Bulletin 435 July, 1940

The Improvement of Naturally Cross-Pollinated Plants by Selection in Self-Fertilized Lines

III. INVESTIGATIONS WITH VEGETATIVELY PROPAGATED FRUITS

DONALD F. JONES AND W. RALPH SINGLETON

Connecticut
Agricultural Experiment Station

CONTENTS

1. A fruit cluster of (P8B x H14B). The evenness in size and shape is derived from the Progressive parent.

The Improvement of Naturally Cross-Pollinated Plants by Selection in Self-Fertilized Lines

III. INVESTIGATIONS WITH VEGETATIVELY PROPAGATED FRUITS

DONALD F. JONES AND W. RALPH SINGLETON

THE heterozygous nature of vegetatively propagated fruits, flowers and vegetables is well known. Seedlings grown from nearly all horticultural varieties are notably variable. Many are weak and unproductive as well as undesirable in other respects. Apples, peaches, grapes, the bush fruits and strawberries have been grown so long by asexual methods of multiplication that they represent a mixture of many diverse germinal elements. The same is true for potatoes and rhubarb, among the vegetables, and dahlias, chrysanthemums, peonies and many other flowers. The history of the origin of most horticultural varieties is a record of continued cross-pollinations made intentionally or by chance. Obtaining a valuable new variety from further cross-pollinations is a lottery in which the chances of securing a winning number are extremely few.

Since inbreeding automatically reduces heterozygous complexes to more nearly homozygous ones and in the process removes the masking effect of hybrid vigor, it is possible to establish lines that are fixed and stable, whose good and bad qualities can be more accurately gauged. Undesirable characters can be eliminated and particular qualities selected and built up. Since this method of concentrating good heredity, followed by crossing to secure the maximum effect of hybrid vigor, has been used so effectively with some of the seed propagated crops, it seems plausible that the same procedure can be used effectively with vegetatively propagated plants.

A preliminary investigation to test this supposition was started in 1923 with strawberries and raspberries. These fruits were selected because they are good seed producers, bear fruit in two or three years from seed, and can be grown in large numbers. The perfect-flowered varieties are easily self-fertilized by enclosing the flower cluster, while in the bud stage, in a small glassine envelope. **No artificial pollination is needed. All varieties used set fruit freely.** When mature the fruits were mashed in dry sand, placed in perforated metal cans and buried in moist soil outdoors until the following spring. In March this sand and seed mixture was spread on the surface of flats containing sterilized soil. Germination was usually prompt. As soon as the seedlings had three or four leaves they were transplanted to other flats and spaced in small squares. When well rooted these squares were cut and planted in shallow furrows in the field during June and July.

The inbred strawberries were set about two feet apart in rows. Runners were pruned off the first year and then allowed to spread after fruiting.

The raspberries were set about six inches apart in cultivated rows the first summer. The plants that survived the first winter were reset the following spring at the usual planting distances. In this way each generation of strawberries required two years and the raspberries three years.

The strawberry varieties selected for self-pollination were Howard (Howard 17 or Premier), Chesapeake, Glen Mary, Marshall and Progressive. Kalicene was used later in some of the crosses but was not inbred. Each of these varieties has valuable characters of plant or fruit. Howard is the leading variety in this section and has productiveness, winter-hardiness, resistance to leaf diseases and a notable adaptability to a wide range of soil and climatic conditions. Chesapeake has unusual firmness and attractiveness of fruit. Glen Mary produces large sized berries and in the past has been one of the most productive varieties in this region. Marshall has desirable flavor and sweetness of fruit. Progressive produces a large number of fruits that are even in size, shape and coloring. It has good fruit quality and is fall bearing. Kalicene is a distinctly different type, mostly *Fragaria chiloensis*, characterized by thick glossy leaves and fruit with very firm flesh.

Three varieties of raspberries were self-fertilized: the Cumberland black, the Ranere red and the Columbian purple. The Cumberland black raspberry is highly susceptible to mosaic. When free from infection it makes a vigorous growth and produces large attractive fruit. The Ranere red is a spring and fall bearing variety, producing bright red fruit of good quality. Columbian is a well known purple variety, productive when free from mosaic and winter killing.

EXPERIMENTS WITH STRAWBERRIES

Results of Inbreeding

The strawberries were self-fertilized for two or three successive generations. All progenies showed a reduction in some characters in each generation. The most noticeable result was the smaller size of plants and fewer runners. Reduced size resulted from fewer crowns, smaller stems and leaves. In many cases the reduction in number of flower clusters and in the number and size of blossoms was more marked even than the reduction in vegetative growth. The number and size of mature fruit were noticeably less in all lines. No yield records were taken but the production of fruit was noted as being reduced to one-half or less in all lines after three generations of selfing. Marked segregation occurred effecting signal difference in size, serration and color of leaf, as well as in size, shape and color of fruit.

Some lines had bluish green leaves, others light green and yellowish green. Some were dull, others bright and glossy. Marked differences appeared in wrinkling and curling of the leaves. In some lines the edges were always turned up as if the plants were suffering from lack of water. Length of leaf stem differed as well as the position of the leaves. Some plants were open with the fruit exposed to the sunlight. In others the leaves were more upright and compact.

Fruit size and color were also variable. A number of lines had a glassy appearance, the surface of the fruit being smooth and shiny. Many shades of red appeared but no other colors were noted. Nearly all of the character differences that distinguish strawberry varieties were to be seen in these inbred lines, in many cases accentuated to a high degree.

All varieties inbred gave about the same results, that is, the progenies of one variety produced about the same range of variation as another. Some resemblance to each parent persisted in a few progenies but it became apparent that strawberry varieties as now grown are so highly heterozygous that the individual characteristics that differentiate strawberry clons are quickly lost by recombination.

Inbred strawberries are much less hardy than the varieties from which they come. It was hoped that the inbred lines could be maintained indefinitely without transplantation but many lines failed to live. Unless the plants are transplanted each year to a new location, it is impossible to keep alive these inbred plants and even then many will fail to survive. In our experiments large numbers were lost by winter-killing, some by leaf diseases and others by root and crown rots. Many lines died during dry spells.

The original plan was to maintain all selected inbred lines used for crossing but after three generations of self-pollination the majority of them had died before it was realized they were so weak and needed special precautions to keep them going. It is essential that young plants be set in new ground every year and provision made for watering them in dry seasons if inbred strawberries are to be kept successfully.

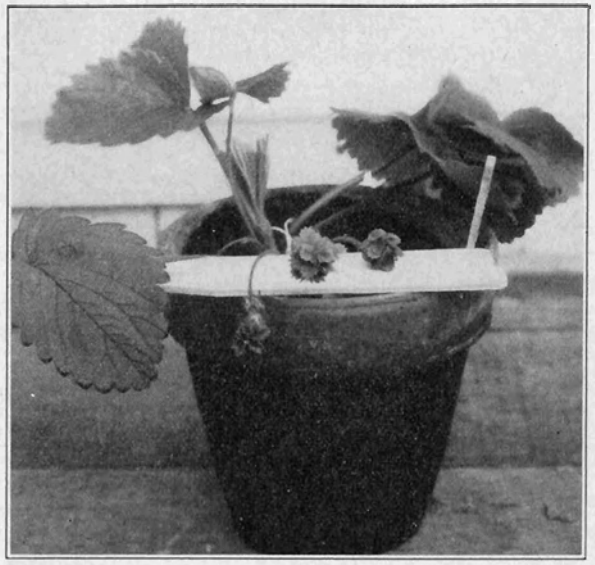
A few abnormalities appeared. One of the most noticeable was an alteration of the flower bud to a proliferating mass of small leaves as shown in Figure 2. Many variations in chlorophyll color appeared, taking the form of yellowish and whitish green leaves. Some were uniformly colored and some streaked and mottled.

In general the behavior of strawberries when self-fertilized follows closely the results obtained with maize. There is about the same amount of reduction in size, viability and reproductive ability. There are fewer clear-cut qualitative differences but fully as much segregation of quantitatively variable characters. Some degree of uniformity was attained after three generations of self-fertilization in a number of lines. Many remained highly variable. The heterozygosity still present was apparent in the differences exhibited in the cross-bred progenies.

All of the self-fertilized progenies had perfect flowers. No entirely pistillate plants were noted although some were much reduced in the number and size of stamens and anthers. Due to the fact that there was an abundance of pollen in the field, all lots had an equal chance of being pollinated. Pollen sterility was not noted, therefore, in the naturally fertilized plants. Some of the bagged flower clusters failed to set seed, an indication of pollen sterility. Some open-pollinated plants also failed to set fruit, due possibly to ovule abortion.

Fall-blooming plants were noted in some of the inbred families of Progressive, although most of these were only spring-blooming, as were all the lines from the other varieties. Crosses of these fall-bearing plants

with spring-blooming lines gave some fall-bearing hybrids. Two of these were grown in comparison with the original Progressive and other named fall-bearing varieties. They were noted as promising in production of good-sized fruit.



2. Inbred strawberry plant showing abnormal fruit stems.

Yellow Leaves

A puzzling abnormality in strawberries is the production of yellow leaves. This condition has appeared in many varieties in various parts of the country and has been noted and described by several investigators. Demaree and Darrow (1937) have given a description and a summary of the known facts concerning it. According to these writers... "the yellowing and variegation of the leaves...varies with the variety, season, and region. Early stages of the disease may show as a faint streaking and mottling of the new leaves with yellow or cream and green. Later the leaves lose more and more of their green color and finally become golden or light yellow or cream color. Each variety has a characteristic yellow and green pattern, some being chiefly mottled, others chiefly streaked. In some varieties the colors are nearly white and green. Badly affected plants become stunted and unproductive depending on how far the yellowing has progressed. Affected plants have never been known to recover, but may live for two or three years, becoming more stunted and yellow each season, and finally dying. Variegated mother plants produce only variegated runner plants. The disease is more conspicuous during early spring and early summer than at any other period of the year." This disease has been called June yellows, yellow leaf, gold leaf and strawberry yellows.

It should not be confused with the yellowing that appears on alkali soils or on soils deficient in manganese and copper. There is a definitely determined virus disease called *xanthosis* that has some of the symptoms of June yellows.

In our trials there has been no spread of the condition from one progeny to another. While it has the appearance of a virus disease, attempts by various investigators to transfer the disease by means of insects, sap injections, or by grafting diseased and healthy runners and roots have failed. From the investigations of Berkeley (1927), Plakidas (1932) and Guba (1933), Demaree and Darrow (1937) state that the evidence shows the disease to be non-infectious and conclude that it must be genetic in origin.

Out of the five varieties inbred, only the Howard variety in one line produced yellow leaves. As this condition was not known by us at that time it may have been overlooked in other lines. Demaree and Darrow (1937) report six selfed lots of seedlings that produced from one to 30 yellow plants. Blakemore selfed produced 30 yellow and 49 green plants. Yellow plants selfed gave a large percentage of yellow seedlings. Some of these showed yellow on the cotyledons.

In our trials no yellow plants were selected for propagation and the lines finally selected for crossing certainly did not show any sign of this condition at any time. Seedlings produced by crossing inbreds have been grown for seven years, transplanting one-year-old plants to new ground each year. The total number grown each year and the number of progenies showing yellow leaves are given in Table 1.

TABLE 1. FREQUENCY OF APPEARANCE OF YELLOW LEAVES IN CROSSBRED STRAWBERRIES

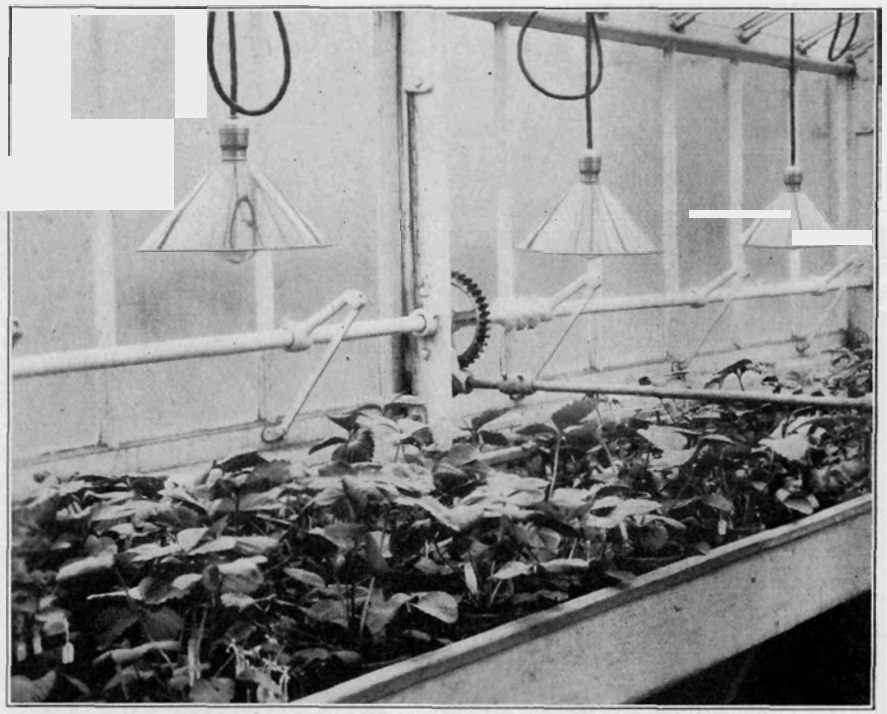
Year Fruited	Number of Crossbred Progenies Grown	Number of Progenies Showing Yellow Leaves
1933	8,845	26
1934	389	8
1935	309	3
1936	53	2
1937	48	3
1938	22	1
1939	15	0

Only selected progenies were grown after the first year. The yellow plants appeared in progenies that previously had been healthy since they were first produced in 1931. Selection was based on desirable plant and fruit characters and total production of fruit. No lots showing any yellow plants were selected for further testing and the progenies that did show yellow did so for the first time in the year stated, some the first year, others not until nine years after the plants were first grown from seed.

All of these abnormal families have in their parentage inbreds out of Howard. This variety has shown yellow plants in many different places. Chesapeake has also shown yellow plants recently. The other varieties inbred have never been reported as showing yellows in commercial fields and no yellows appeared in our self-fertilized lines other than those from Howard. All but four of the crossbred seedlings have either H14 or H44

as one parent. The first generation hybrid of H14 by H44 produced 23 yellow plants out of 24 within two years. The four other crossbred seedlings had either H4, H28, H30 or H40 in their parentage.

There is an inherited basis for the deviation from normal chlorophyll. If there is an infectious agent, the inherited condition is a susceptibility. However no means of transfer is known. Whatever the cause, there is usually a delayed effect such that the condition may not appear until from one to nine years of vegetative propagation and possibly longer. One variety has been reported as producing yellow plants for the first time 50 years after its origin.



3. Strawberries growing in the greenhouse in February for cross-pollination.

The appearance of the abnormality does not follow any simple method of inheritance, at least it is not due to any single dominant or recessive gene. Somatic segregation accompanied by a considerable delay in the appearance of the altered condition may account for this biological puzzle but this does not account for all the plants turning yellow at approximately the same time when these plants are known to come from several mother plants.

A more complete account of this phenomenon is planned for publication elsewhere. The important points, as they affect the production of new varieties of strawberries, are: the inherited nature of the defect

itself or of a susceptibility to a causal agent; the delay in appearance allowing the condition to show up long after a variety is distributed; the widespread appearance of the abnormality possibly affecting all of the descendants of any single plant in time.

Crossing Inbred Strawberries

For the production of crossed seed, runners were rooted in two and one-half-inch pots. As soon as the young plants were well established they were transferred to four-inch pots in good potting soil and placed in a cold frame in late fall. When growth stopped the plants were mulched and allowed to remain outdoors until January. This exposure to low temperatures is necessary for the production of fruit buds. The plants were then brought into the greenhouse and kept for two weeks at a temperature below 50 degrees F. and then raised to about 80 degrees F. The daylight period was extended two or three hours with lights (Figure 3).

4. Two inbred strawberry plants and their first generation hybrid in the center.

Flowers appeared in February and were emasculated by cutting the base of the sepals with a small sharp knife. In this way all of the sepals and petals with their attached stamens were removed as a cap. The anthers were separated from the other parts, spread on a paper and exposed to the air in a warm room for 24 hours, then placed in small vials with a cork stopper. By shaking the vial vigorously, enough pollen adhered to the cork to make several pollinations, the cork being rubbed over the stigmas of the emasculated flowers. This method of preparation and pollination worked equally well for both strawberries and raspberries and has been used successfully with cherries.

From five to ten flowers were pollinated successfully on most plants. They were not bagged as there were no insects flying at that time of year. The growth of the plants and their condition when pollinated is shown in Figure 4. The cross-pollinated fruits ripened from March to the middle of April (Figure 5).

The seeds were handled in the same way as for the inbreds. The seed from each combination was planted separately as soon as the fruit

was ripe. When the young plants had three or four leaves, they were transplanted to flats and set in the field during July and August. The number of plants from each pollination varied greatly. At least five from nearly all parental combinations were set in the field and many had more than 100. Each plant was set 4 by 4 feet and was cultivated both ways. The appearance of the field the following spring is shown in Figure 6. A small clump of plants, from one to ten or more, resulted in most cases. Promising clons were noted while fruiting the first time and marked with a wire stake. The plants were held over and again fruited in the same location the next year. Each square multiplied into many plants and had to be cultivated until late in the fall and trimmed by hand to prevent the runners from mixing. The appearance of the field the second fruiting season is shown in Figure 7.

5. Four individual plants of the first generation hybrid (P8B x H14B). All of the fruit buds were emasculated and pollinated by hand.

The conditions under which the fruit was borne this second year approximated the usual fruiting conditions in a production field where the plants are grown in a matted row. Being cultivated both ways, there were more outside plants bordering on cultivated areas. They were not mulched as it was desired to eliminate all that were not winter hardy.

Most of the selections were made on the basis of their performance in this second fruiting season, noting especially all lots that had been selected the first year. Between each progeny lot, plants of Howard and Chesapeake were set alternately for comparison. Selections were made on the basis of production, fruit characters and plant characters in comparison with these check varieties.

After fruiting, the squares were thinned with a hoe, removing most of the center plants. The field was fertilized and kept cultivated throughout the season, guarding against any mixing of runner plants. The following spring, plants were taken from each selected progeny and set in a row 15 feet long, made up of eight plants, 2.5 feet apart in rows 3.5 feet wide.

6. Crossbred strawberry seedlings in blossom the first year after setting in the field in July.

In all, 8,845 crossbred seedlings were grown. They represented 284 different combinations made up of single crosses of two inbreds, tri-crosses combining three inbreds, double crosses combining four inbreds, crosses of varieties that had not been previously inbred and varietal crosses combined with single crosses and with inbreds. It was planned to have about the same number of plants produced by crossing varieties that had not been inbred as from crosses of inbreds. Due to the better growth of the crosses of inbreds under greenhouse conditions, many more seedlings of these combinations were produced and set in the field. This was probably

due to the varietal plants being started later rather than to any inherent difference.

The crossed plants were much more vigorous and productive than the inbreds. Comparable plants are shown in Figure 4, grown under similar conditions. The hybrids produced a far larger number of blossoms and were more easily worked with under greenhouse conditions since they produced more pollen and more seed from each flower. Therefore the seedlings finally grown for testing were largely double crosses.

7. The same field shown in figure 6 the second year.

In amount of growth, viability and productiveness, there was no noticeable difference in any of the several types of crosses made under field conditions. Those of inbred parentage were no more productive or otherwise more desirable than varietal crosses. It happened that all of the final selections saved for propagation and distribution contained two or more inbreds in their parentage, but this is due, no doubt, to the larger amount of material from which to select. Two single crosses of inbreds, both from the same variety, were noted as promising. Most of the final selections were three-way and double crosses combining inbreds of three or four different varieties.

A single cross (P8B by H14B), combining inbred number 8 out of Progressive with inbred number 14 out of Howard, each selfed twice, is shown in Figure 9 growing in the field. This single cross has the leaf characters of Howard and the fruit shape and color of Progressive. A fruit cluster is shown in Figure 1. Four individual plants of this first

generation hybrid are illustrated in Figure 5. The uniformity in amount of growth, leaf characters and size and shape of fruit is apparent. The fruits are all cross-pollinated and due to the emasculation process have no calices.

8. Crossbred strawberries differ in amount of plant growth and winter hardiness.

These four plants, due to their desirable plant characters and fruitfulness under greenhouse conditions, as well as in the field, were used in combinations with nearly all of the selected plants grown for crossing. Fifteen selections survived the rigorous selection from the original 8,845 progenies fruited first in 1932. Out of these 15, seven had one of these four (P8 by H14) plants as one parent. These first generation hybrids of inbreds not only had desirable characters themselves but had the ability to transmit these characters to their offspring.

The 15 selected lots have the following parentage:

Succession Number	Pedigree Number	Type of Cross
56	[C3B x (P8B x H14B) 2] 1	Tri-cross
62	[C3B x (P8B x H14B) 3] 5	Tri-cross
72	(C3C x H9C) 1	Single cross
80	(C3C x H44C) 4	Single cross
111	[C8C x (P8B x H14B) 4] 2	Tri-cross
118	[(C x M) 10 x (K x H4B) 5] 1	Double cross
123	[(C x M) 10 x (P8B x H14B) 2] 4	Double cross
143	[(C x M) 10 x (P8B x H14B) 4] 1	Double cross
282	[H20B x (G16B x H14B) 1] 1	Tri-cross
348	(H28B x H20B) 1	Single cross
362	(H30C x H20B) 2	Single cross
373	(H30C x M7A) 2	Single cross
431	[(K x H4B) 33 x (P8B x H14B) 2] 2	Double cross
452	(M24A x H9C) 2	Single cross
454	[M24A x (P8B x H14B) 4] 1	Tri-cross

The first letter of each part of the pedigree is an abbreviation of the variety (C=Chesapeake, G=Glen Mary, H=Howard, K=Kalicene, M=Marshall, P=Progressive). The number following the first letter designates the inbred line. The second letter shows the number of generations self-fertilized (A=1, B=2, etc.). The numbers outside the brackets refer to the individual plants in the progeny. Letters standing alone represent the non-inbred variety.

9. An individual plant of the first generation hybrid (P8B x H14B) growing in the field.

Of the 15 selections, six are single crosses, five are combinations of three inbreds and four represent combinations of four parents, partly inbreds and partly varieties. From this list two have been named and described and are now ready for distribution (Conn. Agr. Expt. Sta. Cir. 137, 1939). These are Hebron (111) and Shelton (123). Two more, 143 and 431, are equally good and probably will be named later. All four combine three or four different varieties. Since more combinations of this type were made and many more progenies grown, the conclusion can not be drawn that multiple crosses are more likely to give valuable combinations than single crosses. Furthermore it cannot be stated positively that crosses of inbreds are any more likely to give good results than crosses of varieties. The original plan was to have an equal number of both types of crosses and to compare the number of selected lots in both groups. However, the number finally selected is no greater than is usually obtained from a large series of varietal crosses and it is not known yet whether or not any of these final selections can compete successfully with the original varieties from which they came or with varietal crosses now being made elsewhere.

What is the advantage, if any, of inbreeding strawberries? Considerable time is required and there is much difficulty in maintaining the inbred plants. Could the same time and effort be expended to better advantage in producing more combinations of the varieties as they now exist? Theoretically every combination that can be obtained by inbreeding and crossing can be obtained by crossing without inbreeding. The advantage of uniformity in seed-propagated plants like corn does not hold for vegetatively propagated fruits since uniformity is automatically obtained by the asexual process of reproduction. It has never been proved that crosses of inbreds will give hybrids that are any more vigorous and productive than individual plants in a naturally cross-pollinated variety. If the outstanding individual plants of a corn variety could be propagated vegetatively, there is every reason to believe that they would be equal to any hybrids obtained by crossing inbreds. They might even be superior due to the many more different genetic combinations from which to select.

If there is any advantage in inbreeding strawberries it must come from the opportunity to select for particular characters. There is a good chance that more combinations of the inbreds that have given good results would give even better results when grown in larger numbers. Resistance to disease, winter hardiness, firmness of fruit, bright color can be fixed in self-fertilized lines of strawberries just as heritable characters are established in inbred lines of corn and other naturally cross-pollinated plants.

If inbred strawberries were reduced to a homozygous condition before crossing, it should be possible to cross inbred strawberries and grow only a short row of each cross to test the possibilities of any hybrid. If both inbreds and parents were homozygous, a dozen plants of the hybrid would tell about as well as 100 plants whether the hybrid were good. In this way much effort would be saved in testing large populations of any hybrid, as must be done with varietal crosses.

Unfortunately, many of the best combinations resulting from this program have the H14 inbred which in other combinations has exhibited the yellow leaf condition. This potentiality was not seen in the inbred itself and was not brought out until the crosses had been grown several years. In this case inbreeding did not eliminate this undesirable character. There is reason to believe that the inbreds which did not transmit this abnormal chlorophyll tendency to any of their offspring could be used with some assurance that the trouble would not appear later.

Somatic Segregation

As previously stated, there is some evidence which indicates that the yellow leaf results from some form of somatic segregation. Any heterozygous plant may change as the result of many types of chromosome aberration. All asexually reproduced plants which are being continually renewed from growing points originating from single cells, like the strawberry, may be genetically altered at any time. In nearly every case the change is a degenerative one, the most noticeable result being the uncovering of recessive deleterious factors (Jones 1936). A shift of chromatin into a new position or the doubling of particular sections of chromosomes may conceivably result in increased growth or improvement in some desirable character. Valuable horticultural varieties have undoubtedly originated

in this way, notably the dark red strains of apples. No improved varieties of strawberries are known to have resulted from any change of this kind but the running out of old varieties could be due in some cases to this process. Strawberry nurserymen should compare their varieties with strains from other sources from time to time to make sure that no degenerative changes are being propagated. Nearly all changes of this type weaken the plants and in the course of natural competition are soon eliminated. A systematic search for superior strawberry clons is not justified since the chance of finding any is too remote. But degenerative changes that lessen fruit production or fruit quality without reducing plant-making ability are particularly to be guarded against.

EXPERIMENTS WITH RASPBERRIES

Results of Inbreeding

FIVE lines of the Ranere red raspberry were self-fertilized two generations. All were reduced in amount of growth and showed segregation in plant and fruit characters. All eventually became infected with mosaic and were discarded. A few crosses were made with inbred lines out of Cumberland black raspberry and produced typical purple fruited plants. None of these had sufficient value to be increased.

From the Columbian purple variety, 57 self-fertilized seedlings were grown. Marked segregation in fruit color occurred. Some were nearly red, some true black while the majority were mostly purple resembling the parental type but varying in shade of color and in amount of bloom on fruit. All of these seedlings were less vigorous than the parental variety, killed badly during the winter and soon became so infected with mosaic that no selfed seed was obtained so that inbreeding could not be carried further.

Out of the Cumberland black raspberry, 134 lines were self-fertilized for two generations and two of these were continued to the third generation. These black raspberry inbreds differed markedly from the red and purple lines in that they showed little or no reduction in amount of plant growth and in production of fruit as compared with the original variety. In fact these seedling raspberries seemed more vigorous than the parent and some were clearly more productive. This may have been due to the fact that the seedlings started free from mosaic.

Marked segregation occurred in all plant characters as well as in size and amount of fruit. In the number and size of thorns on the stems and leaf petioles there was marked variation, some being more thorny than the parental variety and some much less; none was entirely free from thorns but there was a good indication that varieties almost entirely thornless could be selected out of a large number of self-fertilized seedlings. When the records were taken many plants were badly stunted by mosaic. Of the healthy plants, 86 were classified for thorniness as follows: more thorny than parental variety, 2; about the same, 54; less thorny, 20; few thorns, 9; almost no thorns, 1. In color of stem, 57 were red, 12 green, 16 greenish red and 1 blue green. Marked segregation occurred in the color of the young leaves on the new sprouts: 59 green, 17 red and 7 light red.

There was much variation in time of flowering, appearance of ripe fruit and in size of berry. All of the healthy plants were productive although the development of the fruit varied widely. In about half of the plants it was well filled, indicating complete fertility of the individual ovules. The others showed partial abortion with consequent imperfect development of the fruit. With these results in mind there can be no doubt about the heterozygous condition prevailing in the original variety of black raspberry. In view of this marked segregation in both qualitative and quantitative characters, it is surprising that the plant growth and fruitfulness held up so well. In the second generation many progenies were as uniform as the original variety and some were even more productive. Two of the most promising lines were again self-fertilized and have been grown for several years in an isolated field with the original variety for comparison in yield and fruit characters. So far both inbred lines have proved to be more productive.

10. A field of black raspberries two generations self-fertilized.

All of the inbreds in the original field, where there were many red raspberries growing that were infected with mosaic, sooner or later became badly diseased and finally died. Some lines remained free from disease symptoms for several years. Whether this is a partial immunity or simply an accidental delayed infection can not be stated. The two selected lines have remained freer from infection than the variety alongside of which they have been grown.

Since raspberries are easily raised from seed, it is possible that this might be a worthwhile nursery practice. With inbred varieties that come reasonably true to seed it would be possible to have plants started entirely free from mosaic. This disease is so destructive to black raspberries that the procedure should be worth trying. Seed would have to be saved from plants grown in an isolated field removed from any kind of raspberry, or the flowers could be bagged to prevent outcrossing. Raspberry seeds must be kept moist and cool to insure proper germination. The seedlings would have to be started in a cold frame or greenhouse, transplanted to the nursery field and grown one or two years until large enough to set in the fruiting field.

It is possible that the plants would be reduced in yield by continued inbreeding. The original third generation self-fertilized plants can be maintained by tip layers in the usual manner and seed from naturally pollinated plants grown in isolation would prevent further inbreeding. The advantage of having plants started free from mosaic may justify this somewhat more expensive and difficult method of propagation.

Crossing Raspberries

The most promising lines of the inbred black raspberries were crossed with a number of varieties of red raspberries. The red varieties used were Ranere, Newman, Erskine Park and Herbert. The first generation hybrid plants were highly variable both in plant growth and in fruit characters. In color of fruit most of the plants were the intermediate, so-called purple, characteristic of this type of fruit. Some were dark red in color and a few were black. The plants started with considerable vigor and a number were selected and transplanted for further testing but all soon became so infected with mosaic that they had to be discarded.

The inbred blackcaps were also crossed with the Columbian purple. This represents a backcross as the Columbian itself is a red and black hybrid. In the offspring there were noted 21 black and 63 purple fruited plants. The purples were highly variable, ranging from the parental purple to almost black. On many plants the fruit was so heavily covered with bloom as to appear dusty. A number of plants were noted to be partially sterile. A few were quite productive and if they could be kept free from mosaic might have promise. Apparently no natural resistance to mosaic was present in this combination.

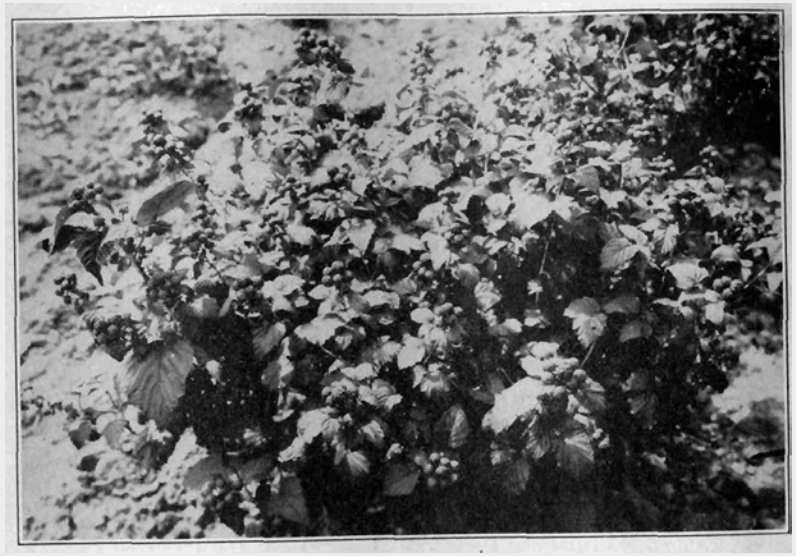
Some of the purple plants originating from the inbred blackcaps crossed by various red varieties were backcrossed with the red parents and with other red varieties. Some attractive and productive plants with bright red fruit were obtained. Most of these produced neither root sprouts nor tip layers and therefore could not be propagated by the ordinary means of vegetative reproduction. Some other means such as root or bud cuttings would have to be used for plants of this kind. Before these were tried the plants were so badly diseased that it seemed useless to propagate from them.

It was expected that some natural resistance to virus disease would appear in some of these hybrids. For that reason the plants were kept in a field in which there were a large number of diseased plants. Since no appreciable immunity appeared, it probably will be necessary, in any future breeding program, to remove diseased plants as fast as they appear and to isolate promising individual plants as quickly as possible.

RASPBERRY AND BLACKBERRY HYBRIDS

A large series of crosses was made between locally grown blackberries and red, purple, and black raspberries. The varieties of blackberries used were Snyder, Eldorado, Blowers and Mercereau. The varieties of red raspberries were Latham, Cuthbert, Newman, La France and Erskine Park. The Columbian purple and Cumberland black were also used. The cross pollinations were made both ways. Only the crosses of Newman, La France, and Erskine Park and the various blackberries produced true hybrids.

The fruit produced by these pollinations contained few seeds and what seeds were produced germinated poorly. Several hundred blackberry-raspberry hybrids were grown. In addition a number of plants were purely parental in type, indicating either contamination of pollen or apogamous development. The hybrid plants were extremely diverse. Many were low, stiff-caned bushes with numerous branching stems. Others had long trailing stems with few branches. The leaves were mostly dark green in color, deeply serrated and in general more like the blackberry in type. Many plants were notably susceptible to rust. Some were entirely free from this disease, winter-hardy and seemed to be exceptionally vigorous. In nearly every case the thorns were larger and more numerous than those of either parent.



11. An individual plant of the Cumberland black raspberry after two generations of self-fertilization.

Nearly all plants were less fruitful than the parental varieties. Some were completely barren and all but a few of the others were partially sterile, many of the drupelets being aborted. Where well-formed fruit was produced, the drupelets failed to adhere like the blackberry and did not part readily from the receptacle like the raspberry. In color the fruit was mostly a dark red verging on black.

Open-pollinated seed from these first generation hybrid plants was grown but no more desirable plants appeared in the second generation. Some of the seedlings were treated with colchicene in the hope that a doubling of chromosomes might make the plants more fruitful. So far no satisfactory results have been forthcoming.

From these preliminary crosses it was thought that plants of the loganberry type might be obtained that would be hardy in the Northeast. It was found that winter hardiness can be secured. So far nearly all of

these plants have been free from virus diseases. In type and amount of growth, satisfactory plants can be obtained from these crosses but their increased thorniness is an undesirable feature. Their most serious fault is the unsatisfactory nature of the fruit. The color is too dark; the flavor is strong and acid. The failure of the drupelets to adhere properly and to detach from the receptacle readily are the greatest difficulties to be overcome if hybrids of this origin are to be useful.

Other investigators have obtained similar results. The prospects of obtaining valuable new fruits from crosses of raspberries and blackberries are not very good. It would seem now more worthwhile to grow seedlings of the loganberry types already available, subjecting them to the conditions prevailing in this part of the country. There is a possibility that some of them would be winter-hardy and as productive in this part of the country as the varieties now grown in the West.

SUMMARY

Five varieties of strawberries were self-fertilized for two and three generations. Marked segregation in plant and fruit characters resulted, accompanied by a reduction in size of plant and fruit and in total number of fruits.

Abnormalities in fruit buds and in chlorophyll formation appeared in different lines.

Some uniformity was attained in the third generation in some lines although many were still segregating.

Crossing inbred lines fully restored size and vigor. Combinations of three and four inbreds in the form of three-way or double crosses gave desirable hybrids that have been named and released for production.

One variety each of red, purple and black raspberries was self-fertilized from one to three generations. Both the red and purple showed marked reduction in growth after inbreeding accompanied by segregation. One variety of black raspberry retained full vigor and productiveness after three generations of self-fertilization. It also segregated for plant colors and fruit form showing that the original variety was heterozygous for many characters.

Since raspberries grown from seed start free from mosaic, it is suggested that true-breeding black raspberries may be grown from seed as a regular nursery practice.

Hybrids of black and red raspberries backcrossed to red varieties produced some promising red-fruited plants with good fruit color. Many of these plants could not be propagated in the usual way.

Neither the inbred or crossbred raspberries showed any improvement in resistance to mosaic and all became so badly infected that they had to be discarded.

Crosses between the three types of raspberries and several varieties of blackberries were grown. Some of the hybrid plants were vigorous in plant growth. All were extremely thorny; only a few were productive of fruit and in these the fruit had undesirable color and flavor. The drupelets failed to adhere properly and did not part from the receptacle easily. Crosses of this type do not offer promise for further improvement.

LITERATURE CITED

Berkeley, G. H. 1927. Strawberry mosaic. Rept. Dom. Bot. Canada, 1927: 128-130.

Demaree, J. B. and Darrow, G. M. 1937. Leaf variegation in strawberries not considered a virus disease. Plant Disease Reporter, Dec. 1, 1937.

Guba, E. F. 1933. Suspected mosaic of strawberry. Phytopathology **23**: 654-661.

Jones, D. F. 1937. Somatic segregation and its relation to atypical growth. Genetics **22**: 484-522.

Plakidas, A. G. 1932. The June yellows of strawberries. Phytopathology **22**: 22.