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# Maine Agriculthral Expperiment Station 

## ORONO

APRIL 1921

## STUDIES IN ORCHARD MANAGEMENT

CONTENTS
PAGE
Summary ..... 53
Introduction ..... 54
Relation between seed set and fruit development ..... 57
Relation between seedless carpels and weight of fruit ..... 71
Influence of tree vigor on fruit development ..... 72
Effect of seed set on shape of apple ..... 75
Conclusions ..... 80

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## BULLETIN 298

## STUDIES IN ORCHARD MANAGEMENT.

## II. Factors Influencing Fruit Development of the Apple. ${ }^{1}$

By Karl Sax

## SUMMARY

The development of the apple is dependent on food supply and seed content. Both factors are essential from a practical standpoint.

Apples which fall in the "June drop" contain fewer seeds than apples which set and develop. There is a high degree of correlation between seed content and weight of apple for both "drop" and "set" apples at the time of the "June drop."

There is usually little correlation between seed content and size of apple when the fruit is mature. The correlation varies from 0 to .66 for trees of different varieties under different conditions. In the Baldwin trees used the correlation is greater in apples from unthinned trees, presumably due to competition for food supply among many-seeded and few-seeded apples. In case there is an abundant food supply due to thinning of the flowers, there is little or no correlation between seed content and weight of apple. In the Ben Davis trees, however, the relationship is reversed. The vigorous tree and the thinned tree show some correlation between seed content and weight of apple, while there is no significant correlation between seed content and apple weight for the unthinned tree which bore heavily. The variation in different varieties indicates that seed and apple weight relationship found in a single tree or one variety can not be applied to all trees of all varieties.

Abundant food supply alone is not sufficient to cause fruit to set. A Ben Davis tree which bore over 11,000 flowers was thinned to 264 flowers. These flowers were self-pollinated and since the Ben Davis is self-sterile no seeds should result. A.

[^0]large proportion of these flowers should set fruit even without seeds if food supply is the only factor involved. No seedless fruits were produced. Only nine small apples set and these contained seeds probably due to cross pollination. No seedless apples were produced on other trees that were severely thinned. The presence of seeds is necessary for fruit set and development under conditions as found at Highmoor Farm.

Food supply does, however, play an important part in the set of fruit. Thinned trees, with abundant food supply for the remaining blossoms, set a much larger percentage of flowers pollinated than trees not thinned. After the apples are set their subsequent development is largely dependent on food supply.

A Ben Davis tree near the center of a block of only Ben Davis trees set as many seeds per apple when open pollinated as another Ben Davis tree set when cross pollinated by hand. Since the Ben Davis is self sterile the bees must have carried the pollen from trees at least 100 yards away and probably also from a small orchard of many varieties about a quarter of a mile away.

The uniform development of the apple is dependent on the seed content. Apples with several adjacent seedless carpels are usually irregular in shape. The presence of only one seedless carpel in an apple is of little consequence since the seeds in adjacent carpels stimulate sufficient development to insure uniform shape of fruit.

There are a large number of factors which may prevent an apple tree from bearing a good crop even tho it may have an abundant bloom. The formation of seeds is an important factor in the development of the apple. The blossoms must be pollinated with pollen which will grow and cause seeds to set. Most varieties of apples will not set seeds when pollinated with their own pollen. They are self-sterile and must be pollinated with pollen from some other variety. The pollen is carried from one tree to another almost entirely by honey bees. It is obvious that compatible combinations of varieties must be grown in the same vicinity so that the bees can visit different varieties and carry the right kind of pollen to the various trees. If single varieties are planted in large blocks and are isolated from other
varieties there is much less chance for the bees to carry the right kind of pollen and as a result little fruit is set.

Unfavorable weather conditions at blossoming time may prevent the bees from working. Extremely dry weather may wither the floral organs so that fertilization of the ovules can not occur. A frost at blooming time may injure the stigmas so that the pollen cannot grow. These factors are beyond the control of fruit growers.

Not only is proper pollination necessary for the development of fruit, but the general vigor of the tree is an important consideration. A tree which is vigorous and healthy will set more fruit than a tree which is stunted and is not properly nourished. Some varieties have a tendency to bear only in alternate years. In general the set and development of fruit in the apple is dependent on formation of seeds and on the vigor and condition of the tree.

The development of the apple is generally considered to be largely dependent on the number of seeds set. Waite (7) first showed that cross pollination results in more and larger seeds and larger and more uniform fruit. The relation between seed and fruit development has been dealt with by a number of writers. Lewis and Vincent (5) noted that with the increase in weight of the apple there was a proportional increase in weight of seeds. Heinicke (3) states that in general the weight of the fruit is proportional to the number of seeds in the fruit. The size as well as the number of seeds is also a factor in increased size of the fruit. It is recognized by all of these writers that the vigor of the tree and environmental conditions also play an important part in fruit development.

Ewert (I) and others consider the general vigor of the tree of most importance in fruit development. According to Ewert seedless apples grown on a branch with apples containing seeds are smaller because the food is drawn to the seed bearing apples. The seeds are of value because they stimulate an additional flow of sap to the seed bearing apples. In the competition for food the seed bearing apples have the advantage and the seedless fruits fail to develop due to lack of nourishment. Ewert believes that if only seedless apples are present on a branch they will grow as large as normal fruits.

Heinicke (3) finds that the weight and vigor of the fruit spur plays an important part in determining the weight of the fruit. Apples with short thick stems contain fewer seeds than those with long stems. Apples which fall in the "June drop" contain fewer seeds than those which remain on the tree.

There are varieties of apples which are normally seedless, but they are small and of little value. Altho they are seedless they contain the cartilagenous carpels and in this respect have no advantage over the seed bearing varieties. Varieties which normally contain seeds occasionally set seedless fruits due to unusual climatic conditions. In the Imperial Valley of California the frequent appearance of seedless apples is thought to be due to the dry hot weather at blooming time. (6) The reproductive organs of the flowers are withered and fertilization rarely occurs altho the flowers may be properly pollinated by bees. The unusual vigor of the trees causes fruit to set and develop even though no seeds are produced. Injury by frost may prevent fertilization and seed development. Young (8) reports that apples and pears injured by frost may remain on the tree and mature, but such fruits are mis-shapen and more or less seedless.

The shape of the apple is also dependent to some extent on seed formation. When only a few seeds are formed the fruit is often irregular in shape. It is generally known that irregular shaped fruit is often, at least, due to the failure of seeds to develop in several of the carpels. The side of the apple which contains seeds is found to be well developed while the seedless side is small. This correlation is more striking in "June drop" apples than in the mature fruits.

The various factors which effect the set and development of fruit will be considered in the following order. (I) The relation of seed formation to set and development of the apple. (2) The relation between vigor of tree and seed and fruit development. (3) The influence of seed formation on the shape of the fruit.

## Trees Used for These Experiments.

The varieties of trees used include Ben Davis, Baldwin, Golden Russett and Spy. The Ben Davis trees were about twenty-five years old. Tree Nos. 1-29, 2-26, 4-25, and 15-28
were located in the sod half of Ben Davis orchard No. I at Highmoor Farm. All were in good condition and fairly vigorous. Ben Davis tree No. II-II was in the cultivated part of the orchard and was unusually vigorous. Trees I-29 and 2-26 were heavily thinned,-at least $90 \%$ of the flowers were removed. The Baldwin trees were in good condition. Tree No. C-42 was much more vigorous than $\mathrm{C}-45$ as indicated by yield for the last five years. The latter was heavily thinned before crossing work was commenced. The Spy tree used-No. F. I3-is one of the largest and most vigorous trees at Highmoor. Altho it blooms very late it usually produces a good crop.

The following table gives the yield of the above trees for the past 5 years.

TABLE 1.

|  | Yield in lbs. of fruit |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1916 | 1917 | 1918 | 1919 | 1920 |
| Ben Davis 1-29 | 0 | 23 | 14 | 60 | - |
| Ben Davis 2-26 | 20 | 59 | 31 | 148 | - |
| Ben Davis 4-25 | 177 | 134 | 181 | 168 | 262 |
| Ben Davis 11-11 | 159 | 83 | 155 | 221 | 183 |
| Ben Davis 15-28 | 59 | 17 | 31 | 3 | 94 |
| Baldwin C-42 |  | 216 | 253 | 242 | 516 |
| Baldwin C-45 | 4 | 34 | 23 | 133 | 99 |
| Russett D-8 | 405 | 97 | 374 | 143 | 428 |
| Spy F-13 | 863 | 715 | 206 | 705 | 753 |

Most of the data have been obtained from apples resulting from crossing experiments, so in many cases the pollen parent is known. Trees designated open pollinated are those pollinated by bees and of course the source of the pollen is unknown.

## Relation Between Seed Set and Fruit Development.

At the time of the "June drop" it was found that most of the drop apples contained few seeds. In order to determine the relation between seed formation and fruit set ioo "pairs" of apples were picked from the Ben Davis trees on the sod half of the orchard. In each case two apples were borne on a single spur. One apple of each pair selected was about to drop as indicated by the color of the stem. On touching such an apple it fell immediately. These drop apples were usually the smaller
of the pair. It was believed that if large and small apples-or "drop" and "set" apples, were selected from the same spur that each type of apple would have equal advantages so far as food supply is concerned. Any difference in size or set must then be attributed to the individual fruits. It was also desired to get the relation between number of seed set and size of fruit at this stage of development. The total number of seeds and weight of apple in grams was determined for each apple. Table 2 shows the relation between number of seeds and weight for the drop apples and for the set apples.

## TABLE 2.

Ben Davis apples-borne 2 per spur-one of each pair about to fall in "June drop."

DROP APPLES


In these tables the number of seeds is plotted against apple weight. For instance in table 2 for drop apples there are 6 apples, each of which contains one seed and weighs 2 grams,-weight taken to the nearest gram. The average or mean number of seeds for the 100 apples used is 3.52 and the average weight is 3.28 grams. The variability of seed number and weight of apples is indicated by the standard deviation, S. D. In a large population nearly all of the individuals will lie in a range of 6 times the standard deviation. The correlation coefficient, $r$, may range from +1 to 0 to -1 . A correlation of .51 for drop apples in table 2 indicates that in general as the number of seeds increases the weight of apple increases. If the weight of apple was absolutely dependent on seed number the correlation coefficient would be 1 , while if there was no relationship between seed number and weight of apple the correlation would be 0 , and if the apple weight decreased as the number of seeds increased there would be a minus correlation coefficient.


The "drop" apples have an average of 3.52 seeds per apple as compared with 4.94 for the "set" apples. The average weight of the "drop" apples is 3.28 grams as compared with 9.02 grams for the "set" apples. It is evident that the apples which contain many seeds are larger and do not drop as readily as apples with few seeds. The correlation between number of seeds and weight of apple is rather high and practically the same for both classes of apples.

The results with the Ben Davis apples at the time of the "June drop" might lead one to expect the same correlation between seed content and weight in the mature apples. It is generally believed that the size of the apple is largely dependent on the number of seeds it contains. In order to get data on this problem "twin" apples were selected in the same way as in the case of "June drop" apples. Only mature apples which were borne two per spur were used. In most cases the two apples of each pair varied considerably in size. Since they were borne on
the same spur both apples should have equal advantages. The weight and seed content of the large and small members of the "twin" apples is shown in Table 3 .

## TABLE 3.

Mature Ben Davis apples-borne 2 per spur.


LARGE APPLES


Number of Seeds Weiget of Apple

$$
\begin{array}{rr}
\mathrm{M}=4.56 \pm .13 & \mathrm{M}=67.80 \pm 1.28 \\
\text { S.D. }=1.73 \pm .09 & \text { S.D. }=17.13 \pm .90
\end{array}
$$

The average weight of the smaller apples is 49.88 gms. while the larger apples have an average weight of 67.80 gms. Altho there is considerable difference in weight the seed content of both classes of apples is identical. The small apples have as many seeds as the large apples altho the large and small apples were borne in pairs,-each pair on a single spur. The correlation between number of seeds and weight of apple is only $.18 \pm .07$ in each case and can hardly be considered significant. Since the seed number is the same for the rwo classes,-small and large apples, we would not expect much correlation between seed number and weight of apple in either class. The larger apples in the small group have practically the same number of seeds per apple as the smaller apples in the small group.

Casual observation indicated that individual trees vary greatly in regard to seed content and weight of apples. We would expect that size of fruit would vary corsiderably due to difference in vigor of various trees, but the seed content of apples might be expected to remain rather uniform. For infor-

## TABLE 4.

Ben Davis 15-28. Open pollinated. Mature apples.


| Number of Seeds | Weifint of Apple |
| :---: | :---: |
| M $=5.26 \pm .17$ | $\mathrm{M}=50.70 \pm 1.34$ |
| S. D. | $=1.82 \pm .12$ |
|  | $\mathrm{r}=-.12 \pm .09$ |

mation on this question two Ben Davis trees were selected in different parts of the orchard. Ben Davis tree No. 15-28 is located in the sod half of the Orchard No. I at Highmoor Farm. It has never been fertilized and is in a rather unfavorable location, altho it is apparently free from injury or disease. It bore 94 lbs . of fruit in 1920. Tree 11-il , one of the largest and most vigorous trees in the orchard, is located in the most favorable part of the cultivated half of Ben Davis Orchard No. I. It has been fertilized at the rate of 2000 lbs . of fertilizer per acre for several years. In 1920 it bore 183 lbs . of fruit. This tree is located near some trees which were grafted with scions from seedlings in 1916. Many of these grafts blossomed last year and afforded greater opportunity for cross pollination in this portion of the orchard. Tables 4 and 5 show the relation between seed content and weight of apple for these two trees.

TABLE 5.
Ben Davis II-II. Open pollinated. Mature apples.


Number of Seeds Weight of Apple

$$
\begin{array}{rl}
\mathrm{M}=3.32 \pm .15 \\
\text { S.D. }=1.57 \pm .11 & \mathrm{r}=.39 \pm .08
\end{array} \begin{array}{r}
\mathrm{M}=85.60 \pm 2.50 \\
\mathrm{~S} . \mathrm{D} .=26.20 \pm 1.77
\end{array}
$$

The apples from tree $15-28$ contain 5.26 seeds per apple and the average weight is 50.70 gms . The apples from tree II-II contain only 3.32 seeds per apple but the average weight is 85.60 gms . The more vigorous tree bore apples which were larger but contained fewer seeds. Apparently the vigorous tree could set and develop fruit without the stimulus of many seeds while the weaker tree needed the stimulation of many seeds in order to set fruit. It is rather peculiar that there is no significant correlation between seed content and size for the apples on tree 15-28. Since seed formation seems to be necessary for fruit development we might expect a high correlation between seed content and size of apple. Just the reverse is the case with tree II-II. Here we might expect fruit devlopment to be comparatively independent of seed number but the correlation between seed number and weight of apple is $.39 \pm .08$. The variations in seed content and size of apples of these two trees shows the necessity for considering the individuality of different trees in such work.

TABLE 6.


The Ben Davis trees considered so far were all open pollinated and were not thinned. Ben Davis tree No. 2-26 was used
for crossing with several varieties. This tree was heavily thinned before working. The pollen varieties used were McIntosh, Spy and Russett. Altho tree No. 2-26 is located in the sod half of the orchard it is a vigorous tree and is in a favorable location. Table 6 shows the relation between seed set and fruit development.

TABLE 7.
Baldwin C-45.


Number of Seeds
$\mathrm{M}=6.34 \pm .07$ S.D. $=1.36 \pm .05$

Weight of Apple
$\mathrm{M}=162.44 \pm 2.31$ $\mathrm{S} . \mathrm{D}=43.82 \pm 1.63$

The number of seeds per apple is 5.5 I , about the same as was found in tree $15-28$ which was in sod but not thinned. Tree 15-28 is in a solid block of Ben Davis trees and is about 100 yards from the nearest graft or seedling tree. It is about 200 yards from the nearest orchard containing compatible varieties. Altho $15-28$ is so isolated from compatille pollen varieties, it set as many seeds per apple when open pollinated as tree 2-26 set when hand pollinated with pollen from compatible varieties. However, tree $15-28$ might have set even more seeds if hand pollinated.

The relation of seed number and weight of fruit of the Baldwin is about the same as for Ben Davis. Two Baldwin trees were used for crossing work. Tree C-42 is a healthy large tree which has usually produced a good crop. Last year it bore ${ }_{51} 6$ lbs. of fruit. Tree C-45 is not in good condition probably due to winter injury. Altho it is as large as $\mathrm{C}-42$ it has never produced a good crop in the last five years and last year it bore only 99 lbs. of fruit. Baldwin C-42 was not thinned while C-45 was heavily thinned before crossing. Pollen from Ben Davis and Spy was used successfully on Baldwin C-45 and 164 apples were produced. The seed number and weight of these apples afe given in table 7 .

The seed number is 6.34 per apple and the average weight is 162.44 gms . In this case there is no correlation between seed number and weight of apple. Since tree C-45 was heavily thinned the remaining apples should be well nourished and should develop regardless of seed content. Thus no correlation between seed number and size of apple would be expected so long as the seed number is sufficient to stimulate uniform development.

Baldwin C-42 was successfully pollinated with pollen from Ben Davis, Russett, Greening and McIntosh and 100 apples developed. The average number of seeds and weights of apples is shown in Table 8.

The average weight of fruit is only 108.50 gms . as compared with 162.44 gms . for tree C-45. This difference is undoubtedly due to thinning which insured sufficient food for all apples set while apples borne on $\mathrm{C}-42$ had to compete for food. The effect of such competition is clearly shown in difference in relation of seed number and weight of apple. Altho the apples borne on

TABLE 8.
Baldwin C-42.


C-45 have a larger number of seeds per apple there is no correlation between seed content and weight of apple. The apples borne on tree C-42 show a significant degree of correlation between seed content and weight presumably due to competition for food supply. The apples containing many seeds are apparently able to draw more nourishment than apples containing few seeds and since there is not sufficient food for the full development of all apples the size of the apple will depend to some extent on the number of seeds it contains. The weight of apples is more variable for the $\mathrm{C}-45$ than for $\mathrm{C}-42$, but this increased variability is evidently due to causes other than seed content.

Baldwin C-42 when open pollinated produced practically as many seeds per apple as hand pollinated flowers altho the average weight is somewhat less. The seed content and weight of 50 open pollinated apples is shown in table 9.

There is a significant correlation between seed content and weight of fruit and the degree of correlation is nearly the same as in the case of hand pollinated apples on the same tree. Baldwin C-42 is only about 50 yards from the Ben Davis orchard so it is not surprising that it produced as many seeds per apple when open pollinated as when hand pollinated.

TABLE 9.


The varieties Spy and Russett were also studied for the relation between seed content and weight of apples. Spy F-I3 is the largest and most vigorous tree on Highmoor Farm. It has always been a high yielder and last year produced 753 lbs . of fruit. Although it is self-sterile and blossoms after most varieties are thru blooming it usually produces a good crop. The tree is very large and even tho it produced 753 lbs . of fruit last year the apples were not crowded on the tree.

The data on seed content and weight are shown in Table 10.
The average number of seeds per apple, - 3.88 , is much greater than found in any other variety studied. The average weight is 141.18 gms. and the weight distribution is quite vari-

TABLE 10.

able as indicated by the standard deviation of 39.47 . Attention is called to the fact that several of the largest apples have the fewest number of seeds. The correlation between seed content and weight of apple is hardly significant. Since this tree is very vigorous apples can, in many cases at least, develop without the stimulation of many seeds. As will be shown later, however, some seeds are necessary to insure uniform development of the fruit.

The apples of Russett D-8 have an average seed content of 6.54 and the average weight is 70.80 . As indicated in table II the correlation between seed content and weight of apple is rather high.

Russett D-8 is a vigorous tree and bore 428 lbs . of fruit last year. Such a large crop, however, probably caused some
competition among the apples for food supply and therefore the high correlation between seed content and weight of apple. It is also probably that varietal differences exist in regard to the effect of seed content on fruit development.

TABLE 11.
Golden Russett D. 8. Open pollinated. Mature apples.


It is of interest to compare the seed set in apples of different trees and varieties when pollinated with pollen of known origin. Trees of the same variety vary considerably in number of seeds per apple even when pollinated with the same kind of pollen. Different kinds of pollen used on the same mother tree also result in differences in number of seeds per apple. The available data for five trees is presented in Table 12.

The mother trees are arranged in order under the heading "number of seeds." The pollen varieties are listed at the left of the table. In the first column under the heading " $F$." is given the fertility of the cross. The fertility is determined by the

TABLE 12.
Fertility and seed development in various crosses.

$\sigma^{\prime}$
Ben Davis
Spy
Ben Davis
Russett
Greening
McIntosh
Russett
McIntosh
Spy
$\sigma^{\prime}$
McIntosh
Ben Davis
Baldwin
Russett
MeIntosh
percentage of crossed blossoms that develop into mature apples. Thus $74 \%$ of the flowers of Baldwin C-45 which were pollinated with Ben Davis pollen set and developed into mature fruit. Baldwin C-45 when pollinated with Ben Davis set more fruit with more seeds per apple than did Baldwin C-42 when pollinated with Ben Davis pollen. In general there is some correlation between compatibility of varieties and number of seed set. For instance Baldwin C-42 pollinated with Greening resulted in only $1 \%$ of mature fruit and the number of seeds per fruit is only 3.28 . A similar case is found in the cross of Spyof x Baldwin ${ }^{3}$. Here only $6 \%$ of the Spy flowers pollinated developed into mature apples. The average seed content of these apples is only 4.60 as compared with 14.53 when Ben Davis is the pollen parent. These apples altho they contain few seeds are among the largest on the tree. The percentage of fruit set on different trees when the same pollen is used will be considered later.

## The Relation Between Seedless Carpels and Weight of Fruit.

When an apple contains less than five seeds one or more carpels will be seedless. An apple may have more than five seeds and yet have one or more seedless carpels if most of the seeds are produced in one or two carpels. Since as a rule there is little correlation between number of seeds and weight of apple it is possible that so long as each carpel contains a seed that sufficient stimulation is provided for maximum growth. However, there is no sudden drop in apple weight when the seed number falls below five and the line of regression for seed content and apple weight is apparently linear. Therefore the correlation between the number of seedless carpels and apple weight would not be expected to be any greater than the correlation between seed content and weight of apple. Data on the seedless carpels and apple weight was obtained for Baldwin $\mathrm{C}-42$ and $\mathrm{C}-45$ and for Ben Davis 2-26. When the average seed number is considerably over 5 as in case of Spy F-I3 there are of course few seedless carpels and such apples cannot be used for a study of the relation of seedless carpels and apple weight. Data for Baldwin C-42 is given in Table 13.

TABLE 13.


Most of the apples recorded have one or no seedless carpels. The correlation between number of seedless carpels and weight of apple is negative. This means that as the number of seedless carpels increase the weight of the apple decreases. Altho the correlation coefficient is three times as large as its probable error it is not very marked. Similar relations were found in apples from Baldwin C-45.

## The Influence of Vigor of the Tree and Food Supply on Fruit Development.

Two of the main factors in influencing the set and development of apples are numbers of seed set and general vigor of the tree. The vigor of the tree may depend on many factors such as natural fertility of the soil, abundance of plant food applied
as fertilizer, sufficient water supply, pruning and habit of bearing. If a tree, potentially able to produce a good crop, is heavily thinned the remaining apples on the tree should be better nourished and have a much better chance of reaching maturity.

The data previously analyzed gives us some information on this question particularly on the influence of thinning on fruit set. Baldwin C-45 was heavily thinned before crossing and bore 99 lbs. of fruit while Baldwin C-42 was not thinned and bore 516 lbs. of fruit. Both trees were pollinated with pollen from Ben Davis tree No. I-26. From the 144 flowers of Baldwin C-45 pollinated with Ben Davis pollen 107 apples matured. Thus $74 \%$ of the flowers pollinated set fruit when the tree was thinned prior to crossing. Baldwin C-42 which was not thinned set only 26 apples from 264 flowers pollinated. Only 10\% of the flowers set fruit when the tree was not thinned. Baldwin C-42 is the more vigorous of the two trees and has always borne a larger crop, but C-45 set a larger percentage of fruit because it was thinned and the remaining apples were presumably better nourished and did not fall in the "June drop."

Similar data is available for two Ben Davis trees. Tree r-26 was thinned before crossing work was commenced while 4-25 was not thinned. In both Baldwin and Ben Davis trees the thinning was severe,-at least $90 \%$ of the flowers were removed in each case. The data on the Ben Davis tree is shown in the following table. (Table 14).

TABLE 14.

| Female parent |  |  | Thinned | Pollen Parent | Flowers worked | Frult Set | \% Set |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Ben | Davis | 4-25 | No | McIntosh H. O . | 361 | 21 | 5.8 |
| Ben | Davis | 2-26 | Yes | MeIntosh H. O. | 142 | 26 | 18.3 |
| Ben | Davis | 2-26 | Yes | Ben Davis 1-26 | 180 | 0 | 0 |

Tree 2-26 which was thinned set a much higher percentage of fruit than did tree 4-25 which was not thinned. Tree 2-26 is naturally not as vigorous as tree $4-25$ as shown by the yield for the last five years which is recorded in Table I.

It is evident that thinning increases the food supply for the remaining fruits so that they develop and are not lost in the "June drop." If thinning provides additional nourishment for
the remaining fruit, then fruits should develop without the stimulation of seed formation. According to Ewert the vigor of the tree, or in other words sufficient nourishment, is the essential factor in fruit development. One entire branch of tree $2-26$ was thinned and the remaining 180 flowers were pollinated with pollen from Ben Davis i-26. Since Ben Davis is self sterile few or no seeds would be expected to form. Thus only seedless apples would set on the entire branch and there would be no competition for food against seed-containing apples on the same branch. Flowers pollinated with Ben Davis I-26 did set in a few cases but fell off very early-even before the "June drop." It is evident that nutrition alone was not sufficient to set and develop the apples even on the thinned tree.

A more extensive experiment was conducted in order to determine the effect of thinning on fruit development. If nutrition is the most important factor in setting fruit then a tree which is severely thinned should be able to set and develop seedless fruit. Ben Davis tree No. r-29 bore 60 lbs. of fruit in I919 and had an unusually heavy bloom in 1920. The tree bore about II,000 blossoms. All but 264 of these flowers were removed before they were fully opened. The remaining flowers were bagged and self pollinated. Since the Ben Davis is self sterile no seeds would be expected to set. Only 9 fruits developed and all contained seeds. It is possible of course that the Ben Davis is not completely self sterile, but it is more probable that these few flowers developed unnoticed outside of the bags and were cross pollinated by the bees.

We do not know of course how much fruit tree I-29 would have produced if it had been open pollinated by bees. The surrounding trees all bore relatively good crops so that it would be safe to say that tree I-29 was potentially able to produce at least 20 or 30 lbs. of fruit. If seed formation is not necessary for fruit set and development, tree $1-29$ should have set at least 20 or 30 lbs. of fruit. Only 9 apples were produced of an average weight of about 50 grams and all contained seeds. Cases have been cited where seedless fruits have been produced due to climatic conditions and unusual vigor of the trees, but under conditions as found at Highmoor Farm seed formation seems to be necessary for the setting of fruit in practically all cases. Only a few rare exceptions have been found.

## The Effect of Seed Set on the Shape of the Apple.

It is well known that irregularly shaped apples are due to absence of seeds in one or several carpels. The percentage of irregular apples is especially large in apples which fall in the "June drop." These apples contain few seeds and many seedless carpels.

It is necessary to know the structure of the apple in order to understand the influence of seed on fruit development. According to Kraus (4) the apple is composed of five drupe-like carpels surrounded by a fleshy torus or receptacle. The carpels consist not only of the cartilagenous tissue but include part of the fleshy portion of the fruit. The pith and the fleshy portion of the carpels extend to the fibro-vascular bundles which lie in a circle around the carpels. (Fig. 36) The remainder of the


Fig. 36
fleshy portion of the apple is the enlarged receptacle or in other words the enlarged stem. In addition to the ten primary fibrovascular bundles surrounding the carpels there are three main fibro-vascular bundles in each carpel-one at the outer or dorsal side and one in each of the infolded edges of the carpels. The
seeds are attached to the placenta and are supplied with food by the fibrovascular bundles in the infolded edges of the carpels.

When several carpels are seedless the corresponding portion of the apple is usually poorly developed. Such a case is shown in a diagrammatic cross section of the apple in Fig. 36. Two of the five carpels contain seeds and the corresponding side of the apple is larger than the side containing the seedless carpels. The dotted line indicates the dimension of the apple if it were uniformly developed. The fibrovascular bundles are indicated by small circles. The bundles in the infolded edges of the carpels are poorly developed if no seeds are present. The dotted portion is composed of the pith and fleshy tissue of the carpels. An "open cored" variety is shown to emphasize the carpel and seed development.

In order to determine the effect of seedless carpels on shape of fruit two of the five stigmas on each of 142 flowers were cut off. The remaining three stigmas were pollinated with McIntosh polleni. From the 142 flowers thus pollinated 26 apples developed. All were borne on a single branch of Ben Davis tree No. 2-26. Twenty of the twenty-six apples were irregular in shape most of them so misshapen that they were of no commercial value. Only six of the twenty-six apples were of normal shape.

The weight and position of seeds was recorded for each apple. Of the twenty-six apples which matured seven had no seedless carpels, five had only one seedless carpel, eight had two seedless carpels, five had three seedless carpels, and one apple-the largest of the lot, had four seedless carpels. It is evident that when only three stigmas are pollinated it is no guarantee that only three carpels will set seed. The pollen tubes in their growth down the style apparently do not always follow a definite route to the corresponding carpel. Since the styles are united at the base it is possible for a pollen tube to wander in different directions and fertilize one of several ovaries in different carpels.

When an apple contains both seedless and seeded carpels there may be considerable difference in the size of the various segments. The apples resulting from pollinating Ben Davis flowers which had two stigmas removed, contained a large percentage of seedless carpels. The apples were cut in five sections as indicated in Fig. 36. -the dotted lines showing the method

TABLE 15.
Ben Davis $x$ McIntosh．Only 3 stigmas pollinated．

|  | Section Number |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1 |  | 2 |  | 3 |  | 4 |  | 5 |  | To |  |
|  | $\begin{aligned} & \frac{y}{z} \\ & \frac{00}{2} \\ & \frac{1}{2} \end{aligned}$ | $\begin{aligned} & \text { n } \\ & \text { " } \\ & \text { © } \\ & 0 \\ & 0 \end{aligned}$ | 盛 | $\begin{aligned} & \text { Q } \\ & \text { U } \\ & 0 \\ & 0 \\ & 0 \end{aligned}$ | 宸 |  | 号 | 08 0 0 0 0 |  | 等 | 家 | ch |
| 1 | 12 | 1 | 16 | 0 | 26 | 2 | 26 | 2 | 18 | 0 | 98 | 5 |
| 2 | 20 | 0 | 16 | 1 | 18 | 1 | 22 | 1 | 24 | 1 | 100 | 4 |
| 3 | 12 | 0 | 26 | 2 | 16 | 0 | 12 | 0 | 20 | 1 | 86 | 3 |
| 4 | 20 | 2 | 18 | 1 | 18 | 1 | 22 | 1 | 10 | 0 | 88 | 5 |
| 5 | 14 | 1 | 14 | 0 | 16 | 1 | 18 | 2 | 10 | 0 | 72 | 4 |
| 6 | 8 | 0 | 10 । | 0 | 14 | 1 | 14 | 1 | 14 | 2 | 63 | 4 |
| 7 | 14 | 1 | 20 | 1 | 29 | 2 | 12 | 0 | 14 | 1 | 89 | 5 |
| 8 | 24 | 2 | 24 | 1 | 14 | 0 | 10 | 0 | 16 | 2 | 88 | 5 |
| 9 | 20 | 2 | 20 | 2 | 24 | 2 | 26 | 2 | 26 | 1 | 116 | 9 |
| 10 | 26 | 1 | 26 | 1 | 34 | 1 | 26 | 0 | 24 | 0 | 136 | 3 |
| 11 | 22 | 1 | 18 | 0 | 24 | 1 | 24 | 0 | 2.4 | 1 | 112 | 3 |
| 12 | 12 | 3 | 8 | 0 | 8 | 0 | 8 | 0 | 19 | 1 | 40 | 4 |
| 13 | 18 | 0 | 28 | 2 | $3)$ | 2 | $2)$ | 0 | 16 | 0 | 113 | 4 |
| 14 | 12 | 0 | 20 | 1 | 20 | 1 | 18 | 1 | 22 | 2 | 92 | 5 |
| 15 | 16 | 0 | 24 | 1 | 22 | 1 | 27 | 1 | 12 | 0 | 94 | 3 |
| 16 | 23 | 2 | 18 | 0 | 20 | 1 | 20 | 2 | 29 | 1 | 102 | 6 |
| 17 | 12 | 2 | 14 | 0 | 14 | 1 | 12 | 1 | 8 | 0 | 67 | 4 |
| 18 | 20 | 2 | 29 | 1 | 14 | 0 | 23 | 2 | 22 | 1 | 98 | 6 |
| 19 | 26 | 1 | 20 | 1 | 28 | 2 | 29 | 0 | 22 | 1 | 116 | 5 |
| 20 | 22 | 0 | 38 | 2 | 38 | 1 | 22 | 0 | 20 | 0 | 140 | 3 |
| 21 | 22 | 2 | 24 | 2 | 18 | 1 | 18 | 2 | 14 | 1 | 96 | 8 |
| 22 | 22 | 2 | 29 | 0 | 20 | 2 | 20 | 2 | 20 | 1 | 104 | 7 |
| 23 | 26 | 1 | 18 | 0 | 20 | 1 | 26 | 1 | 26 | 1 | 116 | 4 |
| 24 | 14 | 1 | 14 | 1 | 12 | 1 | 12 | 1 | 14 | 1 | 66 | 5 |
| 25 | 20 | 2 | 24 | 1 | 24 | 2 | 18 ， | 2 | 16 | 0 | 102 | 7 |

of division．This division of the apple was considered better than taking segments corresponding to the carpels．because the seed set on one side of the carpel appeared to affect the develop－ ment of the section of the apple between the carpels to a greater extent than the segment corresponding to the carpel．As shown
in Fig. 36 the ten fibrovascular bundles are arranged symmetrically around the carpels. The segments between carpels were obtained in a uniform way by cutting thru the posterior end of the carpel and the corresponding fibrovascular bundle. The presence or absence of seeds influences the size of the sections but the nature of the seed content of adjacent sections must also be considered. Therefore the seed arrangement was classified as follows: I-seedless section with adjacent section seedless; 2-seedless section with an adjacent section seedless and the other seeded; 3-seedless sections with both adjacent sections seedless; 4-seeded section with both adjacent sections seedless; 5-seeded section with one adjacent section seedless; 6-seeded section with both adjacent sections seeded. The relation of the seed number and weight of section is shown in Table 15.

The average weight of the seeded sections is 2 I .84 grams as compared with 16.38 grams for the seedless sections. The correlation between seed arrangement and weight of section is $.25 \pm .06$. It is evident that presence or absence of seeds is of considerable influence in the development of the fruit. Practically the same correlation would undoubtedly be obtained by comparing seed arrangement with sections corresponding to the individual carpels. The weight of the apples varied considerably and might influence the correlation between seed arrangement and weight of sections. For instance the apples containing many seeds may be much larger than those with few seeds so that there may be a correlation between seed arrangement and size of section simply due to the fact that the many seeded fruits are larger. In order to hold the apple weight constant so that seed arrangement and weight of section are the only factors involved the partial correlation was computed. The correlation was obtained for seed arrangement and weight of section, seed arrangement and total weight of apple, and weight of section and total weight of apples. The partial correlation between seed arrangement and weight of section was determined by using the formula

$$
\mathrm{r}=\frac{\mathrm{r}_{12}-\mathrm{r}_{13} \cdot \mathrm{r}_{23}}{\left(\mathrm{I}-\mathrm{r}_{13}{ }^{2}\right)^{1 / 2}\left(\mathrm{I}-\mathrm{r}_{23}{ }^{2}\right)^{1 / 2}}
$$

where ${ }_{1}==$ seed arrangement, ${ }_{2}=$ weight of section and ${ }_{3}=$ total weight of apple. The correlation coefficient thus found is $30 \pm$ .05 when the apple weight is held constant.

As would be expected the presence of seeds in one carpel or one section stimulated growth not only in the corresponding section but also in adjacent sections. Altho the data recorded are not numerous enough to show the relation between seedless carpels with adjacent carpels seedless and seedless carpels with one or both adjacent carpels seeded, yet observations on hundreds of apples examined indicates that seeded carpels stimulate growth in adjacent seedless sections of the apple. A study of the fibrovascular bundles shows that the bundles of the carpels which lie along the placenta where the seeds are attached do not develop fully if no seeds are present. These bundles, when developed, undoubtedly supply nourishment not only to the seeds but to some extent to the carpels and surrounding tissue. Thus the presence of seed is correlated with the development of the fibrovascular bundle in the carpel which may bring nourishment to the fleshy portion of the apple as well as the seeds. Failure of seeds to develop results in small undevoloped fibrovascular bundles which conduct little sap to that portion of the apple. However, a more careful study of the conducting system of the apple is necessary before we can draw definite conclusions regarding the relation of seed set to sap flow. If only the bundles in the incurved edge of the carpels are affected by the seed content then the decreasd or increased development of the apple might be expected only in the fleshy tissue of the carpels and the pith which extends only to the ring of fibrovascular bundles surrounding the carpels. This, however, is not the case. Increased development of one side of the apple is due to greater growth not only in the tissue immediately surrounding the cartilagenous portion of the carpels but also in the cortex region of the apple which lies outside of the ten primary fibrovascular bundles. Thus the presence of seeds in a carpel stimulates the development of all of the surrounding tissue.

The absence of seeds in only one of the five carpels has little effect on the development of the corresponding section of the fruit. When the adjacent carpels contain seeds the stimulation of fruit development affects also the growth of the seedless section. If, however, two adjacent carpels are seedless there is
usually some decrease in size of corresponding sections and if three adjacent carpels are seedless the apple is quite likely to be irregular in shape due to the cumulative effect of several adjacent seedless carpels. However, cases have been observed where normal apples contained several seedless carpels.

## Conclusions.

The presence of seeds in an apple is an important factor in fruit development especially at the time of the "June drop." Apples which contain many seeds remain on the tree while those which contain few seeds fall at an early stage of development. As a rule many more blossoms are produced than can possibly develop into mature fruits. Heinicke (3) states that only three to seven per cent of the total number of flowers finally develop into fruits. If all of the blossoms on the tree are well pollinated and many seeds are produced in all apples it does not follow that all fruits will develop to maturity. Since there is sufficient food for only a small percentage of the flowers to develop into mature fruits only those having the largest number of seeds will develop. The presence of seeds seems to be a stimulus to the sap flow and in the competition for food the many seeded apples have the advantage. When all apples bear many seeds the tree will mature as many of these apples as its vigor and food supply will permit. In fact such a tree often bears more fruit than it can develop properly, at least from the horticulturist's standpoint. If, on the other hand, the weather is unfavorable for the work of bees, and only a few seeds are produced, it does not mean that all apples will drop. The percentage of set will undoubtedly be lower than when many seeds are set, but many apples containing a comparatively large number of seeds will develop. When few seeds are present it is probable that fewer fruits will set than the tree is able to mature. For maximum crops it is therefore necessary to insure cross pollination. Cross pollination is dependent on the action of bees and the presence of several compatible varieties in the same vicinity. The problem of self and cross sterility has already been considered in a previous bulletin. (2).

A number of writers have recognized the necessity for mixed plantings of compatible varieties to insure cross pollina-
tion. But how close together do varieties need to be planted to insure cross pollination?

Some interesting data have been obtained on numbers of seed set by open pollination and hand pollination of the same variety. Ben Davis tree $15-28$ set as many seeds per apple when open pollinated as did Ben Davis 2-26 when hand pollinated. The Ben Davis trees are self sterile and will set no seed when self pollinated or when pollinated with pollen from other Ben Davis trees. Tree $15-28$ is near the venter of the sod half of Ben Davis orchard No. I at Hgihmoor Farm. It is located in a solid block of Ben Davis trees. There are some large grafts from seedlings about 100 yards to the west. A small orchard of mixed varieties is at the edge of the south side of the orchard about 200 yards to the south. There are a few scattered trees about 200 yards north of tree $15-28$ which may be compatible as pollen parents. About a quarter of a mile to the north there is a small home orchard of about 25 trees containing over a dozen varieties, most of them compatible with Ben Davis.

Six hives of bees were kept in the home orchard during the spring and summer of 1920. Most of the trees on the Farm were presumably pollinated by these bees. Since the isolated Ben Davis tree set as many seeds as hand pollinated trees it must have been liberally supplied with compatible pollen carried by the bees. The bees must have visited the trees bearing compatible pollen before visiting Ben Davis tree No. 15-28 in the center of a block of Ben Davis trees. It is probable that the bees visited the trees in the home orchard frequently and carried pollen from these trees to the Ben Davis orchard. If cross pollination can be effected when the varieties are so scattered it would explain the cases where solid blocks of self sterile varieties produced good crops. However, more work must be done on the cross sterility problem especially on the distance that pollen is carried by bees when the weather is unfavorable for the work of bees. At present it is safe to follow the system of mixed plantings as previously recommended. (2) Hives of bees should be scattered thruout the orchard at the rate of one hive per acre of trees.

Although the presence of seeds is an important factor in the early development of the fruit it is of less importance in the later stages of development. There is usually little correlation
between seed number and weight of fruit, but different varreties under different conditions vary greatly in this respect. In the Baldwin tree that was severely thinned there is no significant correlation between seed number and weight of fruit. Presu.nably there is sufficient food for all apples and the apples develop regardless of seed content so long as sufficient seeds are present to insure uniform development. This does not mean that all apples will attain the same size. In fact the variability of size of apples is much greater in Baldwin C-45 which was thinned than in Baldwin C-42 which was not thinned. Other factors affect the size of fruit as Heinicke has shown. In Baldwin C-42 however, there is a significant degree of correlation between seed content and size of fruit apparently due to competition for food by many-seeded and few-seeded apples. Since in the unthinned tree there is not sufficient food for the maximum development of all apples, those containing most seeds attract the most food and become larger.

The relation of seed content and weight of fruit for the Ben Davis trees is just the opposite from the relationship found in the Baldwin. The large vigorous tree and the tree that was heavily thinned show some correlation between seed content and weight of fruit while the small tree which bore many apples shows no correlation between seed content and weight of fruit. The number of apples recorded is rather small; but it is evident that the relation of seed content and apple weight is not in accord with the tentative explanation of the relation of seed content and apple weight of apples from thinned and unthinned Baldwin trees.

There is a high degree of correlation between seed content and weight of apple for Golden Russett. The variation in different varieties indicates that seed and apple weight relationships found in one variety or in one tree can not be applied to all trees of all varieties.

The effect of food supply on fruit set and fruit development is well recognized by all writers. Available food supply is not, however, the only factor in fruit development. It is true that in some cases apples have developed which were seedless, but under usual conditions such cases are rare. A careful examination of over rooo apples of different varieties grown at Highmoor Farm revealed only two mature apples which were entirely seed-
less. Both of these were self-pollinated Baldwins. Heinicke states that fruit development is possible without cross-pollination and even under relatively unfavorable weather conditions, so long as the young fruit has an abundant supply of water and of readily available food. This view is also held by Ewert and others. However, the fruit set on the Ben Davis and Baldwin trees at Highmoor Farm seems to be dependent on seed formation. A Ben Davis tree bearing over ir,ooo flowers was thinned to 264 flowers and these were self-pollinated. No seedless apples were produced. The flowers on an entire branch of a Ben Davis tree were pollinated with pollen from another Ben Davis tree. Altho 180 flowers were pollinated no fruit set. Yet this tree was heavily thinned and enough food was available to develop from 5 to 18 per cent of the flowers pollinated with other varieties. It is evident that seed formation is necessary in most cases for the setting of fruit at least under the conditions existing in Maine.

Food supply does, however, play an important part in fruit development. When trees are heavily thinned a much larger per cent of the flowers set fruit than in unthimned trees, even when the same variety of pollen is used. Thinning increases the available food supply and there is less competition for food. Enough food is available to develop a large percentage of apples regardless of seed content to a considerable extent. One might expect that if the thinning was very severe, seedless apples could be produced. Severe thinning has failed to produce seedless apples at Highmoor Farm.

Severe thinning greatly increases the set of fruit and also the size of the mature fruit. The plant breeder would do well to thin trees severely before cross-pollinating work is commenced. A much larger percentage of flowers set fruit and thus many more successful crosses could be made in the short time the flowers can be worked. It is also necessary to consider the individual trees when drawing conclusions in regard to cross-fertility of varieties. For instance Baldwin C-45 was pollinated with Ben Davis 1-26 and $74 \%$ of the flowers developed into mature fruits, while Baldwin C-42, which was not thinned, set only $10 \%$ of the flowers when pollinated with Ben Davis 1-26. Baldwin C-42 when pollinated with Russett set $39 \%$ of the flowers worked. If comparison were made between the
compatibility of Ben Davis and Russett pollen with the Baldwin it would make considerable difference which cross of Baldwin x Ben Davis was considered. In one case Russett would be rated as about half as compatible as Ben Davis, and in the other case it would be rated as much more compatible than Ben Davis pollen when used with the Baldwin as the female parent.

Seed development is usually essential for uniform development of the apple. Apples with very few seeds must have several seedless carpels. When two or three adjacent carpels are seedless and the remaining carpels contain seeds the fruit is usually irregular in shape. Apples which develop with few seeds as the result of frost injury are also irregular in shape (8). Thus an abundant seed supply is essential not only for insuring sufficient set of fruit but also for the stimulation of uniform development of the apple.

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