "giant sports." Triploid seedlings may be found to occur at a low rate among the seedlings of diploid varieties, and natural tetraploids may occasionally be found among the seedlings of triploids.

A tetraploid apple seedling at Kentville

These apparently occur as a result of the formation of an egg cell with the unreduced number of chromosomes. Thus a diploid plant may occasionally form an egg cell possessing two sets of chromosomes instead of the normal one set, while a triploid may occasionally form an egg cell with the whole three sets of chromosomes. When these cells are fertilized by a sperm cell containing another complete set of chromosomes, the results are embryos which possess three and four sets respectively, and thus grow into triploid and tetraploid seedlings.

In the seedling plantations at Kentville six of these natural triploid seedlings have been discovered among the progeny of diploids, and three tetraploids among the progeny of triploids. The tetraploids are of particular interest because at the present time, although there are triploid varieties, there are no commercial tetraploid apples. None of the three trees have produced fruit though they are old enough to do so. This may indicate a genetic upset which is undesirable or they may just be slow. One of them blossomed two years ago but did not set any fruit, even though the blossoms were hand pollinated to insure proper pollination. It was used in a cross with McIntosh, and a number of seedlings with this parentage have been planted in the nursery.

Giant sports occur as a change in the vegetative growth of the branch of a tree in such a way that the terminal bud gives rise to tetraploid cells, and any further growth is tetraploid rather than normal diploid tissue. The result is a single section or branch of a tree which produces abnormally large flowers and fruit. These may be distinguished readily from those on the rest of the tree. Several of these giant sports have already been discovered, but they are probably much more numerous than present figures would indicate.

Although tetraploid apples may not prove to be of commercial value themselves, they may be of considerable value in a breeding program. The tetraploid when crossed with diploid varieties such as McIntosh, Cox, Orange, and Northern Spy will produce seedlings which are triploids or nearly so. Because these have three complete sets of chromosomes they will be perfectly viable, and in addition can be expected to show some of the polyploid characteristics of increased vigor and larger fruit. This may prove of particular value in crosses with such varieties as Jonathan, Cox Orange, and Fameuse, where the progeny tend to produce relatively high quality but small fruit.

If tetraploid seedlings or giant sports can be found or produced in considerable numbers, it will allow the plant breeder to open up an entirely new avenue in apple breeding, namely, the production of triploid varieties in quantity. Up to the present this has been impossible, but it is one aspect of apple breeding which offers promising possibilities.

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