APPLE BREEDING

INHERITANCE AND STATISTICAL STUDIES ON THE FRUITS OF CROSSBRED SEEDLINGS WITH ANTONOVKA PARENTAGE

by

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LITERATURE REVIEW

Inheritance of Fruit Characters

Investigations in fruit breeding have been in progress for over half a century, but it was not until the rediscovery of Mendel's laws in 1902 that any extensive work in fruit breeding was attempted. It soon became apparent to fruit breeders that controlled crossing gave progenies much superior to those produced by chance seedling selection. As a result fruit breeding studies were so largely expanded that by 1935 Alderman (1) reported 32 state stations and 13 federal stations actively engaged in some phase of the work. With an increase in the number of fruit breeding stations came a corresponding increase in the volume of literature dealing with this subject. The following review covers the more important contributions relative to the genetics and general aspects of the subject.

Many problems confronting the fruit breeder were emphasized by Crandall (5) who pointed out that the only way to obtain information about the breeding behavior of the various varieties was to study the progenies resulting from them. Also concurring in this quite obvious conclusion are

Oskamp (23), Hedrick and Wellington (15). Hedrick and Wellington in summarizing the results of the breeding work conducted at the New York Agricultural Experiment Station, Geneva, New York, previous to 1912 suggest the following conclusions: 1) Crosses did not revert to the prototype as it was believed they might; 2) crosses exhibited very marked hybrid vigor; 3) in color of skin the fruits in which yellow predominates over red seem to be heterozygous for yellow and red. The fruits in which red predominates are either homozygous or heterozygous. The pure yellows are homozygous. 4) From the data it was assumed that white flesh color is a recessive to colored flesh. 5) The inheritance of sweetness and sourness has a tendency to segregate in a simple 3 : 1 ratio, sourness predominating. 6) Jonathan carries only red skin color, and sweetness is a recessive. 7) Northern Spy possesses red and yellow skin factors, but evidently carries no genes for sweetness.

They realized full well the difficulties that would beset the fruit breeders of the future for they say, "The chief difficulties in the application of the Mendelian principles to the breeding of apples are likely to be: a) the determination of various factors, b) possibilities of linkage, c) bringing together of complementary characters which may result in the formation of new ones, d) necessity

of working with large numbers of plants--difficult with apples, and e) finally, disappointments will be frequent, and there is likely to be confusion between simple Mendelian characters and blending factors."

In later investigation Wellington (28) was able to confirm the conclusions set forth in the preceeding paper, namely, that fruit characters seemed to be inherited in a very irregular and unpredictable manner. He did say, however, that accumulated evidence concerning the inheritance of size, form, color, quality and season seemed to indicate that they were transmitted as multiple factors rather than as a single factor difference.

The more recent work of Wilcox and Angelo (29, 30) supports the multiple factor hypothesis as far as the inheritance of color and shape is concerned. There seemed to be some indication, however, that when apples were grouped into two classes, red and no red, the inheritance of red and yellow color was governed by a single factor. This is in accord with the conclusions of Crane and Lawrence (7) who suggested that color is regulated by an allelmorphic series of genes, while flesh characters are determined by several complementary genes.

Further evidence in support of the multiple factor hypothesis has been advanced by Lantz (18, 19) and Vincent and Longley (27). In a study of five progenies of Jonathan

and four of Longfield, Lantz drew attention to the differential influence of parental varieties and parental combinations on the size, shape, color, quality and season of the fruit of the various progenies. Vincent and Longley also arrived at similar conclusions.

Working from a slightly different angle Saunders (25) reports demonstrable indications of a gene for earliness which seems to be carried as a partial dominant in the wild Russian crab, Pyrus baccata. Size gave every indication that it was inherited as an intermediate. None of the crosses which he made between the baccata crab and the cultivated varieties of apples produced any fruit as large as the latter, yet an average increase in weight of 12-14 times that of the wild form was obtained. Continued investigations by Patterson (24) with the material originated by Saunders indicate that crossing Pyrus baccata by standard apple varieties and then intercrossing the F_1's will eventually lead to larger apples, although it still remains a question as to how far the size of fruit can be increased and the plant not rendered too tender for the coldest parts of the Great Plains area.

The inheritance of vigor in both tree and fruit characters has been reported on by several workers. Beaumont (2) in reporting on an analysis of 18 crosses between apple varieties found distinct variations in vigor. He grouped the

progenies according to a common parent, and was thus able to obtain a comparison among the varieties used as the variable parents. He found that when Delicious was used as a parent, whether male or female, the progenies were uniformly more vigorous than those of Okabena, Grimes, Duchess, Jonathan and Wealthy. In contrast to the uniform vigor of the trees of the Delicious progeny the seedling trees of Wealthy were unusually low in vigor. The deficiency of vigor was so apparent in Wealthy seedlings that he assumed this variety carried several factors which produced low vigor.

Variations in the vigor of apple seedlings were recorded by Crandall (5) who noted that "there are a few groups of seedlings that have exhibited an excess of vigor from the beginning: a vigor that called forth comment even at the time of germination. Such are seedlings of the 1911 cross Tolman x Malus Toringo, the 1912 cross Tolman x Malus atrosanguinea and the 1914 cross Rome Beauty x Malus floribunda. Seedlings of certain other groups were so uniformly deficient in vigor that none lived through the first year; as an example, I may cite the 1915 cross Malus Ioensis x Collins with 31 germinations and one survived the season. In still other groups exhibiting debility from the beginning, most seedlings die within a few weeks of germination, but a small minority may linger on for four or more years and,

rarely, may attain fruiting maturity." He ranked the following parental varieties in their ability to transmit vigor to their progeny: first, Rome Beauty, then Grimes Golden and lastly Jonathan.

Lantz (17), Edgecombe (10) and Merrill (21) have found that varieties vary considerably in their ability to transmit vigor. Similar reference is also made by Dorsey (9), Gardner (11) and Macoun (20).

The mode of inheritance of skin color in apples is not yet well understood and still remains an interesting problem. Hedrick and Wellington (15), as already noted, indicate that fruits exhibiting a predominance of yellow are heterozygous for yellow and red, while fruits showing an abundance of red coloring appear to be either heterozygous for red and yellow or homozygous for red. The pure yellows are evidently homozygous. They caution the reader not to take their assumptions as final for they were dealing with quite small populations.

Macoun (20) in an early apple breeding report found that if the parents were highly colored the seedlings would be highly colored, and he adds that "it is interesting to note that of 28 seedlings of Golden Russet none have been russeted, while 78 percent have been green or striped." This seems to indicate, although no direct mention was made of it,

that red coloring acts as a partial dominant, and the factors controlling russeting are carried as recessives.

Wilcox and Angelo (29) found from a detailed study of fruit color inheritance of 1,709 seedling apple trees representing 24 combinations that they had a tendency to group themselves into various catagories. The progenies were catalogued into three groups according to the amount of striping: class one, 97-100 percent striped; class two, 72-83 percent striped; and class three 48-53 percent striped. In order to determine whether the progeny of group two were segregating in a 3 : 1 ratio for stripedness, the short method of determining Chi Square was used. The goodness of fit was approximately .55 indicating that these progenies might be segregating on a 3 : 1 basis. The same test was also applied to seedlings of group three, and a probability of .75 suggested that they were segregating in a 1 : 1 ratio. It was, therefore, concluded that Okabena and Duchess probably carry a single factor for striping, and suggested that Delicious also belonged in this same class. King David and Jonathan were believed to carry additional or polymeric genes for red. They were of the opinion that Winesap and Wolf River fall into this same catagory. In the reciprocal, Grimes x Duchess cross, an interesting variation in color inheritance was noted. When Duchess was used as the female parent there were few blushed

or yellow apples, but when the cross was reversed about half of the progeny were blushed or yellow.

Crane and Lawrence (7) concluded from data obtained from an extensive apple breeding program that "the inheritance and distribution of anthocyanin appears to be controlled by a number of genes. The factors determining its inheritance seem to be dominant, since individuals without anthocyanin give progenies with very little or no anthocyanin, whereas colored forms crossed together commonly segregate individuals without anthocyanin." This conclusion checks fairly well with similar observations made by Lantz (18, 19) and Vincent and Longley (27).

The mode of inheritance of skin color among apples has claimed the interest and attention of several investigators. In spite of the heterozygous nature of the apple some definite information relative to color inheritance has been secured. That Jonathan is essentially homozygous for red coloring has been observed by several writers, namely Lantz (18), Vincent and Longley (27), Wilcox and Angelo (29) and Hedrick and Wellington (15). It is recognized, however, that the inheritance of color, as well as other fruit characters, is extremely complex, and this fact has forced investigators to resort to general conclusions and assumptions.

Crane and Lawrence (7) concluded from their review of literature that this complex behavior was probably due to

two causes, "namely, hybridity and an intricate polyploid condition." Darlington and Moffett (8) concluded that in apples the haploid set of 17 chromosomes was composed of two sets of seven with three chromosomes repeated a third time. Table 1 illustrates the chromosome composition as they believe it exists in the apple.

TABLE 1

Ancestral Complement	Haploid n=17	Diploid 2n=34	Triploid 3n=51
A	$A_1A_2A_3$	$A_1A_2A_3A_1A_2A_3$	$A_1A_2A_3A_1A_2A_3A_1A_2A_3$
B	$B_1B_2B_3$	$B_1B_2B_3B_1B_2B_3$	$B_1B_2B_3B_1B_2B_3B_1B_2B_3$
C	$C_1C_2C_3$	$C_1C_2C_3C_1C_2C_3$	$C_1C_2C_3C_1C_2C_3C_1C_2C_3$
D	D_1D_2	D_1D_2 D_1D_2	D_1D_2 D_1D_2 D_1D_2
E	E_1E_2	E_1E_2 E_1E_2	E_1E_2 E_1E_2 E_1E_2
F	F_1F_2	F_1F_2 F_1F_2	F_1F_2 F_1F_2 F_1F_2
G	G_1G_2	G_1G_2 G_1G_2	G_1G_2 G_1G_2 G_1G_2

Crane and Lawrence (7), in interpreting the table by Darlington and Moffett (8), state "since out of a total of 34 chromosomes in the apple there are 18 chromosomes (6 x 3) any one of which is more or less similar to five others, the chances are slightly more than even that a gene will be represented six times or have one to five other genes similar

to or slightly different from itself." The various combinations effected by such an organization would account for the complex range in variations which are present in apple seedlings. Furthermore, as Crane and Lawrence have shown in their work with the tetraploid Primula sinensis and the octaploid Dahlia, there are a number of cumulative and differential factors which govern the same character, and it is quite possible, due to the difficulty in deciding dominance, that a similar situation may exist in the apple.

The inheritance of size, form and season among apple progenies is evidently fully as complex as color inheritance. Wilcox and Angelo (30) working with the inheritance of form reported a tendency toward relative length and away from relative oblateness that was transmitted most consistently by Ben Davis, Delicious, Black Ben Davis and Grimes. In the reverse direction were Jonathan, King David, Patten, Greening, Wealthy and Wolf River. The above mentioned varieties retained their respective positions as far as the inheritance of conic tendencies was concerned.

Macoun (20) found that when the parental varieties were round, the average of the progenies centered about the round category. He also reported similar behavior when size, quality and season were analyzed. It is interesting to note that in analyzing the inheritance of quality virtually none

of the offspring fell into the 'poor' class. Undoubtedly Macoun set the standard of quality too low, for, as general experience indicates, a large percentage of seedlings are discarded on the basis of low quality.

Hedrick and Wellington (15) reported the tendency of Northern Spy progeny to segregate into two distinct size groups, one ranging around three inches in diameter, and the other slightly below 2.5 inches, indicating the possible presence of two different allelomorphic pairs of size genes. They found that the date of maturity of the progeny did not extend, on the average, much more than a month on either side of that of the parents. Relative to maturity they concluded that earliness did not appear to be a recessive character. This observation is entirely in accord with Saunder's conclusion, which was referred to earlier in this review.

Lantz (18, 19) in reporting on the breeding behavior of a group of Jonathan and a group of Longfield crosses suggested that form was transmitted as an intermediate character, while medium and below size appears to be transmitted as a partial dominant when Jonathan was involved. Vincent and Longley (27) reported similar behavior of form and size among their progenies, although they added that Ben Davis seemed to be dominant over Jonathan in its ability to transmit its form when these two varieties were involved in the same cross.

They concluded that there were several factors governing the inheritance of form and size in the parents.

Crane and Lawrence (7) stated in regard to size inheritance: "In all the families we have raised, the mean fruit size of the progeny is smaller than the mean size of their parents, and the results suggest that small size is dominant to large size. The results also indicate that a number of cumulative genes are concerned in the determination of fruit size." Their conclusions regarding the inheritance of maturity check closely with those of other workers, in that when comparatively early ripening varieties have been intercrossed the time of maturity of the offspring is mainly early.

Investigations by Lantz (18, 19) Hedrick and Wellington (15) and Crane and Lawrence (7) on the transmission of quality in apples indicated that this important characteristic was governed by a heterozygous group of multiple factors.

General Considerations Involved in Fruit Breeding

Choice of Parents

The choice of parents is generally recognized as highly important if satisfactory results are to be obtained in fruit breeding. Hayes and Garber (13) made the following

recommendation: "Varieties selected as parents should contain in the highest degree possible the characters desired in the progeny."

Hansen (12) was of the opinion that the intercrossing of heterozygous varieties of apples would not lead to any increase in vigor, since the varieties were already expressing the maximum amount of hybrid vigor possible. He suggested that if homozygous strains could be developed, the breeding of new and improved fruits would proceed at a more rapid pace.

Macoun (20) recognized the importance of selecting the right type of parents for he implied that in order to produce satisfactory varieties of apples it would be necessary to use as parents those varieties which possessed the characteristics desired in the progeny. This was in accord with the work of Lantz (17) who was of the opinion that good varieties of apples could not be produced by using poor varieties as parents.

Although directly concerned with the inheritance of size and maturity among grapes, the conclusions reached by Hedrick and Anthony (14) may be quite applicable to apple breeding. They concluded that a) there was a definite tendency for seedlings to attain approximately the same size as their parents, b) when two early maturing varieties were crossed their progeny were early, c) early x midseason varieties

produced midseason offspring, and d) midseason x midseason varieties gave rise to seedlings of midseason maturity.

Environmental Effects

Fruit breeders in evaluating their materials recognize the effects of external or environmental factors. Michurin (22) reporting upon apple breeding experiments in Russia says of environment: "In general the influence of external factors . . . is so great, that in the majority of cases it subordinates the activity of hereditary transmission of the qualities and characteristics of the plant progenitors."

Not quite as positive was the statement of Tiedjens (26) who, working on the relation of the environment to shape of fruit in Cucumis sativus, found that starvation, delayed pollenation and amount of light were the principle external factors influencing shape. He came to the conclusion that in order to make careful inheritance studies, the maximum and the minimum expressions of factors should be taken rather than the averages.

Hoblyn (16) emphasized the importance of position effect and further cautioned fruit investigators that "once planted many factors may influence the behavior of trees, some of which are unavoidable, while others may be avoided

by constant observation and the greatest care in management of the plantation."

PURPOSE OF INVESTIGATION

Variability between progenies, and within progenies, in tree and in fruit characteristics can be readily observed in the seedling apple orchards of the Iowa Agricultural Experiment Station. Merrill (21) Edgecombe (10) and Bole (3) studied tree variations and showed by their statistical analysis that the differences in the vigor, shape and grade of the trees in the different progenies were due to parental influence.

The purpose of this investigation was to study the fruits produced by 8 progenies of Antonovka to determine 1) whether these variations and differences between the progenies were statistically significant; 2) to determine the breeding value of the various parental varieties involved in these crosses; 3) to examine genetic inheritance of the different fruit characteristics.

These progenies of Antonovka were selected for study because the trees were outstanding in vigor and hardiness, and because these progenies presented an opportunity to study the variations in genetic makeup of the 6 parent varieties used in making the crosses.

EXPERIMENTAL

Materials

The investigation has been divided into two parts. Part one is a study of the inheritance of fruit size of 1398 crossbred apple seedlings, involving 38 parental combinations which are as follows:

Cross	Number Fruited
Antonovka Progenies	
Ant. x Ashton	107
Ant. x Black Oxford	41
Ant. x Delicious	195
Ant. x Jonathan	99
Ant. x King David	67
Ant. x Grimes	16
Grimes x Ant.	43
Jonathan x Ant.	16
	584
Northern Spy Progenies	
N. Spy x Delicious	79
Harrington x N. Spy	34
N.W. Greening x N. Spy	22
Patten 1011 x N. Spy	11

Pewaukee x N. Spy	23
Salome x N. Spy	31
	200

Delicious Progenies

Delicious x Jonathan	13
Antonovka x Delicious	195
Anisim x Delicious	84
N.W. Greening x Delicious	20
N. Spy x Delicious	79
Patten 1000 x Delicious	20
Patten 1011 x Delicious	29
Patten 1015 x Delicious	33
Pewaukee x Delicious	45
Salome x Delicious	13
Black Annette x Delicious	45
Patten 1015 x Delicious	33
Jonathan x Delicious	70
	634

Grimes Progenies

Grimes x Antonovka	43
Grimes x N.W. Greening	20
Grimes x White Pippin	12
Antonovka x Grimes	16

N.W. Greening x Grimes	20
Nelson Sweet x Grimes	26
	137

Jonathan Progenies

Jonathan x Delicious	70
Jonathan x Antonovka	18
Antonovka x Jonathan	99
Delicious x Jonathan	13
Salome x Jonathan	12
	212

N.W. Greening Progenies

N.W. Greening x Delicious	20
N.W. Greening x Harrington	40
N.W. Greening x Grimes	20
Grimes x N.W. Greening	20
N.W. Greening x N. Spy	22
	122

Anisim Progenies

Anisim x Black Oxford	27
Anisim x Delicious	84
Anisim x Black Annette	63
Anisim x Hubbardston	25
	199

Total	2097
Minus duplications	699
Net	1398

Part two is an inheritance study of the fruits of 8 progenies of Antonovka. The characteristics under observation were size, color, form, season and flesh characteristics, which included grain, firmness, texture, juiciness, flavor and quality. The following list includes the crosses and the number of seedling trees of Antonovka parentage that have fruited up to and including 1937.

Cross	No. of trees fruited
Antonovka x Delicious	195
Antonovka x Ashton	107
Antonovka x Jonathan	99
Antonovka x King David	67
Antonovka x Black Oxford	41
Antonovka x Grimes	16
*Grimes x Antonovka	43
Jonathan x Antonovka	18
Total	584

*For all characters except size the reciprocals were combined and treated as a single progeny

The crosses were made during the years 1917 to 1919 inclusive, and the trees were planted in the orchards in the spring of 1924.

Antonovka is an apple of Russian origin. It is one of the hardiest and most productive of the large fruited varieties, and was used as a parent because of the hardiness of the tree. The fruit is above medium to large in size, roundish inclined to conic; the color is a clear, pale greenish-yellow, sometimes with a slight blush; the flesh is pale yellow,

firm, coarse, medium tender, juicy, sprightly subacid, fair quality and the season September. A good culinary apple.

Methods

The data in this paper were obtained from descriptions made by H. L. Lantz during the years 1932 to 1937 inclusive. The fruit description sheets were standardized (see page 76) to insure uniformity of records from year to year and to facilitate summation.

The seedlings concerned in this investigation were planted several years before the present-day methods of field plot technique were in vogue, and the data are not particularly adapted to an analysis of variance. The following facts, however, tend to reduce to a large extent variation that might otherwise be attributed to these seedlings:

1. The entire group of seedlings were planted the same year, 1924, thus reducing variation due to time of planting.
2. Trees of the same cross were set out in a single row, thus practically eliminating position effect, for investigations have shown that soil variations in a single row tend to cancel one another.
3. The trees were all planted exactly the same distance apart, and all received the same treatment as far as spraying, pruning and fertilizing

were concerned.

The seedlings naturally varied as to the age in which they came into bearing, and because of the necessity for ground space, the majority of them were taken out as soon as enough fruit had been harvested to insure an adequate sample (15-20) for descriptive purposes.

It is commonly known that standard apple varieties vary from year to year in the expression of their fruit characteristics. Wilcox and Angelo (29) found that the environment is capable of changing a solid red apple to a highly striped apple from one year to the next, but is not powerful enough to change a solid red apple to a slightly striped apple. Lantz has made similar observations on other characteristics of the apple, and it appears that year to year variations are not great enough to seriously change the results.

All of these facts were taken into consideration in choosing a suitable method of analyzing these data. The method finally selected was a modification of group comparison which involved the standard error of the mean difference. It was selected partly because it was readily adaptable to the data on hand, and partly because it took into account all variance not due to inheritance. The standard error of the mean difference was computed by the formula $\sqrt{(S.E.\ \bar{x})^2 + (S.E.\ \bar{b})^2}$. Wherever the difference of the means in question

between two progenies was at least twice the standard error of the mean difference, the difference was considered genetically significant.

Before this method of comparing averages could be successfully used it was necessary to divide all the characters under consideration into units. These units were then assigned index numbers and the mean, standard deviation and standard error computed. Table 2 (page 28) concerning the analysis of fruit size of the seedlings from the Antonovka x Delicious cross will serve to illustrate the preliminary work involved.

TABLE 2

INDIVIDUAL SIZE RECORD

Antonovka x Delicious

(n = 195)

Fruit Size groups (10 units = $\frac{1}{8}$")		I Index No.	F Frequency	I(F) Product
Large	(3 - 3$\frac{1}{8}$)	5	16	80
Above medium	(2$\frac{7}{8}$ - 3)	4	73	292
Medium	(2$\frac{3}{8}$ - 2$\frac{7}{8}$)	3	59	177
Below medium	(2$\frac{1}{8}$ - 2$\frac{3}{8}$)	2	37	74
Small	(2 - 2$\frac{1}{8}$)	1	10	10
		Total	195	633

Mean = $\frac{S\ (I \cdot F)}{n}$

Sum products = $^{S}\ I \cdot (I \cdot F)$

Sq. products = $\frac{(I \cdot F)^2}{n}$

Sum squares = (Sum prod.)(Sq. prod.)

Standard deviation: $s = \frac{S\ x^2}{\sqrt{n - 1}}$

Where $S\ x^2$ = Sum squares

Standard error = $s/\sqrt{n}$

Index mean 3.246 = 2.55" apple

Sum Prod. 2257

Sq. Prod. 2054.82

Sum Sq. 202.18

s 1.0208

S.E. .0731

PRESENTATION AND DISCUSSION OF MATERIAL

Size Analysis of the Fruits Produced by Crossbred Apple Seedlings

Size is one of the essential fruit characters which make up the components of a satisfactory economic apple variety. A good commercial variety should have an equatorial diameter of at least 2½ inches. An apple variety may be too large in size, but in actual breeding practice the occurrence of oversized apples plays a very minor roll, for as a general rule seedling apples often fail to measure up to the minimum requirements. Seven varieties, Antonovka, Northern Spy, Delicious, Jonathan, Grimes, Northwestern Greening and Anisim, were used in combinations among themselves and with other varieties for a total of 33 different matings.

A careful study has shown that the Antonovka crosses have produced larger apples than most of the other groups of crosses involving common parents. This is shown quite conclusively in table 3* (page 30), which shows a series of comparisons made between the mean index size of all crosses

*In this table and in all similar tables the progenies in the left hand column are to be compared favorably with the other progenies. For example, the mean fruit size of the progeny of Antonovka x Delicious is significantly larger than the mean fruit size of Antonovka x Anisim.

TABLE 3

MEAN FRUIT SIZE OF THE SEEDLINGS OF ANTONOVKA COMPARED WITH THE MEAN FRUIT SIZE OF SEEDLINGS OF DELICIOUS, ANISIM, GRIMES, NORTHWESTERN GREENING AND JONATHAN

Antonovka crosses	Delicious crosses			Anisim crosses		
	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio
	.21	.056	3.75*	1.00	.0457	21.88*

Antonovka crosses	Grimes crosses			N.W. Greening crosses		
	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio
	.49	.0975	5.03*	.50	.1064	4.70*

Antonovka crosses	N. Spy crosses			Jonathan crosses		
	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio
	.18	.079	2.28*	.45	.0766	5.87*

*Significant difference in fruit size

involving Antonovka as a common parent and six other groups which are tied together in a similar fashion. The fruits of the Antonovka group were found to be significantly larger than the fruits of the other six groups when compared to them by means of the standard error of the mean difference. The greatest difference in mean fruit size occurred, as might be expected, when the Antonovka group was compared to the Anisim group. The actual difference between the means of the two groups was a quarter of an inch which gave a ratio value of 21.88 in favor of Antonovka.

By arranging the group means in descending order, from large to small, a relative scale of breeding values was obtained for the seven parental varieties which were used as common parents. Table 4 gives the position of each variety with respect to the mean size of the fruits produced.

TABLE 4

RELATIVE VALUE OF VARIETIES USED AS COMMON PARENT AS GOVERNED BY MEAN FRUIT SIZE OF THEIR PROGENY

Rank	Variety	Mean Index Size of Progeny	Group
1.	Antonovka	2.94*	1
2.	N. Spy	2.76	2
3.	Delicious	2.73	2
4.	Jonathan	2.49	3
5.	Grimes	2.45	3
6.	N.W. Greening	2.44	3
7.	Anisim	1.94	4

*Significantly larger than groups 2, 3 and 4

On a basis of significance as to the inheritance of mean fruit size the table is peculiar in several respects. The parent varieties apparently fall into four distinct genetic groups. Antonovka is in the first group, Northern Spy and Delicious are in the second group, Jonathan, Grimes and Northwestern Greening make up the third group and Anisim is by itself in the fourth group. Each group was compared to the one next to it and in every instance the difference in mean fruit size was found to be significant; i.e. the seedling fruits of Antonovka were significantly larger than the seedlings of the other parent varieties, and Northern Spy and Delicious seedling fruits were significantly larger than the seedling fruits of Jonathan, Grimes, Northwestern Greening and Anisim. Another interesting item is the position of Northwestern Greening with respect to the other varieties. The Northwestern Greening in Iowa is catalogued as an 'above medium' apple--about the same size as Antonovka or Northern Spy, yet the mean of its progenies which was derived from crosses in which it served as a common parent was given a ranking of only six.

None of the seven varieties used as common parents were crossed with exactly the same varieties, so in order to check upon the validity of table 4 comparisons were made between all varieties in the group which were present in crosses involving a common parent. In order to make these comparisons

the seven varieties which are listed in table 4 were transcribed in the same order to table 5 (page 34), and along the top line were listed alphabetically all varieties which were used as the variable parent. The results were most gratifying. Antonovka yielded five direct comparisons, and in every case the progeny of Antonovka was superior in size to the offspring of the variety with which it was compared. Northern Spy compared favorably with Jonathan and Anisim when Delicious was used as a common parent, but was decidedly inferior to Northwestern Greening. Nevertheless, when Northern Spy and Northwestern Greening were compared with Harrington acting as the common parent Northern Spy proved to be the better. Another size reversal occurred between Anisim and Jonathan on Delicious in which Anisim was the favored parent. However, that was the only reversal of any import since the two other reversals were confined to intra-class groups; namely, that Grimes progeny transmitted larger size traits than Jonathan when both were crossed on Antonovka, and Delicious seedling fruits averaged larger than Northern Spy when both were crossed with Northwestern Greening. The evidence on the inheritance of size presented in this table would seem to indicate that, by merely obtaining the mean of a number of crosses involving a common parent and arranging them according to their respective value, a fair prediction of the breeding value of the common parents can be obtained. Several other

TABLE 5

INHERITANCE OF MEAN FRUIT SIZE IN APPLES

Size Ranking	Parental Varieties	Anisim	Antonovka	Black Annette	Black Oxford	Del.	Grimes	Har'ton	Jon.	N. Spy	N.W. Green.	Pat. 1011	Pew.	Salome
							3.19		2.87					
1	Antonovka				3.07	3.25	2.58R		2.89R					
2	Northern Spy					2.96		2.59			2.41	2.73	2.78	2.58
									2.08					
3	Delicious	2.42	3.25	1.67					2.19R	2.96	3.15*	2.69	2.29	2.23
			2.87			2.08								
4	Jonathan		2.89R			2.19R								1.50
			2.58								2.20			
5	Grimes		3.19*R								2.27R			
							2.20							
6	N.W. Greening					3.15*	2.27R	2.28		2.41				
7	Anisim			1.35	1.63	2.42*								

R indicates reciprocal cross

valid comparisons can also be drawn from table 5, but since this paper for the most part is dealing with Antonovka crosses, it was deemed advisable to omit them. There is a strong indication, although no proof, that Antonovka, Northern Spy and Delicious carry factors for large size that are not present or are not able to express themselves in the varieties of classes three and four.

Studies on Seedling Fruits of Antonovka Parentage

Size. A size analysis of the fruits of the Antonovka group furnishes some very interesting material. The frequency distribution of the Antonovka crosses as based on the size classes illustrated in figs 1, 2 and 3 tends to approach a normal curve. This was rather unusual since similar computations of the other groups produced skewed curves with the modes centering around the below medium class. These figures give a graphic comparison of the size of fruit of the seedlings of Northern Spy, Delicious, Jonathan, Grimes, Northwestern Greening and Anisim as compared to the Antonovka seedlings. The graphs demonstrate perhaps more clearly than the tables the genetic position of Antonovka in transmitting large size fruit.

Figures 4 and 5 and tables 6 and 7 (pages 36 and 37) show the distribution and comparison of fruit size of the

individual Antonovka crosses.

TABLE 6

INHERITANCE OF FRUIT SIZE IN ANTONOVKA PROGENIES

Cross	No.	Percent				
		Large	Above Med.	Med.	Below Med.	Small
Ant. x Ashton	107	2.8	18.7	26.2	43.0	9.3
Ant. x Bl. Oxford	41	7.3	29.3	29.3	31.7	2.4
Ant. x Delicious	195	8.2	37.4	30.3	19.0	5.1
Ant. x Jonathan*	116	3.4	24.1	37.9	26.7	8.6
Ant. x King David	65	9.2	15.4	35.3	30.7	12.3
Ant. x Grimes*	59	3.4	13.2	49.1	22.0	11.8

*Includes reciprocal cross

The cross Antonovka x Delicious, while it did not produce the greatest percentage of 'large' apples, threw over 75 percent of its F_1 progeny into the classes medium and above. At the other end of the scale only 47.7 percent of the progeny of the Antonovka x Ashton cross fell within the medium to above medium group. The marked variability between the two crosses indicates that, insofar as these progenies of Antonovka are concerned, Delicious transmitted those factors

TABLE 7

MEAN DIFFERENCES IN FRUIT SIZE OF SIX PROGENIES OF ANTONOVKA

	Ant. x Grimes			Ant. x Bl. Oxf.			Ant. x K. David			Ant. x Jon.			Ant. x Ash.		
	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio
Ant. x Delicious	.06	.2391	.2509	.18	.179	1.005	.37	.1464	2.927*	.38	.1239	3.067*	.62	.12	5.167*
Ant. x Grimes				.12	.2801	.428	.31	.2606	1.189	.32	.2486	1.287	.56	.2476	2.262*
Ant. x Bl. Oxford							.19	.2069	.918	.20	.1916	1.044	.44	.1891	2.327*
Ant. x King David										.01	.1616	.062	.25	.1587	1.575
Ant. x Jonathan													.24	.1382	1.737

*Indicates significant difference in size

which produced larger fruit size than Ashton. Where fruit size is concerned, Delicious proved to be a much better parent than any of the other five varieties with which Antonovka was crossed. In this connection it is important to note that the distribution of the Antonovka x Jonathan and the Antonovka x King David crosses are closely parallel, indicating that apparently both Jonathan and King David carry approximately the same factors for fruit size.

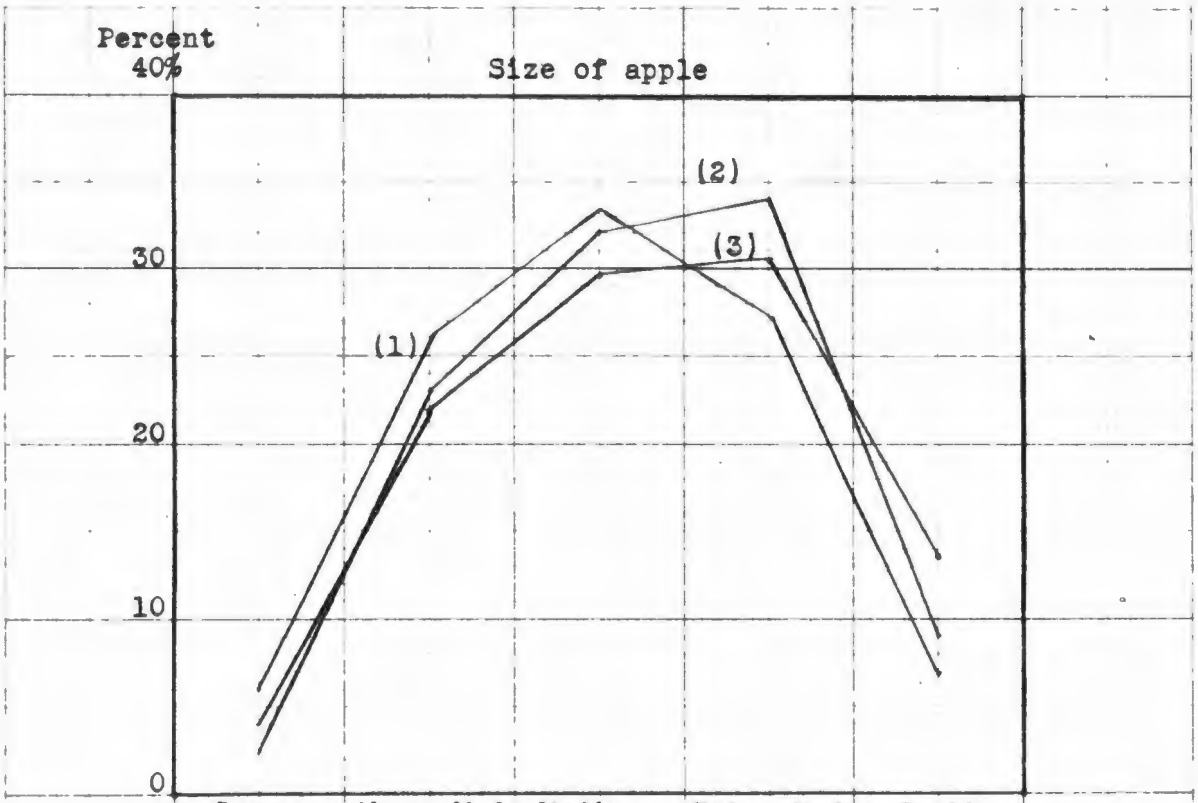


Fig. 1 Comparative Size of Crossbred Apple Seedlings of Antonovka, Northern Spy and Delicious

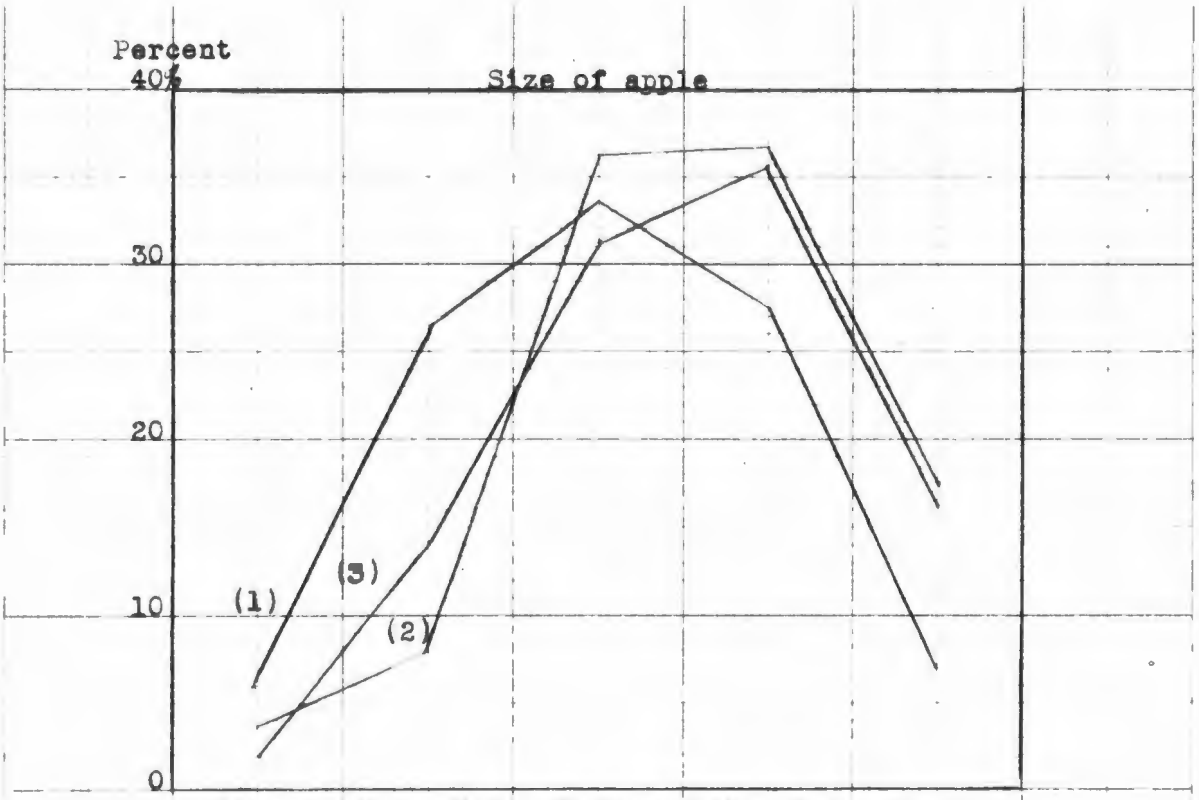


Fig. 2 Comparative Size of Crossbred Apple Seedlings of Antonovka, Grimes and Jonathan.

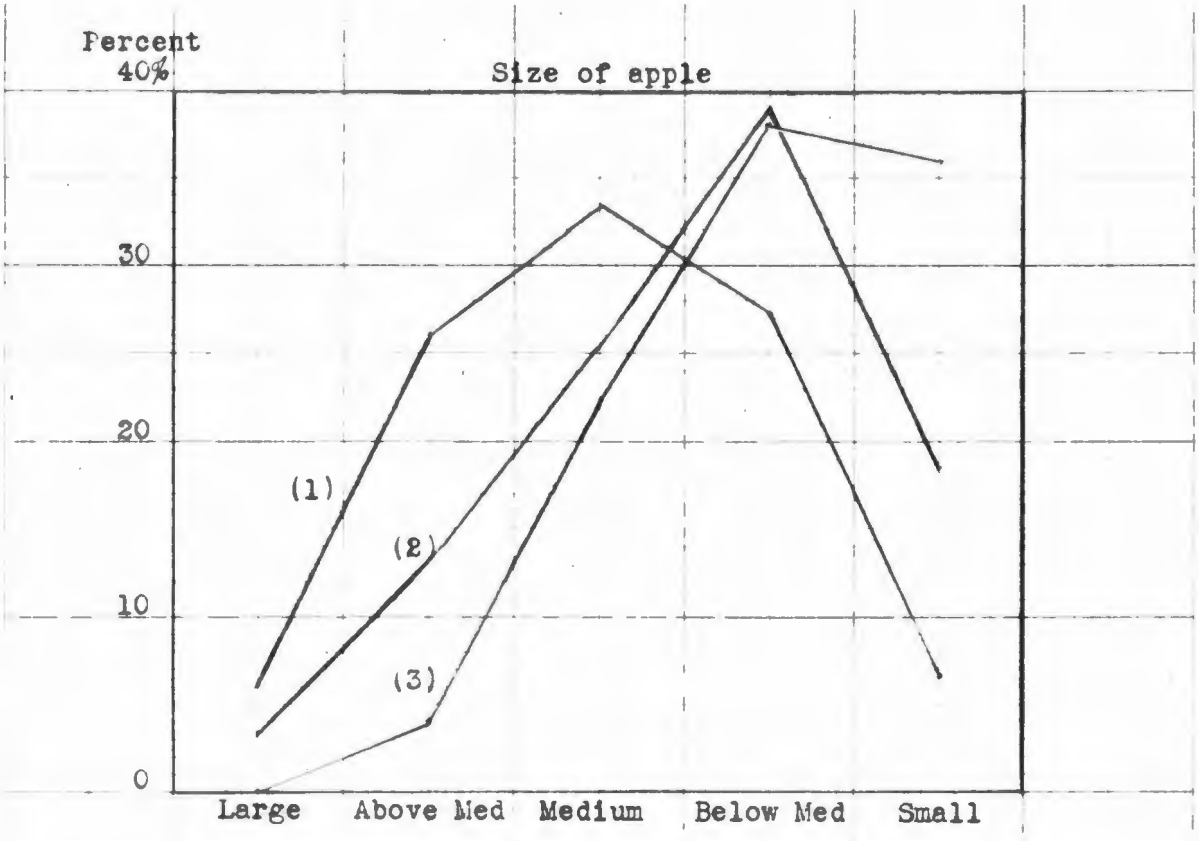
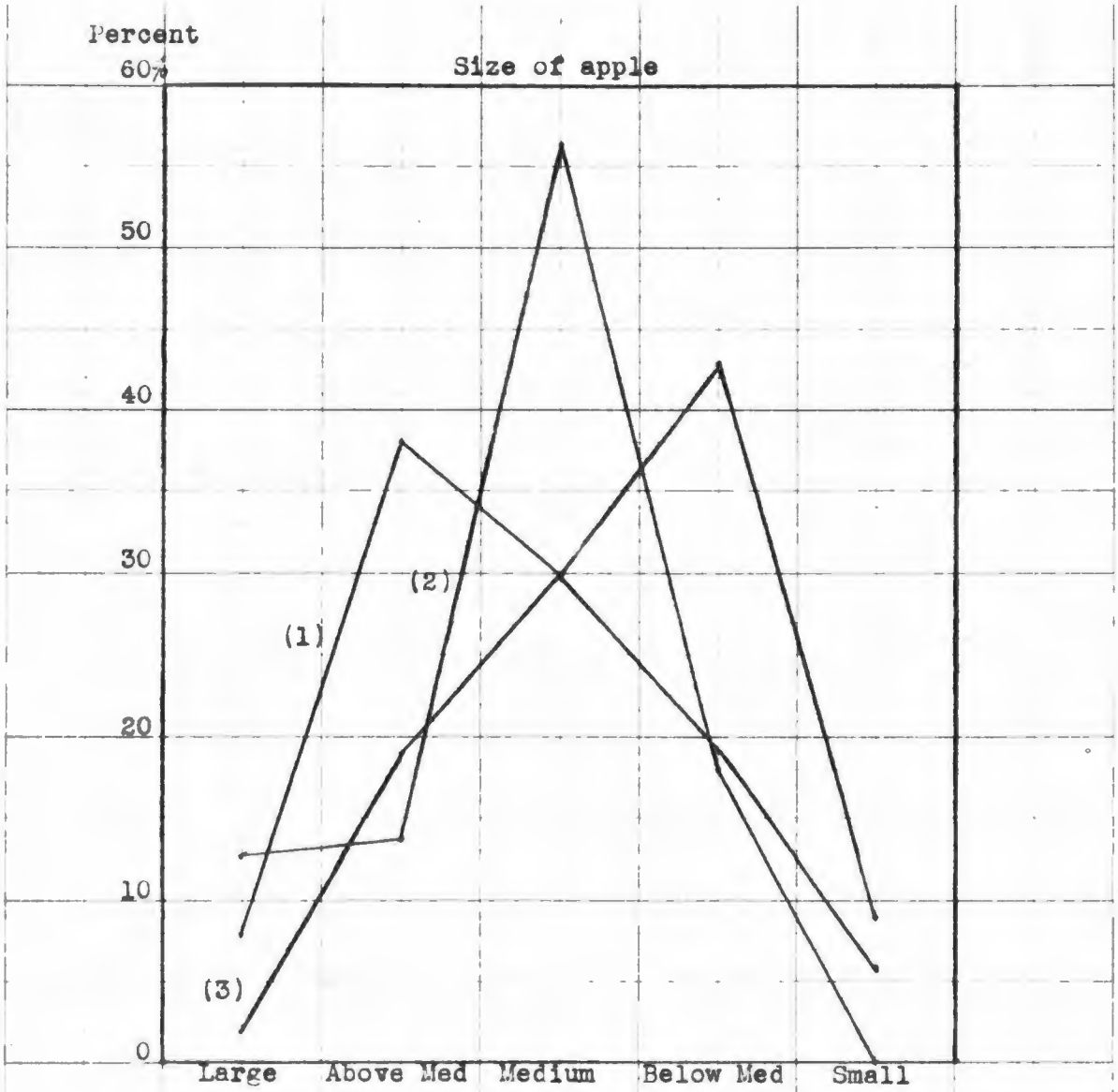


Fig. 3 Comparative Size of Crossbred Apple Seedlings of Antonovka, Northwestern Greening and Anisim

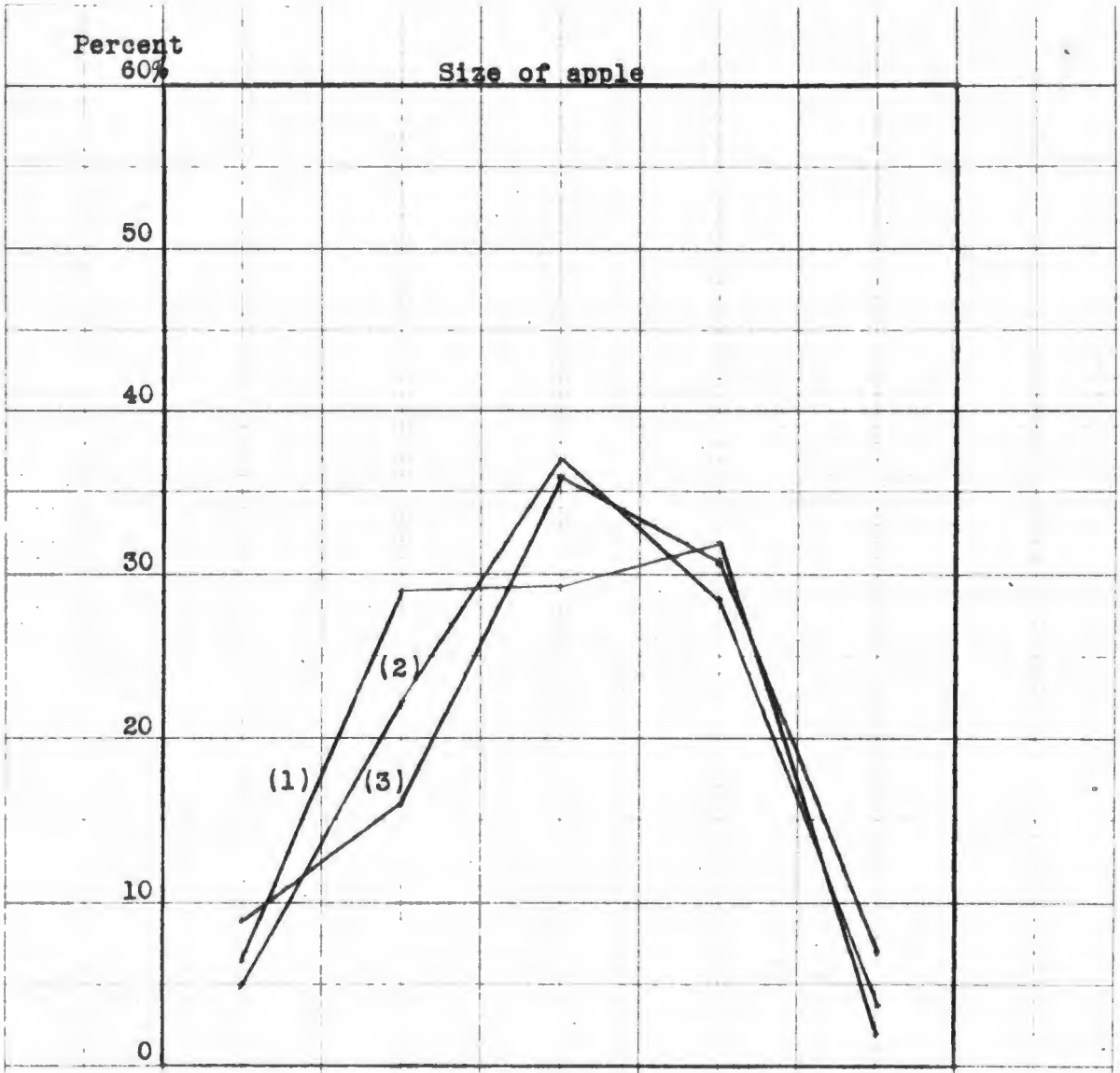


(1) Antonovka x Delicious

(2) Antonovka x Grimes

(3) Antonovka x Ashton

Fig. 4 Comparative Size of Progenies of Antonovka Crosses



(1) Antonovka x Black Oxford

(2) Antonovka x Jonathan

(3) Antonovka x King David

Fig. 5 Comparative Size of Progenies of Antonovka Crosses

Color. An attractive uniform red color is another essential characteristic which an apple variety should possess if it is to command the attention of the commercial fruit grower. Therefore, the inheritance of fruit color is of special interest to determine which parent varieties carry those factors which produce desirable color. The analysis of the Antonovka crosses was limited to a few, although important points. Color groups were chosen as follows: red, striped, blush and no red. Frequency distributions were calculated in percentages for each of the Antonovka crosses, and the results are listed in table 8.

TABLE 8

FRUIT COLOR DISTRIBUTION OF PROGENIES OF ANTONOVKA IN PERCENT

Cross	No.	Red	Striped	Blush	Yellow
Ant. x Ashton	107	16.8	83.2	0.0	0.0
Ant. x Bl. Oxf.	41	22.0	78.0	0.0	0.0
Ant. x Delicious	190	3.0	44.2	9.5	43.1
Ant. x Jonathan	117	23.0	74.6	.9	1.7
Ant. x K. David	65	32.3	66.2	1.5	0.0
Ant. x Grimes	59	1.7	3.4	13.5	81.4

The crosses involving Antonovka and Jonathan and Antonovka and King David gave the highest percentage of red apples, while the cross Antonovka x Grimes and its reciprocal produced almost entirely yellow apples. The interesting observation which may be made from this table, however, is the pronounced segregation of the varieties into three distinct classes or groups as based upon the color distribution of their progeny. The progeny of the four parent varieties, Jonathan, King David, Black Oxford and Ashton, were between 97 and 100 percent red or striped apples; Delicious progeny were divided almost equally between apples which carried red color and no red color, and the Grimes progeny were 95 percent yellow or blushed apples. Obviously there was no significant difference for color between the first group of four varieties.

TABLE 9

COMPARISON OF AMOUNT OF RED COLOR BETWEEN THREE ANTONOVKA PROGENIES

	Antonovka x Grimes			Antonvoka x Del.		
	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio
Antonovka x Jonathan	/1.9	.356	5.34*	/1.1	.356	3.09*
Antonovka x Grimes				- .8	.397	2.02*

/ Indicates redder than Ant. x Grimes and Ant. x Del.
- Indicates yellower than Ant. x Del.
* Indicates significant difference in amount of red color

Table 9 shows, however, that there was a significant difference for red coloring between the progenies of group 1 and the progeny of groups 2 and 3. Furthermore, there was a significant difference between groups 2 and 3.

TABLE 10

RANK ACCORDING TO DEGREE OF RED COLOR DISTRIBUTION AMONG ANTONOVKA PROGENIES

Cross	Rank	Index mean	Group
Ant. x King David	1	3.3	1
Ant. x Jonathan	2	3.2	1
Ant. x Ashton	3	3.2	1
Ant. x Bl. Oxford	4	3.2	1
Ant. x Delicious	5	2.1	2
Ant. x Grimes	6	1.3	3

Unfortunately the scope of this paper does not permit a complete color analysis for the entire group of seedlings, but it should be noted that Wilcox (29) reported that the parental varieties segregated into definite groups with respect to their ability to transmit color to their offspring. He observed that, in reference to stripedness, the progeny segregated into three classes: a) between 95 and 100 percent; b) 78 and 83 percent; c) between 43 and 52 percent.

These percentage groups check fairly well with information derived from the present study of Antonovka crosses, save that there was obtained no group between 78 and 83 percent, but another group which centered around 4 percent was added. The failure of group b to show up in the Antonovka crosses and the appearance of the low percent group is undoubtedly due to the fact that the concern was with only one group of crosses, which involved as one common parent, a yellow apple, while Wilcox was reporting on several groups of crosses.

Genetic implications. The results shown in table 8 were obtained by placing the seedlings into two categories: red color and no red color. In the red-color group all the apples are included which possess solid red color as well as those with lesser amounts of red color. The no-red-color group encompassed all apples showing either a slight blush or an entire lack of red coloring. In the first four crosses which involved four dark red varieties no semblance of a genetic ratio appeared, and the results very strongly indicated that the four paternal varieties, Jonathan, King David, Black Oxford and Ashton, carry homozygous factors for red color. The cross Antonovka x Delicious suggested a single factor difference, and when the Chi Square test of goodness of fit was applied the probability of correctness was over 90 percent. The cross, Antonovka x Grimes, and reciprocal, indicated segregation on a

three factor basis, but when fitted to a Chi Square test for goodness of fit gave a probability of correctness of only 10 percent which is scarcely high enough to warrant the above assumption.

Form. In order to study the form of the Antonovka crosses the fruits were divided into four categories: roundish, conic, oblate and oblong. Frequency distributions were then made for each of the Antonovka crosses, and from these the percentage of fruits falling into each of the four classes was calculated. Border-line cases, where there was some question as to whether a fruit went into the 'roundish' class or the 'conic' class, tend to make these percentages only rough estimates. For this reason it was decided that a more careful analysis would not be worth while.

According to table 11 (page 49) there is a tendency toward conic apples as far as the entire Antonovka group is concerned, but as table 10 shows, when individual crosses are compared marked variations appear. Antonovka x Delicious, as might be expected, threw 42.6 percent of their progeny into the conic class, while Grimes x Antonovka threw 51 percent of its progeny into the roundish class. The tendency toward oblong apples is noticeably lacking, and it may be that oblong is a recessive factor. The data indicate that the phenotype form of fruit, in the parent variety, is a fairly good index

of the genotype of the parent variety. That is, conic apple varieties produce seedling fruits which tend to be conic in general form.

TABLE 11

FORM OF SEEDLING FRUITS OF ANTONOVKA CROSSES

Measure	No. fruits	Percentage
Roundish	162	27.7
Conic	221	37.8
Oblate	143	24.5
Oblong	58	9.9
Total	584	99.9

Flesh characteristics.

Color, firmness, texture and grain. The minor flesh characters in the apple include color, firmness, texture and grain. The overlapping tendency among the four characters limited the analysis to a percentage distribution from which it was possible to make only a few general inferences. It is quite apparent from table 12, column A, (page 50) that surprisingly few apples with pure white flesh were produced by these crosses. Pale yellow flesh color appeared in all crosses. From 70 to 88 percent of all the fruits produced

TABLE 12

DISTRIBUTION OF FLESH CHARACTERISTICS

Percentage

		A Color			B Firmness			C Texture			D Grain		
	No.	Pale Yellow	White	Colored	Firm	Medium	Soft	Tender	Medium	Tough	Fine	Medium	Coarse
Ant. x Ashton	107	85.0	.93	14.0	59.8	38.3	1.9	52.3	36.4	11.2	.93	27.1	63.6
Ant. x Bl. Oxford	41	73.2	0.0	26.8	85.3	12.2	2.4	26.8	41.5	31.7	4.9	36.6	58.5
Ant. x King David	65	75.4	0.0	24.6	58.5	40.0	1.5	52.3	32.3	15.4	13.8	38.5	47.7
Ant. x Jonathan*	116	84.5	.86	14.7	69.0	29.3	1.7	43.1	37.1	19.8	5.2	54.8	40.0
Ant. x Delicious	195	88.2	1.5	10.3	58.5	39.0	2.6	59.0	32.8	9.2	8.7	33.8	57.4
Ant. x Grimes*	59	69.5	1.7	28.8	79.7	20.3	0.0	50.8	35.6	13.4	10.2	47.5	42.4

*Reciprocal indicated

were of pale yellow color. Fruits with colored flesh varied from 10 to 28 percent in the different progenies. The parental varieties appear to transmit flesh color to their progeny in approximately the same proportions, although there is a marked variability between Delicious and Grimes progenies with respect to yellow flesh color. The extent of variation between the several progenies is illustrated when it is noted that 88 percent of the Delicious x Antonovka progeny were pale yellow and only 69 percent of the Antonovka x Grimes and its reciprocal were pale yellow.

The distribution of the firmness of flesh was somewhat more irregular, although the percentages under table 12, column B, seem to indicate that soft flesh is recessive. The cross, Antonovka x Grimes, and the cross, Antonovka x Black Oxford, produced more firm apples among their progenies than did any other mating, indicating that Grimes and Black Oxford carry those factors which produce firm flesh.

The progeny of Antonovka x Delicious were the best textured apples of the entire group, table 12, column C, with only 9 percent falling in the tough category. The poorest progeny from the standpoint of texture was that of the Antonovka x Black Oxford cross in which nearly 32 percent were tough and only 26.8 percent were tender. This differential distribution of texture suggests that the parental varieties

carry at least two independent sets of factors governing inheritance of texture. On the whole, however, the texture rating on the majority of the progeny was good.

The cross producing the greatest number of coarse-fleshed apples was Antonovka x Ashton in which 63.6 percent of the apples were classified as coarse, table 12, column D. It is rather difficult to choose one cross that produced the most satisfactory progeny, insofar as grain of flesh is concerned, but Antonovka x Grimes, Antonovka x Jonathan and Antonovka x King David progenies group themselves fairly well and tend to produce satisfactory percentages of desirable textured apples. The data indicate that tough flesh is inherited as a partial dominant.

The fruits of Antonovka x Delicious were, taken as a whole, somewhat superior from the standpoint of all four characters to the progeny of the other crosses.

Juice. The amount of juiciness in an apple is one of the major points checked by the fruit breeder in his quest for a new variety. The amount and variability of the amount of juice among the Antonovka progeny were measured in much the same manner as size and color. The apples were divided into three groups: juicy, medium and dry. Index numbers were then assigned to the groups and an index mean for each cross was computed. From these data table 13 (page 53) was prepared

showing the ranking of each cross as judged by the average amount of juiciness exhibited by its progeny.

TABLE 13

RANK OF CROSS ACCORDING TO JUICINESS

Cross	Rank	Index mean	Juicy	Med.	Dry	No.
Ant. x Jonathan	1	2.6	65.5	29.3	5.2	116
Ant. x K. David	2	2.43	60.0	30.8	9.2	65
Ant. x Grimes	3	2.34	49.2	35.6	15.3	59
Ant. x Delicious	4	2.29	48.7	31.8	19.5	195
Ant. x Ashton	5	2.23	40.2	43.0	16.8	107
Ant. x Bl. Oxford	6	2.09	29.3	51.2	19.5	41

There is no clear cut segregation, but rather, a gradual graduation in juiciness from Antonovka x Jonathan down to Antonovka x Black Oxford. When progenies were compared among themselves, however, only the cross Antonovka x Jonathan proved to be outstanding as far as juiciness was concerned. The progeny of the Antonovka x King David, however, as table 14 (page 54) shows, were significantly juicier than the progeny of the Antonovka x Black Oxford cross. Table 13 clearly shows the trend of juiciness (computed in percent) of the Antonovka crosses. As in the preceding interpretation

TABLE 14

COMPARISON OF JUICINESS AMONG ANTONOVKA PROGENIES

	Ant. x K. David			Ant. x Grimes			Ant. x Del.			Ant. x Ash.			Ant. x Hl. Oxf.		
	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio
Ant. x Jonathan	.17	.111	1.53	.26	.11	2.36*	.31	.0778	4.0*	.37	.0718	5.15*	.51	.1221	4.18*
Ant. x King David				.09	.135	.67	.14	.1106	1.27	.20	.1182	1.7	.34	.145	2.34*
Ant. x Grimes							.08	.110	.45	.11	.174	.63	.25	.145	1.72
Ant. x Delicious										.06	.088	.68	.20	.122	1.64
Ant. x Ashton													.14	.129	1.09

*Indicates significant difference in juiciness

of grain and texture, juiciness seems to be inherited as an intermediate factor. The lack of clear-cut segregations strongly indicates the presence of several determining factors. Here again it is worthwhile to call attention to the close parallelism existing between Jonathan and King David.

Flavor. Flavor is an important characteristic in determining the value of a variety. It is obviously a character that involves the judgment of the observer to a high degree. For purposes of analysis the progenies of the Antonovka seedlings were divided into four flavor categories: sweet, mild subacid, sprightly and sour; corresponding index numbers of 4,3,2 and 1 were assigned, and the usual procedure of computing the standard error and standard deviation of each of the Antonovka crosses and then running a group comparison among them was carried out for this characteristic. The results of this comparison are shown in table 15 (page 56). The Antonovka x Delicious cross is significantly sweeter than all the other crosses save Antonovka x Grimes. In this test, no apparent tendency to grouping was observed such as was noted with other characters. The averages of the crosses ranged from almost sweet to sprightly. Significant differences in flavor were found between the progenies of nearly all of the crosses. The one notable exception to this was the small (.12) non-significant difference between the progenies of Antonovka x Jonathan and of Antonovka x

TABLE 15

COMPARISON OF FLAVOR AMONG FRUITS OF ANTONOVKA PROGENIES

	Ant. x Grimes			Ant. x Ash.			Ant. x Bl. Oxf.			Ant. x Jon.			Ant. x K. David		
	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio
Ant. x Delicious	.18	.119	1.51	.27	.0899	3.003*	.65	.142	4.58*	.93	.095	9.79*	1.07	.0895	11.96*
Ant. x Grimes				.09	.1284	.70	.47	.169	2.78*	.75	.1322	5.67*	.89	.128	6.95*
Ant. x Ashton							.58	.1506	2.53*	.66	.1072	6.17*	.90	.101	8.91*
Ant. x Bl. Oxford										.28	.154	1.82	.42	.150	2.8 *
Ant. x Jonathan													.14	.1079	1.31

*Indicates significant difference in flavor

King David. This illustration serves to exemplify further the close parallelism which has been apparent between these two varieties. The production of sour fruits appears to behave as a recessive character, for, as table 16 shows, only about 4 percent of all the fruits were classified as sour.

TABLE 16

INHERITANCE OF FRUIT FLAVOR IN ANTONOVKA PROGENIES

		Percent			
Cross	Number fruits	Sweet	Mild acid	Sprightly subacid	Sour
Ant. x Ashton	107	38.3	41.1	20.5	0.0
Ant. x Bl. Oxford	41	21.9	41.4	31.7	4.8
Ant. x Delicious	195	22.0	47.2	29.7	1.0
Ant. x K. David	65	0.0	43.1	52.3	4.61
Ant. x Jonathan*	116	17.2	23.2	53.4	6.0
Ant. x Grimes*	59	18.6	44.0	32.2	5.0

*Includes reciprocal crosses

Quality. Quality in apples is based upon the flesh characteristics--firmness, texture, grain, flavor and juice. This characteristic in apples also encompasses a wide range of variation. In these studies the seedling fruits were place in 4 categories,

i.e. very good, good, fair and poor. In evaluating seedling apple fruits as to quality, the standard was based on a horticultural conception of those flesh characteristics which determine the quality of each seedling. Therefore, seedling fruits which were rated as 'very good' in quality were similar to standard named varieties which are recognized as 'very good' in quality. The mean, standard deviation and standard error were computed and with these statistics comparisons of quality were made between the Antonovka crosses. The information derived from these comparisons and shown in table 17 is interesting.

TABLE 17

RANK ACCORDING TO QUALITY

Cross	Rank	Index mean	Group
Ant. x K. David	1	1.85	1
Ant. x Grimes	2	1.83	1
Ant. x Delicious	3	1.82	1
Ant. x Jonathan	4	1.77	1
Ant. x B. Oxford	5	1.54	2
Ant. x Ashton	6	1.44	2

It is interesting to note that, first, the position of the cross Antonovka x King David is rather surprising for

neither King David nor Antonovka are exceptional in quality, and one would scarcely suspect that a combination of the two varieties would produce apples of a quality superior, although not statistically so, to those derived from a cross involving Delicious. The two distinct groups into which the progeny have segregated is the second item of interest. The quality differences among the progeny of the first four crosses were statistically insignificant, as were the differences between the last two crosses, but a significant difference was found to exist between all the crosses of group one and the two crosses of group two. The close parallelism which seems to exist between Jonathan and King David was not quite as apparent in this instance, although, as table 18 (page 60) shows, there was no significant difference between them in quality.

It is interesting to note on a 4,3,2 and 1 basis, where four equals a very good quality of apple, that the Antonovka progenies are all low in quality. This would seem to suggest that poor quality is partially dominant to good quality. (Table 19, page 61).

TABLE 18

COMPARISON OF QUALITY AMONG ANTONOVKA CROSSES

BASED ON MEAN DIFFERENCES

	Ant. x Grimes			Ant. x Del.			Ant. x Jon.			Ant. x Bl. Oxf.			Ant. x Ash.		
	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio
Ant. x King David	.02	Not sig.		.03	Not sig.		.08	.1348	.5934	.31	.145	2.30*	.41	.127	3.23*
Ant. x Grimes				.01	Not sig.		.06	Not sig.		.29	.1132	2.56*	.39	.084	4.64*
Ant. x Delicious							.05	Not sig.		.28	.099	2.83*	.38	.088	4.32*
Ant. x Jonathan										.28	.126	1.83	.33	.10	3.00*
Ant. x Bl. Oxford													.10	Not sig.	

*Indicates significant difference in quality

TABLE 19

DISTRIBUTION OF FRUIT QUALITY AMONG ANTONOVKA SEEDLINGS

Cross	No.	Percent V. Good	Good	Fair	Poor
Ant. x Ashton	107	0.0	8.4	27.2	64.5
Ant. x Black Oxford	41	0.0	7.3	39.0	53.6
Ant. x King David	65	1.5	26.3	27.7	44.3
Ant. x Jonathan*	116	1.7	20.7	30.1	47.4
Ant. x Delicious	195	3.0	20.5	31.2	45.1
Ant. x Grimes*	59	1.7	30.5	17.0	50.8

* Reciprocal crosses included

Season. The season of maturity of the fruit was treated statistically in the same manner as were the other characteristics studied. The five periods, August, September-October, November-December, January-February, and March and later, were assigned index numbers, 5,4,3,2 and 1 respectively; the mean, standard deviation and standard error were computed and the crosses were compared with one another on the basis of season. The date of ripening is dependent upon a good many external factors, but the overlapping of fruits in the various classes undoubtedly largely cancel one another,

and this method of study was believed to be as free from errors as a more conciliatory one.

The results of the comparisons shown in table 20 (page 63) seem to indicate that when Antonovka, a fall apple, is crossed with a winter apple the progeny will fall into an intermediate season of maturity. Again the almost equal ripening dates of the progenies of Antonovka x Jonathan and Antonovka x King David crosses indicate the close relationship existing between Jonathan and King David. Only one cross out of the six gave any indication that it carried factors for late maturity, and that was the cross Antonovka x Black Oxford, which, according to the results presented in table 20, was significantly later in maturity than any of the other crosses. The variation which existed between time of fruit maturity in these progenies is clearly brought out in table 21 (page 64), where 65.8 of the seedling fruits of Antonovka x Black Oxford ripened after January. In sharp contrast to these seedlings are those of the cross Antonovka x Ashton in which 82.1 percent matured from August through December and only 18 percent ripened after December.

An examination of table 20 shows rather clearly that the season of maturity of the seedling fruits tends to be in the general direction of the parents. For example, the seedling fruits of the Black Oxford cross on the average were

TABLE 20

COMPARISON OF FRUIT MATURITY IN ANTONOVKA CROSSES BASED ON MEAN DIFFERENCE

	Ant. x Del.			Ant. x Jon.			Ant. x K. David			Ant. x Grimes			Ant. x Bl. Oxf.		
	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio	Dif.	S.E.	Ratio
Ant. x Ashton	.03	Not sig.		.15	.125	1.2	.25	.145	1.72	.29	.153	1.9	.78	.169	4.62*
Ant. x Delicious				.12	Not sig.		.22	Not sig.		.26	.142	1.83	.75	.161	4.66*
Ant. x Jonathan							.10	Not sig.		.14	Not sig.		.63	.169	3.73*
Ant. x King David										.04	Not sig.		.53	.184	2.88*
Ant. x Grimes													.49	.19	2.58*

*Indicates significant difference in earliness of maturity

later than those of the other crosses.

TABLE 21

INHERITANCE OF FRUIT MATURITY IN ANTONOVKA PROGENIES

Cross	No.	5 Aug.	4 Sept. Oct.	3 Nov. Dec.	2 Jan. Feb.	1 March and later
Ant. x Ashton	107	9.3	27.1	43.9	16.8	1.8
Ant. x Bl. Oxf.	41	4.9	9.8	19.5	60.9	4.9
Ant. x Del.	195	6.1	42.5	23.1	25.6	2.5
Ant. x K. David	65	4.6	39.2	29.2	36.9	0.0
Ant. x Jon.	116	8.0	27.6	35.3	27.6	1.7
Ant. x Grimes	59	5.1	28.8	25.4	40.6	0.0

The seedling fruits of the Jonathan and King David crosses are much alike in season. Whereas in the case of the Antonovka and Delicious crosses the seedling fruits tended to be somewhat earlier in season than were the fruits of the other progenies. In all progenies very few late keeping apples appeared. Antonovka is an early season apple and the evidence here shows that the season has been influenced quite strongly in that direction in all the progenies. Table 22 (page 65) shows that the mean index of season for the various

progenies has been influenced by season of the respective parents.

TABLE 22

RANK ACCORDING TO EARLINESS

Cross	Rank	Index mean
Ant. x Ashton	1	3.27
Ant. x Delicious	2	3.24
Ant. x Jonathan	3	3.12
Ant. x King David	4	3.02
Ant. x Grimes	5	2.98
Ant. x Bl. Oxford	6	2.49*

*Significantly later than other Antonovka crosses

CONCLUSIONS

The results of this investigation have definitely shown that the parental varieties differ in their genetic makeup. The progenies of Antonovka, for example, were significantly superior in fruit size to the progenies of Northern Spy, Jonathan, Delicious, Northwestern Greening and Anisim. The mean of the variations in fruit characteristics of the progenies of the Antonovka crosses were, for the most part, statistically significant, and indicated that real genetic differences exist between the parental varieties studied.

Genetic Implications

Size. Irregular segregation in progenies of different crosses supports the hypothesis held by the majority of fruit breeders that size of fruit is governed by more than one factor character. It is also apparent that Antonovka reacts in a different manner with different varieties, and it is quite probable, although adaquate data are lacking, that inheritance of size is on a quantitative basis. When Antonovka was used as a common parent in 8 progenies, including 2 reciprocals, fruit size was found to be significantly larger than fruits produced by the progenies of Anisim, Delicious, Jonathan, etc.

In the two reciprocal crosses which were studied, Antonovka with Grimes and Antonovka with Jonathan, no apparent fruit size differences were observed between the Antonovka-Jonathan reciprocal, but the Antonovka-Grimes reciprocal produced a statistically significant fruit size difference. When Antonovka was used as the female parent the mean size of the progeny was over two and one-half inches, but when Grimes served as the female parent the mean size of the seedlings was only two and three-eighths inches. No adequate explanation of this phenomena can be offered with our present knowledge of the genetics of the apple, but in all probability it is due to some underlying genetic factor in Grimes which has as yet not been detected.

It is worthy of record at this time to note that other stations have reported unusual behavior in color of fruit when Grimes reciprocals were studied. Wilcox and Angelo (29) say in relation to color of fruit that "a striking difference was found between the reciprocal matings of Grimes Golden with Oldenburg, that such a higher percentage of red fruits was obtained when Oldenburg was used as the female parent."

Color. Color has been studied perhaps more intensively than other fruit characteristics of the apple, and as yet very little information is available concerning its mode of inheritance. The results of this investigation strongly indicate

that red coloring is practically homozygous in Jonathan, King David, Black Oxford and Ashton. The inheritance of yellow suggests that this color is transmitted as a recessive to red, and that Antonovka carries yellow in a nearly homozygous condition. This assumption is borne out quite conclusively by the cross Antonovka x Grimes in which 95 percent of the progeny were either yellow or slightly blushed.

Judging from the behavior of Delicious this variety is heterozygous for red and yellow and the high probability obtained from the Chi Square test (.90) seems to indicate that there is but a single factor difference governing the inheritance of these two colors insofar as Delicious and Antonovka are concerned.

Form. The inheritance of form among the Antonovka crosses is rather difficult to interpret from a genetical standpoint. The conic form exhibited by Delicious seems to be inherited as a partial dominant over roundness, while the barrel-shaped character of Grimes appears to be a recessive trait. It is quite apparent from the data that several heterozygous factors or genes are responsible for the expression of form among the Antonovka crosses. Interpreting the results in a slightly different manner, it may be stated that in general 'like begets like', i.e., the average form of the progeny resulting from

a cross of two round apples would be round, etc.

Flesh characters.

Color, firmness, texture and grain. The varieties which were crossed with Antonovka transmitted color, firmness, texture and grain on an almost equal basis. In all of the crosses the inheritance of white flesh is undoubtedly transmitted as a recessive to yellow. Soft flesh is without question a recessive trait, while firm flesh appears to be transmitted as a partial dominant over medium flesh. Tender and medium textured flesh is evidently inherited as a dominant over tough flesh, while fine grain is a recessive to medium and coarse-grained flesh.

Juice. Juice was the most variable of the fruit characters which were studied, and because of this it is virtually impossible to draw any inference regarding the specific inheritance of this character. The results indicate quite conclusively that it is governed by several factors which are apparently distributed in a heterozygous condition among the parents. Indications are, however, that juicy apples are more prevalent than the less juicy and dry apples. In this connection it should be pointed out that juiciness in Jonathan is in a more homozygous condition than in any of the other varieties.

Flavor. The inheritance of flavor, like the majority of the

fruit characters, gives every indication that it is transmitted on a multiple factor basis. Delicious and Grimes carry factors for sweetness which do not seem to be present in Jonathan, Black Oxford, King David and Ashton, and judging from Antonovka, which is sprightly subacid, the mild flavor of Delicious and Grimes is transmitted as a partial dominant. Sourness is definitely a recessive trait, while the preponderance of apples inheriting a subacid flavor indicates that this character is intermediate to sweetness.

Quality. Fair to poor quality, according to the results of this investigation, gives every evidence of dominance over good and very good quality. King David, Grimes, Delicious and Jonathan carry approximately the same factors for average quality, while Black Oxford and Ashton transmit fruits of a quality below average. The lack of distinct groups of segregates suggests that quality is also controlled by several genes.

Season. The majority of the genetic considerations pertinent to season were discussed in the previous section and only the more important ones need to be recalled at this time. It is evident that the variations in season are controlled on a multiple factor basis, and that these controlling factors are present in all of the varieties in an extremely heterozygous

condition. No degree of dominance of lateness over earliness could be detected, although Black Oxford gave a slight indication that it possessed partially dominant genes for late maturity.

Practical results. All data which have been derived from fruit breeding material show the apple to be heterozygous for many characteristics. Continuous variation in most of the observed characteristics is believed by a majority of fruit breeders as due to a multiple factor situation in apple varieties. It has been shown that the trees in many progenies may vary from weak to strong growers, from tender to hardy, from drooping to upright in habit of growth, and from early fruiting to late fruiting. Likewise, the fruits may vary from small to large in size, from yellow to red with varying amounts and types of red coloring, from sweet to sour, from poor to very good quality and early to late season. While the variations referred to above are commonly noted in apple progenies, yet parent varieties and parent variety combinations exert a powerful influence insofar as the characteristics of hardiness of the tree and desirability of the fruits produced are concerned.

Studies at this station have shown the Antonovka progenies to be superior in vigor, habit of growth and hardiness of trees. The tree of the Antonovka variety is among the

most hardy of the Russian group of apples, and it has transmitted its hardiness to its progenies regardless of the other parent involved in the cross. The fruit of Antonovka is 'above medium' to 'large' in size, and the seedling fruits of Antonovka likewise tend to be of desirable size. The seedling fruits produced by all of the Antonovka crosses were generally deficient in desirable red color and in quality. However, these studies have shown that the seedling fruits of Antonovka produced by the crosses of Jonathan, King David and Delicious were superior, in all respects, to those produced by the other parent varieties. A number of fruits were found which were much superior to the Antonovka, and the following 9 seedlings were selected for the second test.

1. A533 Antonovka x Ashton 78/14211; large, oblate attractive red, good quality, January-February season
2. A534 Antonovka x Delicious 42/14906; medium size, roundish, solid red, very good quality, January-February season
3. A540 Antonovka x Delicious 146/14210; a handsome pale yellow apple of good quality, November-December season
4. A565 Antonovka x Delicious 132/14906; medium size fruit which resembles Yellow Transparent in form, color and quality, mid-August season. Tree much superior to Yellow Transparent in habit of growth.

5. A566 Antonovka x Delicious 14/14210; above medium size, roundish, yellow, flesh tender with mild subacid flavor, good quality, September season

6. A535 Antonovka x King David 27/14215; above medium size, striped with red, juicy, sprightly, very good, September season

7. A542 Antonovka x King David 101/14215; medium size, roundish, Esopus type of red color, good quality, January-February season

8. A548 Antonovka x Jonathan 32/14213; medium size, red striped, attractive, flesh tender, juicy, rich, mild subacid flavor, very good, oval, mid-August season

9. A543 Jonathan x Antonovka 29/14912; medium size, resembles Jonathan in form, striped red, sprightly subacid, good quality, January-February season

SUMMARY

1. A statistical and inheritance study was made of fruit size of 1398 crossbred seedling apples produced by 33 parental combinations in an effort to determine whether the size differences between progenies of various parental combinations were due to hereditary variations. A similar study was also made of the fruit characteristics of 586 crossbred apple seedlings of Antonovka parentage. The seedling fruits of Antonovka parentage were found to be significantly larger in size than the fruits produced by progenies of other parentage.

2. Jonathan, King David, Ashton and Black Oxford appeared to carry dominant homozygous factors for red skin color. The inheritance of yellow skin color gave every indication that it was transmitted as a recessive. Seedlings of Antonovka x Delicious were catalogued for skin color on the basis of 'red' and 'no red'. There were 47.4 percent yellow and 52.6 percent colored. When the data were subjected to a Chi Square test, a probability of goodness of fit of 95.2 percent strongly indicated that the transmission of red and yellow skin color was governed by a single factor in this cross.

3. The data obtained from this study of other fruit characteristics, such as texture, grain, juice and flavor, suggest that the observed variations are governed by complex genetic factors.

4. There was a very pronounced parallelism between the progeny of Antonovka x Jonathan and Antonovka x King David which appeared in all of the fruit characteristics studied. Hence it is quite possible that Jonathan and King David may possess similar genetic constitutions.

5. The standard error of the mean difference proved to be quite satisfactory in evaluating genetic differences between parental varieties through their progenies.

Parentage _____

Br. Rec. No._____ ...Described by _____

APPLE BREEDING
FRUIT DESCRIPTION

				SIZE					FORM									COLOR																		SKIN				
																		Pattern						Tone												Wax		Bloom		
LOCATION	Br. Rec No.	Date Picked	De-scribed	Large	Above medium	Medium	Below medium	Small	Roundish	Conic	Oblate	Oblong	Oblique	Slightly oblique	Roundish	Roundish	Unlike parents	Yellow	Green	Solid red	½-¾ red	Blushed	Striped	½-¾ striped	1-2 striped	Deep red	Medium	Pale	Roundish	Roundish	Unlike parents	Attractive	Medium	Unattractive	Waxy	Not waxy	Much	Medium	Slight

FLESH																											RECOMMENDATION			
Color			Firmness			Texture			Grain			Juice			Flavor							Quality				Season							
Pale yellow	White	Colored	Firm	Medium	Soft	Tender	Medium	Tough	Fine	Medium	Coarse	Juicy	Medium	Dry	Sweet	Mild acid	Sprightly	Sour	Aromatic	Astringent	Insipid	Very good	Good	Fair	Poor	August	Sept.-Oct.	Nov.-Dec.	Jan.-March	March—later	Dessert	Fruit spots	Bread	Processing

Fig. 6. Apple Breeding Fruit Description Record Blank.

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