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A. E. MURNEEK

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The Nature of Shedding of Immature Apples

A. E. MURNEEK

Abstract.—The shedding of non-setting flowers and immature fruits of the apple was studied for four years by observation and periodic counting of drops from trees of known pollination. The varieties involved were Delicious, Stayman, Winesap, Rome, Grimes, Jonathan, and Ben Davis. All of them exhibited in the "on" year and to some extent in the "off" year four waves of abscission or dropping of young fruits. These waves occurred at intervals of approximately 12-14 days and apparently are controlled by hereditary factors. The first drop is the largest, of a compound character, and probably includes many unpollinated flowers. It is followed by three others, made up of fruits of various but quite definite sizes in which embryo abortion may be the immediate and most important cause of abscission. Some apple varieties show a typical and apparently stable course in fruit shedding. When self-pollinated, the first wave of abscission of non-setting flowers is usually pronounced. The second and third drops of fruits are, as a rule, larger under cross-pollination. A discussion is presented regarding the probable causes of the various drops.

INTRODUCTION

It is commonly known that though an apple tree may be literally white with flowers in the spring, only a relatively small percentage of these become mature fruit. The vast majority of blossoms drop either soon after full bloom or at subsequent stages in their further development. Frequently this shedding of immature apples is so great that the yield may be seriously reduced. Thus time and again the proper setting of fruits becomes an important problem for the grower, which he attempts to solve by attending to or adjusting certain orchard practices.

Though considerable experimental work has been done on the subject, our information on the real causes of shedding of flowers and fruits is still very incomplete indeed. We do not know even the time factors involved in this so common a phenomenon. The general idea seems to be that abscission of apples, and several other tree fruits, or the natural separation of the stem from the fruit spur, is not a continuous process but that it occurs in several more or less distinct waves. There appear to be certain "critical periods" during which relatively large numbers of fruits shed, or absciss.

The prevailing opinion among investigators seems to be that non-developing flowers and young fruits of the apple absciss mostly at two periods (5, 16, 17, 10, 6, 8, 15)*. An early shedding is usually referred to as the "first drop" and a much later one as the "second" or "June drop," whether it occurs exactly in this month or not. Comparatively recent, though limited, studies of the dropping of immature apples seem to emphasize these two periods (2, 8).

This conception, however, is by no means definite and universally accepted. A critical review of the extant literature on the

*A list of the literature cited appears on page 34.

subject will disclose the fact that a considerable diversity of opinion exists regarding the time of occurrence and the nature of these drops in the apple. Under "first drop" are frequently considered non-setting flowers as well as small abortive fruits, while by "June drop" are understood later drops consisting of larger fruits, varying in size up to about 1 inch in diameter. This is indeed a very rough and highly unsatisfactory classification, for even a cursory inspection of abscised flowers and fruits of the apple will show several (certainly more than two) quite distinct and rather typical groups. Moreover, there appear to be fairly definite periods or waves of shedding.

Little as we know of the nature of non-setting and dropping of the apple, our information of the causes of this phenomenon is even less satisfactory. The various factors that may or may not be responsible in a particular case for shedding may be arbitrarily separated into five classes: (a) The genetic constitution of the plant, which changes but rarely in clonally propagated plants. (b) The physiological condition of the tree or part of it. This is frequently a heritage from the previous season, but subject to amelioration by certain orchard practices, such as pruning, fertilization, irrigation, etc. (c) Type of pollination and effectiveness of fertilization (gametic union). Much work has been done on this phase of the problem with rather profitable results. (d) External environmental factors; numerous, indeed, and diverse in their effect on the plant. They include the weather, soil, moisture supply, pollen-carrying insects, etc. (e) Diseases and insect pests. In general, these may be considered as abnormal environmental factors. The possible effects of certain sprays also come under this heading.

No attempt will be made at this time to analyze in detail the character and intensity of these factors in their relationship to fruit setting. A general discussion of this subject may be found in a number of publications (6, 1, 10, 13). A careful study of the available data and results will make it obvious that much more investigation is required in order that the abscission of flowers and fruits be more clearly understood. An important phase of the basic work on this problem seems to be a detailed analysis of the nature and time of occurrence of various drops. The present publication embodies the results of a study of abscission of non-setting flowers and immature apples over a period of four years.

Object of the Investigation.—Since it is commonly believed that, other conditions remaining the same, the setting and subsequent shedding of apples is determined very largely by the type of pollination, it was thought highly desirable to study it in certain varieties when self- and cross-pollinated. The use of the screen-

ed-cage method of pollination* offered an excellent opportunity for such an investigation, which the more conventional paper-bag and branch-unit methods do not. More specifically, it was thought desirable to answer the following questions: (a) What is the difference, if any, in time and nature of shedding of flowers and fruits of some of our standard apple varieties? (b) To what extent is this "normal" abscission altered by self- and cross-pollination? (c) Does the kind of pollen (as to variety) exert an influence in this respect? (d) Pollination being the same, is there a difference in dropping in "on" and "off" years?

Material and Methods of Procedure.—Commercial varieties of apples, 19 to 23 years old in the respective years of investigation, served as material. These trees are growing on rather typical loess soil, are healthy, and vigorous, and bear good crops. But, because of age and considerable crowding, many of the trees have acquired more or less a biennial bearing habit. The orchard is maintained in bluegrass sod. Each tree received approximately 4 to 5 pounds of ammonium sulfate in the spring, was pruned moderately, and sprayed well. The following varieties are included in this study: Jonathan, Delicious, Grimes, Rome, Winesap, Stayman, and Ben Davis.

In all instances the so-called screened-cage-package-bee method of pollination was used, which reproduces more closely natural pollination by insects than any other method yet devised. The construction of the cages, supply of pollen, methods of its distribution, and other details of procedure are described fully in previous publications (12, 14) and hence will not be discussed here.

As soon as the flowers were past the receptive stage, all cages were cleared and a cloth spread on the ground to facilitate gathering of the various drops. At the same time, the screens were removed from the tops and sides of the cages to expose the trees to a maximum amount of light and other environmental factors.

On the day of collection, all branches were jarred carefully but firmly by means of a long pole to which was attached a well-padded hook. This was done by a trained assistant, who was supervised almost continuously by the author. Emphasis must be placed on the necessity of shaking the branches previous to gathering the drops. Unless there be a strong wind, many of the shedding flowers and fruits will adhere to the spurs for a considerable period. Jarring will make them abscise at a more normal time. Most of the collections were made every second day, some at slightly less frequent intervals. Previous experience had shown that not much could be gained by more frequent, daily, gathering of apple drops.

*Murneek, A. E. Apple pollination: An evaluation of methods and pollenizers. Mo. Agr. Exp. Sta. Res. Bul. 175, 1932.

As a rule, all collections were made and the drops counted on the same day. When the numbers were extremely large, as in the case of shedding of non-setting flowers, representative samples were weighed and counted. Repeated checks showed a close agreement between sample and total counting, the error being around $\pm 3\%$. All extraneous matter must be previously removed, however, from the samples.

In order to assure oneself that other trees of the same variety, when open-pollinated, behave similarly in respect to shedding of fruits, observations and in some cases counts were made on numerous trees in this orchard. At the same time, typical drops from most of the caged and from open-pollinated trees were gathered for histological observation of embryo development. This material is being studied and will be the subject of another publication.

When all drops were over, the percentage of flowers set from each type of pollination was determined on 10 representative and previously tagged branches. This was done early in July. The results are presented graphically on the charts. All things considered, this set probably is the best indication of the normal performance of a tree. Windstorms, insect pests and other abnormal environmental factors frequently cause in the Middle West an "unnatural" abscission of apples before the regular harvest time.

RESULTS

The seasonal progress of abscission of non-setting flowers and fruits is expressed in this report by the quantity of fruit shed on the respective days of collection. The data are presented in both tabular and graphic forms. This is by no means a duplication of effort. Because of the great numbers involved early in the season, the ordinates of the graphs had to be plotted on a comparatively large scale, even when the high points are cut off. Consequently the numerically smaller waves of drops are not given their due prominence. Thus, perforce, being minimized, they may be overlooked. Figures in the tables will serve to bring them out.

Excepting where otherwise indicated, each chart presents the shedding performance of the same tree, two quarters of which were exposed to different pollination. The other half of the tree was open-pollinated. The percentage of flowers set was determined after the final drop.

The Four Waves of Abscission.—An examination of all the data will show quite clearly that practically all the considered varieties exhibit more or less distinctly four waves of drops. The first two usually overlap, hence in some cases only a careful analysis will lead to their distinction. In other instances they are unmistakably separated. But always they are marked by differences in the development of the fruit, this being the most deciding cri-

terion. Although numerically smaller, the two later drops overlap less and are more clearly distinguishable as to size of specimens and their time of shedding. During our investigation the crests of these four characteristic waves of abscission of immature apples occurred approximately at intervals of 12 to 14 days. In one year, at least, the intervals were, however, only 8 to 12 days, thereby showing a possible seasonal variation.

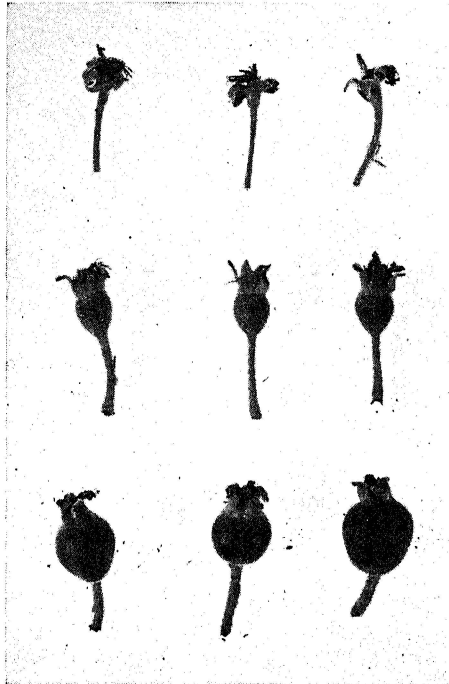


Fig. 1.—Typical flowers (fruit) of the first (top), second (middle), and third (bottom) drops. Approximately two-thirds natural size. Variety, Jonathan. Open pollinated. Note the position of calyx lobes and enlargement of torus.

The first drop consisted largely of non-setting flowers* with petals abscised and anthers, stigmas and styles dead. It began about 8-12 days after full bloom. The calyx lobes of these flowers are fully open (Fig. 1, top) and the pedicels usually yellowed. Seldom is there a noticeable swelling of the torus. During our studies this drop occurred largely between April 25 and May 2, or 9-16 days after anthesis or full bloom. These non-setting flowers or fruits dry up rapidly, occasionally while still attached to the

*If fertilization has occurred in such a flower, leading to initiation of development of the zygotes, then it may be called a *fruit*.

spur. Having fallen on the ground, they disintegrate promptly and, therefore, are not conspicuous.

It is more than probable, however, that this fruit drop began in most varieties earlier than on April 25. It was thought desirable, however, not to remove the bees and open the cages till it was positive that no receptive flowers were present on the trees. In some cases this, perforce, has caused the drop records to begin rather abruptly.

One can often distinguish beforehand potential early drops from fruits that have set at least temporarily, by an upward bending of pedicels of the latter, even though there may not be a great difference in their relative sizes (Fig. 2).



Fig. 2.—Showing upward bending of fruit that have set, at least temporarily. Time of first drop. Variety Jonathan. Open pollinated.

The second drop of apples is made up of fruits considerably larger than those of the first drop, generally .5 to .7 centimeters in diameter. Their calyx lobes are either partly or completely closed and the torus enlarged (Fig. 1, middle; also Fig. 3, right). There is a characteristic yellowing of the pedicel, which often extends into the torus. Frequently when a spur does not shed any fruit during a first wave of dropping, it will do so in the second (Fig. 3). In most mid-season varieties the peak of this drop occurred between May 7 and 14, and may be said to appear about 9-10 days later than the first one. But in most cases the two overlap considerably.

Although varying in intensity, these two drops of apples seem to take place in all varieties and under all conditions of pollination. The later drops, however, are comparatively small. They may be reduced greatly in numbers or almost completely absent, as in the case of meager flowering and fruit setting in the "off" year.

Separated from the second drop by about two weeks or less, there usually comes a third abscission of immature fruit. In our orchard the majority of specimens of this drop were gathered between May

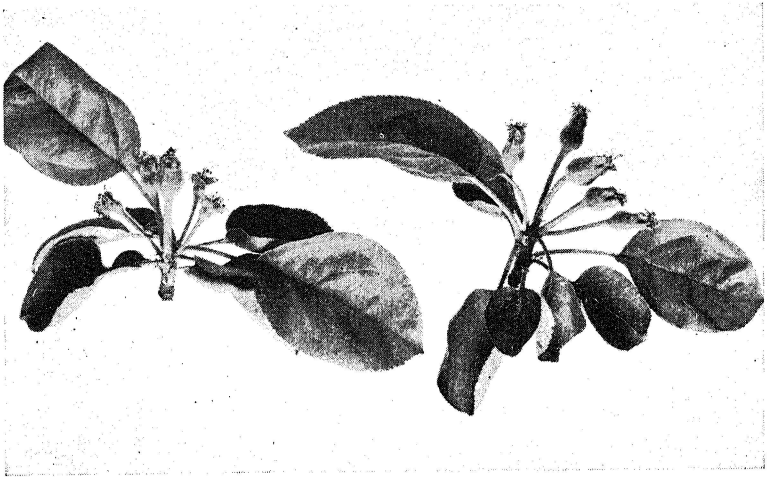


Fig. 3.—Spur on the left will shed most of its fruit during the first drop; one on the right during the second.

23-29. Apples of this wave of shedding are considerably more enlarged, rounded out, and average approximately 1 centimeter in diameter (Fig. 1, bottom). The difference in development between fruits of the second and third drops and those remaining on the spur at the time of the third drop are shown in Figure 4.



Fig. 4.—Showing difference in development of fruit of second (center) and third (right) drops and one (left) developing further at the time of the third drop. Approximately one-half natural size. Variety Rome. Open pollinated.

Fruits that absciss during the third wave remain on the ground for several days. When in large numbers their presence is very conspicuous. Undoubtedly, this drop is often referred to in literature and by growers as the "June drop," or part of it.

The peak of the wave of the last normal abscission of immature apples was reached about 12-14 days after the third one. As a rule it is numerically the smallest but commonly the most noticeable, chiefly due to the size of the specimens which are shed at this period. The fruits are now fully rounded out—about 2 centimeters in diameter. In many summer and fall varieties they are larger. But in all instances apples that absciss normally at this time are very much smaller than those that will continue to develop to maturity (Fig. 5). During our studies this drop appeared between June 8-13. Should it be listed as the real "June drop"?

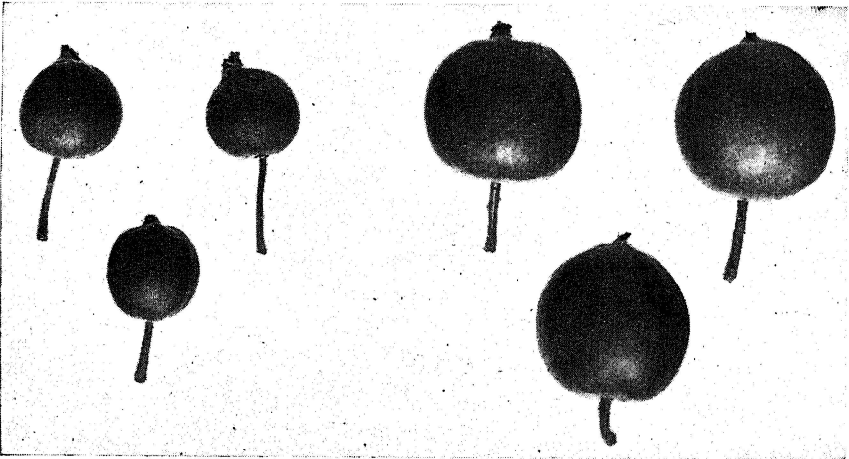


Fig. 5.—Relative, approximately two-thirds natural, sizes of fruit that are shed during the fourth drop (left) and those remaining on the tree (right). Variety Jonathan. Open pollinated.

In addition to these normal waves of shedding, apples may absciss in considerable numbers as a result of effects of various abnormal environmental factors or injuries to the fruit or vegetative parts of the tree by disease or insects. Severe wind storms may tear off many apples in the summer months. Scab and other diseases occasionally cause heavy shedding early in the spring. Curculio, codling moth, aphid and other insects may bring about dropping at various times. In one year the writer noted a marked shedding of apples that were much larger than those of the normal fourth drop due to an attack of the Lesser Apple Worm. Such abnormal abscission of young fruits, of course, is not included in this study.

Varietal Differences.—Not all varieties of apples shed their immature fruits in the same manner. In this respect there appear to be characteristic group and individual differences. Many summer and early fall varieties, such as Duchess, Wealthy, etc., have a relatively light early but an extremely heavy late drop. The reverse is true of a large number of winter apples. But within each group there are also marked varietal differences in this respect.

Referring to our records, it will be noted that Delicious exhibits an unusually heavy early drop (Figs. 6-8, tables 1, A-F). Most of the fruits (flowers) are shed promptly after the petals have fallen. Quite often the set is reduced to a single specimen or two per spur after this first drop (8, 12). The succeeding waves of abscission may or may not be pronounced, the fourth one usually being light (Fig. 6 vs. Figs. 7 and 8). Pollination appears to be an important factor in this respect in all varieties, determining in a large measure the severity of each drop. This phase of the problem will be discussed forthwith.

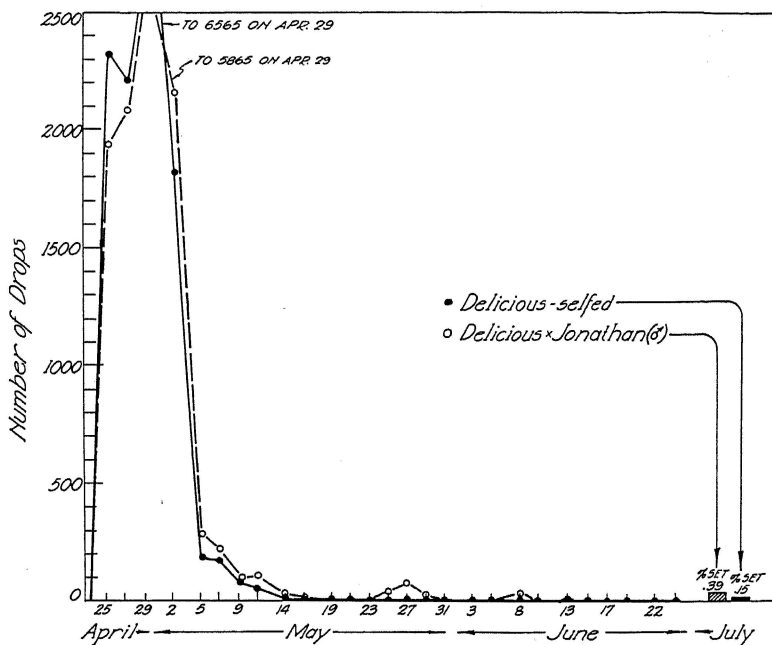


Fig. 6.—Distribution of drops of the Delicious variety when self-pollinated and pollinated with Jonathan. See Table 1, A and B.

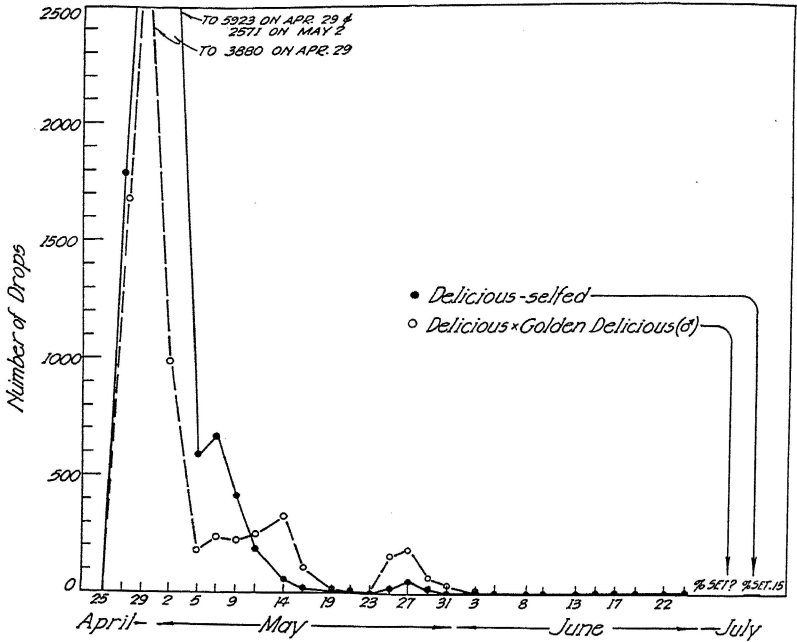


Fig. 7.—Distribution of drops of the Delicious variety when self-pollinated and pollinated with Golden Delicious. See table 1, C and D.

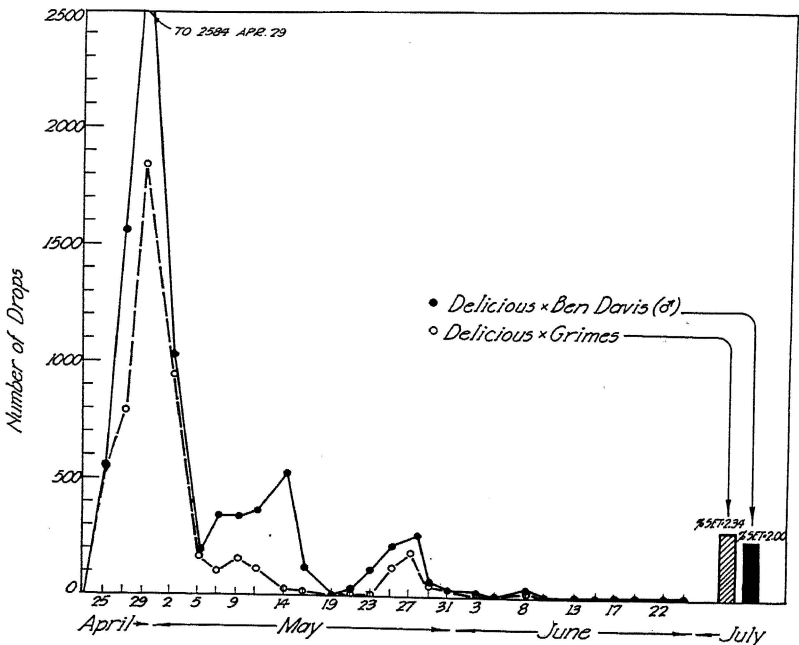


Fig. 8.—Distribution of drops of the Delicious variety when pollinated with Ben Davis and Grimes. See table 1, E and F.

TABLE 1.—FRUIT SHEDDING RECORDS IN “ON” YEAR OF THE *Delicious* VARIETY WHEN SELF-POLLINATED AND CROSS-POLLINATED WITH KNOWN POLLEN.

Date of collection of drops	A Self-pollinated	B Pollinated with Jonathan	C Self-pollinated	D Pollinated with Golden Delicious	E Pollinated with Grimes	F Pollinated with Ben Davis
April 25	2322	1934	----	----	542	506
April 27	2207	2081	1784	1678	781	1543
April 29	6565	5865	5923	3880	1825	2584
April 2	1829	2161	2571	986	937	1114
May 5	186	288	585	172	157	172
May 7	180	219	666	233	160	332
May 9	85	87	412	223	147	330
May 11	54	106	193	243	100	355
May 14	12	27	53	322	21	515
May 16	2	19	14	109	14	105
May 19	0	0	0	12	6	8
May 21	0	9	5	9	7	26
May 23	0	0	0	0	0	104
May 25	5	47	13	152	115	206
May 27	10	79	55	184	179	252
May 29	5	22	19	62	38	46
May 31	0	10	5	26	23	19
June 3	2	9	1	5	5	10
June 5	1	4	1	2	3	3
June 8	0	43	0	7	14	29
June 10	3	4	3	0	1	6
June 13	2	9	2	4	5	7
June 15	0	0	2	0	2	2
June 17	0	0	0	0	0	0
June 19	0	1	0	0	0	2
June 22	0	0	0	0	3	0
June 25	0	3	0	0	2	0
June 29	0	0	0	3	2	3
July 2	0	0	0	1	0	1

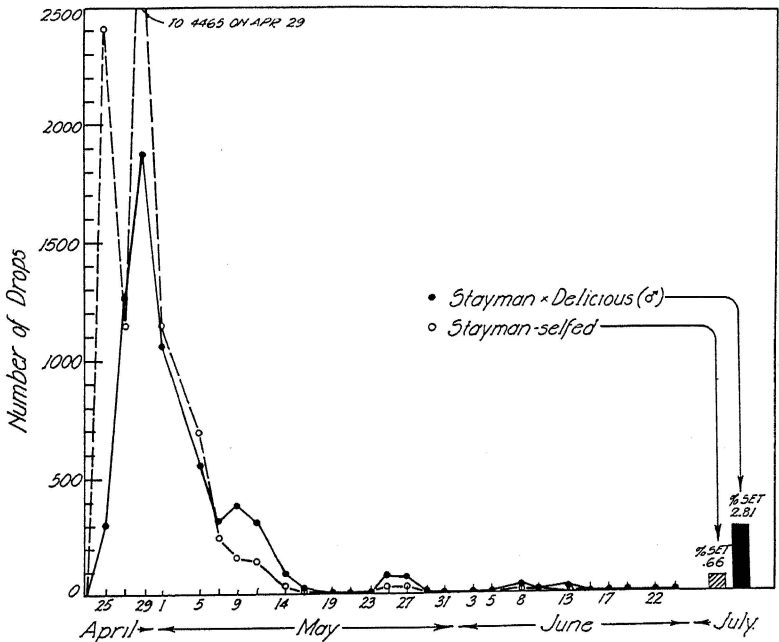


Fig. 9.—Distribution of drops of the Stayman variety when self-pollinated and pollinated with Delicious. See table 2, A and B.

Varieties of the Winesap group seem to have similar characteristic early drops—a behavior well known to many fruit growers and horticulturists (?). The two Stayman trees under our close scrutiny shed almost all their flowers and young fruits during the first two drops. The third and fourth ones were very light indeed (Fig. 9-10, Tables 2, A-D). Similarly, Winesap trees dropped almost all of their potential fruits soon after the bloom was over. A much lighter second shedding made its appearance, and a somewhat heavier third drop than in the Staymans, but there were practically no fruits left to absciss in June (Figs. 11 and 12, Tables 3, A-D).

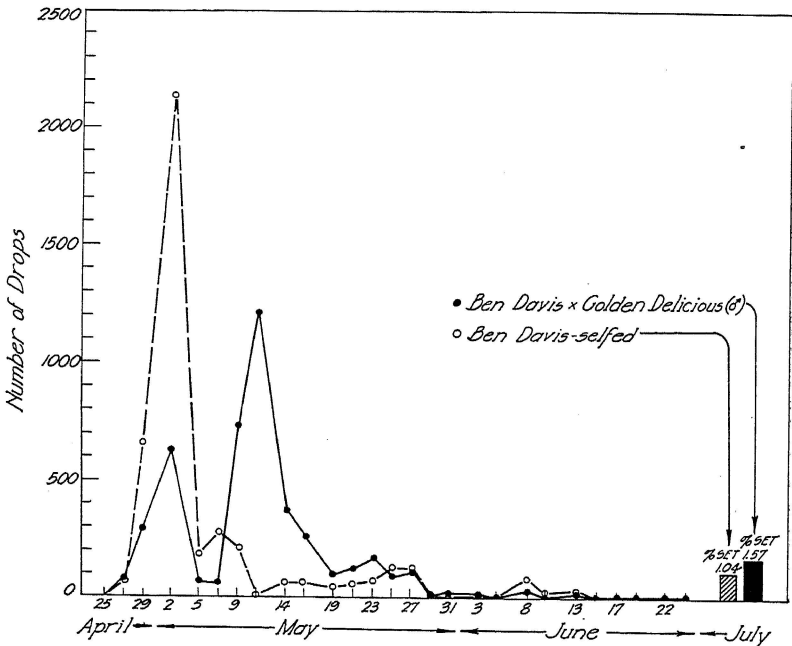


Fig. 10.—Distribution of drops of the Stayman variety when pollinated with Golden Delicious and Jonathan. See table 2, C and D.

TABLE 2.—FRUIT SHEDDING RECORDS IN “ON” YEAR OF THE *Stayman* VARIETY WHEN SELF-POLLINATED AND CROSS-POLLINATED WITH KNOWN POLLEN.

Date of collection of drops	A Self-pollinated	B Pollinated with Delicious	C Pollinated with Golden Delicious	D Pollinated with Jonathan
April 25	2397	290	2812	521
April 27	1147	1262	511	289
April 29	4465	1861	2423	1416
May 1	1137	1058	1388	1467
May 5	691	549	622	633
May 7	243	315	544	205
May 9	156	378	416	141
May 11	143	306	344	152
May 14	31	87	45	14
May 16	11	28	27	17
May 19	0	0	0	0
May 21	0	0	0	0
May 23	0	0	0	0
May 25	27	75	67	38
May 27	30	73	53	33
May 29	12	2	2	2
May 31	5	8	9	0
June 3	2	6	1	3
June 5	2	8	3	4
June 8	15	30	34	13
June 10	11	17	11	3
June 13	8	21	14	3
June 15	4	0	0	4
June 17	9	4	2	3
June 19	7	4	4	1
June 22	0	0	0	0
June 25	2	0	0	0
June 29	2	0	0	0
July 2	0	0	0	0

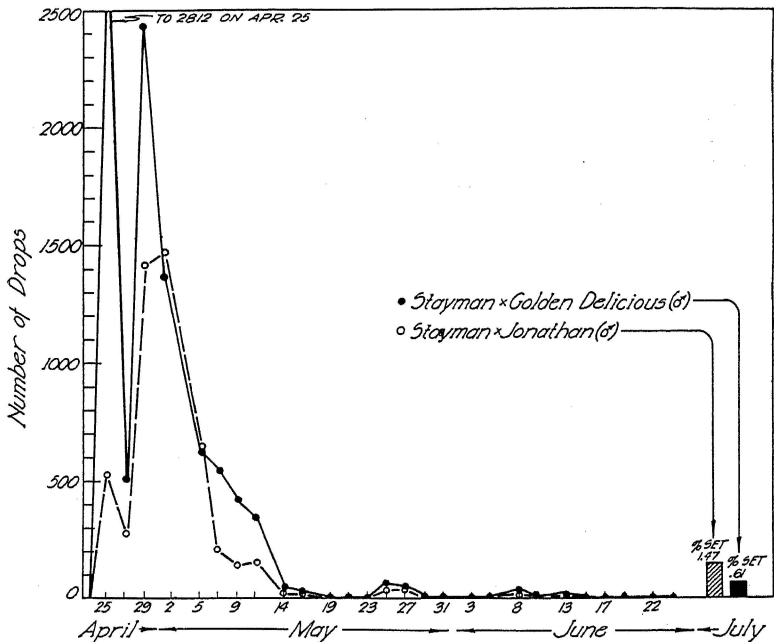


Fig. 11.—Distribution of drops of the *Winesap* variety when self-pollinated and pollinated with *Jonathan*. See table 3, A and B.

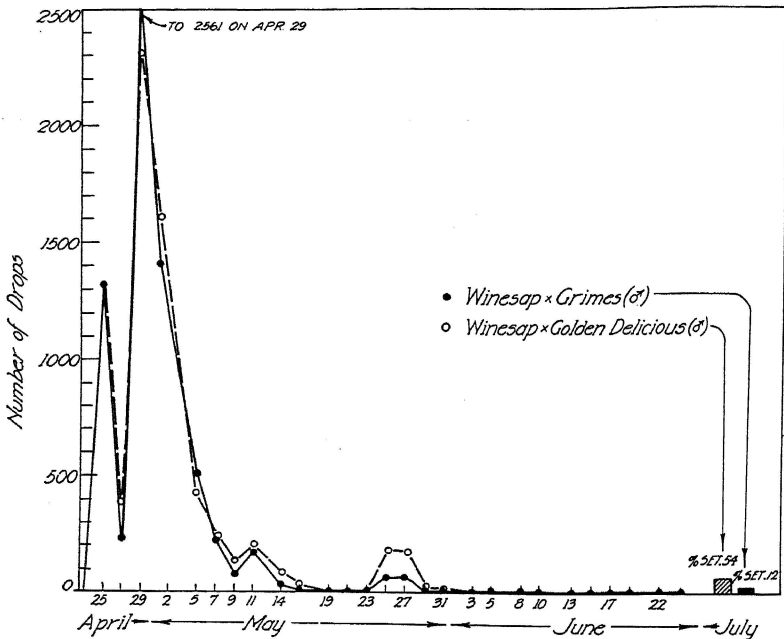


Fig. 12.—Distribution of drops of the Winesap variety when pollinated with Grimes and Golden Delicious. See table 3, C and D.

TABLE 3.—FRUIT SHEDDING RECORDS IN “ON” YEAR OF THE *Winesap* VARIETY WHEN SELF-POLLINATED AND CROSS-POLLINATED WITH KNOWN POLLEN.

Date of collection of drops	A Self-pollinated	B Pollinated with Jonathans	C Pollinated with Grimes	D Pollinated with Golden Delicious
April 25	624	1432	1416	1403
April 27	375	257	223	379
April 29	896	950	2561	2303
May 1	1076	1030	1410	1613
May 5	263	346	500	429
May 7	68	128	225	240
May 9	14	108	72	138
May 11	13	145	177	196
May 14	0	20	14	70
May 16	0	0	0	27
May 19	0	0	0	0
May 21	0	0	0	0
May 23	17	0	0	0
May 25	0	135	52	179
May 27	0	52	61	161
May 29	0	2	1	17
May 31	0	0	0	12
June 3	0	0	0	0
June 5	0	0	6	3
June 8	0	0	5	5
June 10	0	0	0	1
June 13	0	0	1	2
June 15	0	0	0	0
June 17	0	0	0	0
June 19	0	0	0	0
June 22	0	0	0	0
June 25	0	0	0	0
June 29	0	0	0	0
July 2	0	0	0	0

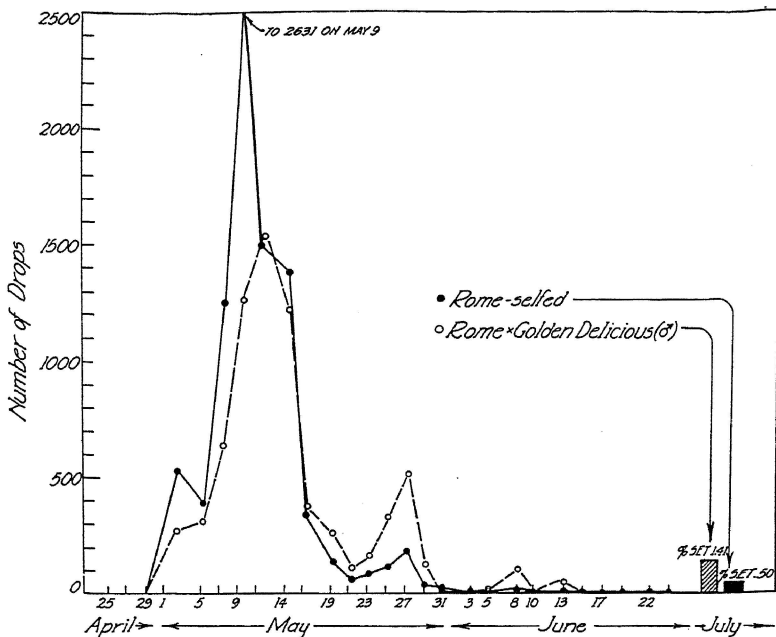


Fig. 13.—Distribution of drops of the Rome variety when self-pollinated and pollinated with Golden Delicious. See table 4, A and B.

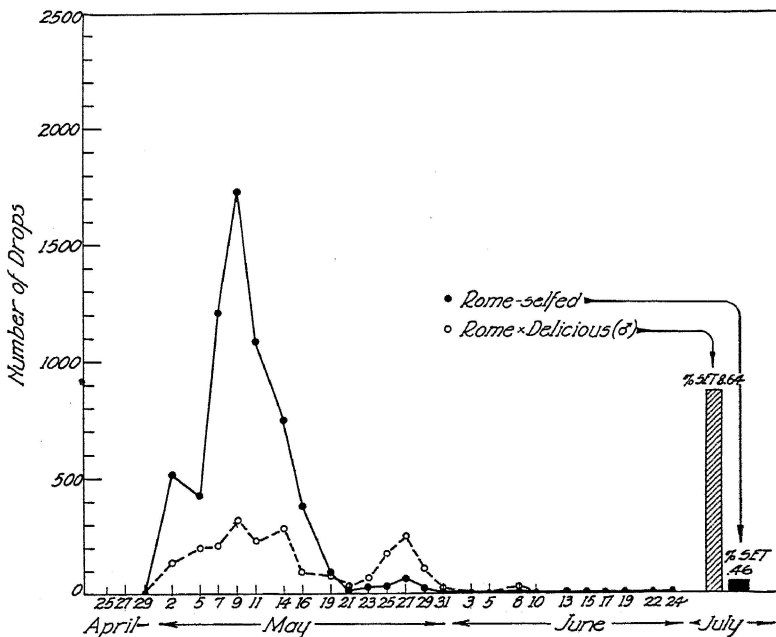


Fig. 14.—Distribution of drops of the Rome variety when self-pollinated and pollinated with Delicious. See table 4, C and D.

In a good bearing year the Rome variety is relieved of a large proportion of its young fruits during the first and second waves of shedding. With good pollination, the third drop may also be pronounced and the fourth noticeable (Figs. 13 and 14, Tables 4, A-D). Thus the four drops are more evenly distributed in this variety than in members of the Winesap group.

TABLE 4.—FRUIT SHEDDING RECORDS IN "ON" YEAR OF THE *Rome* VARIETY WHEN SELF-POLLINATED AND CROSS-POLLINATED WITH KNOWN POLLEN.

Date of collection of drops	A Self-pollinated	B Pollinated with Golden Delicious	C Self-pollinated	D Pollinated with Delicious
May 2	521	263	515	134
May 5	379	310	422	199
May 7	1242	639	1209	206
May 9	2636	1251	1729	320
May 11	1500	1531	1089	229
May 14	1383	1318	747	276
May 16	348	373	383	96
May 19	145	270	95	80
May 21	69	107	19	28
May 23	92	157	22	64
May 25	120	336	29	183
May 27	185	522	65	250
May 29	42	132	21	102
May 31	15	5	0	24
June 3	3	12	0	2
June 5	5	14	0	8
June 8	22	111	6	23
June 10	19	23	10	6
June 13	12	69	5	5
June 15	3	7	0	0
June 17	4	6	0	0
June 19	1	4	0	1
June 22	0	0	0	0
June 25	0	0	0	0
June 29	0	0	0	0
July 2	0	0	0	0

Counts were made of drops from one Grimes tree when the flowers were self-pollinated and pollinated by Jonathan. Moreover, the shedding was closely observed on a number of other Grimes trees under open orchard pollination. This variety likewise has a pronounced first drop but, when properly pollinated, the second and third drops are also conspicuous (Fig. 15, Tables 5, A and B). In our orchard, King David behaved quite similarly to Grimes in this respect.

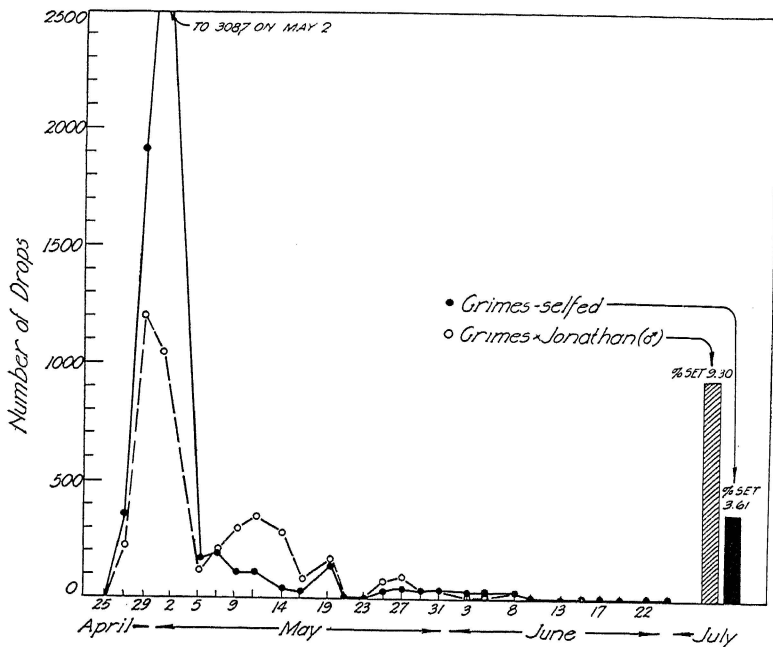


Fig. 15.—Distribution of drops of the Grimes variety when self-pollinated and pollinated with Jonathan. See table 5, A and B.

TABLE 5.—FRUIT SHEDDING RECORDS IN “ON” YEAR OF THE *Grimes* VARIETY WHEN SELF-POLLINATED AND CROSS-POLLINATED WITH JONATHAN.

Date of collection of drops	A Self-pollinated	B Pollinated with Jonathan
April 25	----	---
April 27	356	220
April 29	1907	1200
May 2	3087	1046
May 5	158	117
May 7	191	199
May 9	110	295
May 11	109	343
May 14	36	286
May 16	21	84
May 19	143	162
May 21	5	6
May 23	0	0
May 25	30	70
May 27	43	97
May 29	22	32
May 31	26	34
June 3	20	3
June 5	15	9
June 8	19	27
June 10	0	6
June 13	8	1
June 15	0	2
June 17	0	0
June 19	1	2
June 22	0	0
June 25	0	0
June 29	0	0
July 2	0	0

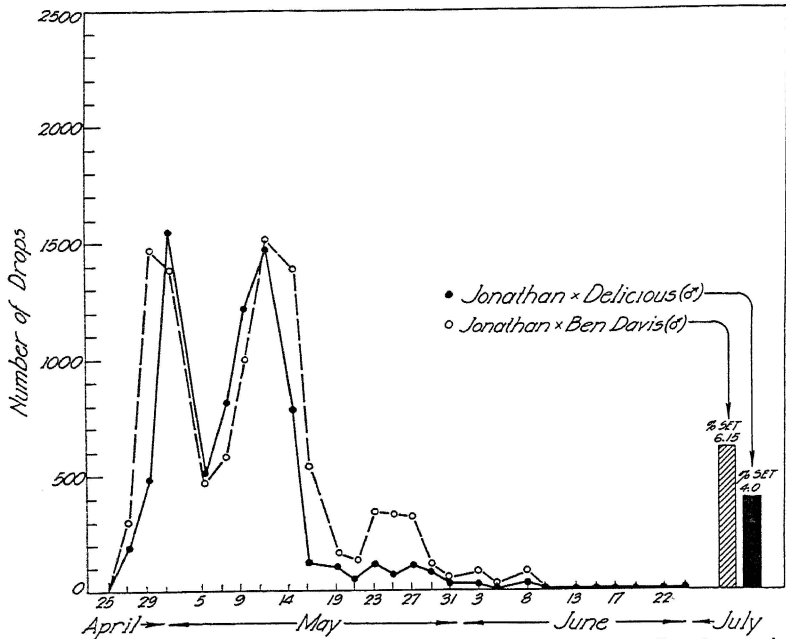


Fig. 16.—Distribution of drops from two separate trees of the Jonathan variety when pollinated with Delicious and Ben Davis. See table 6, A and B.

TABLE 6.—FRUIT SHEDDING RECORDS IN "ON" YEAR OF THE Jonathan VARIETY WHEN SELF-POLLINATED AND CROSS-POLLINATED WITH KNOWN POLLEN.

Date of collection of drops	A Pollinated with Delicious	B Pollinated with Ben Davis	C Self-pollinated	D Pollinated with Golden Delicious	E Pollinated with Grimes
April 25	189	297	279	306	285
April 27	480	1464	1682	1987	2069
April 29	1542	1376	4497	4350	6518
May 2	505	461	469	451	825
May 5	808	575	581	605	1588
May 7	1207	977	331	649	1877
May 9	1474	1503	600	1044	1301
May 11	781	1381	387	799	974
May 14	124	535	20	115	189
May 16	101	164	42	60	47
May 19	45	142	12	54	115
May 21	118	340	18	149	149
May 23	66	328	20	161	76
May 25	108	313	32	208	109
May 27	85	104	32	94	40
May 29	31	45	16	41	43
May 31	16	80	30	16	12
June 3	3	16	3	16	10
June 5	24	90	24	20	12
June 8	4	12	1	4	2
June 10	4	15	8	18	3
June 13	3	5	0	3	0
June 15	4	4	3	0	1
June 17	0	4	8	6	0
June 19	2	0	0	0	0
June 22	0	0	0	0	0
June 25	0	0	0	0	0
June 29	0	0	0	0	0
July 2	0	0	0	0	0

Unlike Delicious, Stayman and Winesap varieties, Jonathan trees will hold a large proportion of their fruit until the second wave of abscission, which is frequently almost as heavy as the first one. Figure 16 and Tables 6, A and B, record the shedding performance of two trees when pollinated by Delicious and Ben Davis respectively. The similarity of the curves is very striking, the only difference being at the time of the third drop. In three other instances when the trees were either self-pollinated or pollinated by Grimes and Golden Delicious, there was likewise a very pronounced second drop (Fig. 17 and Tables 6, C-E).

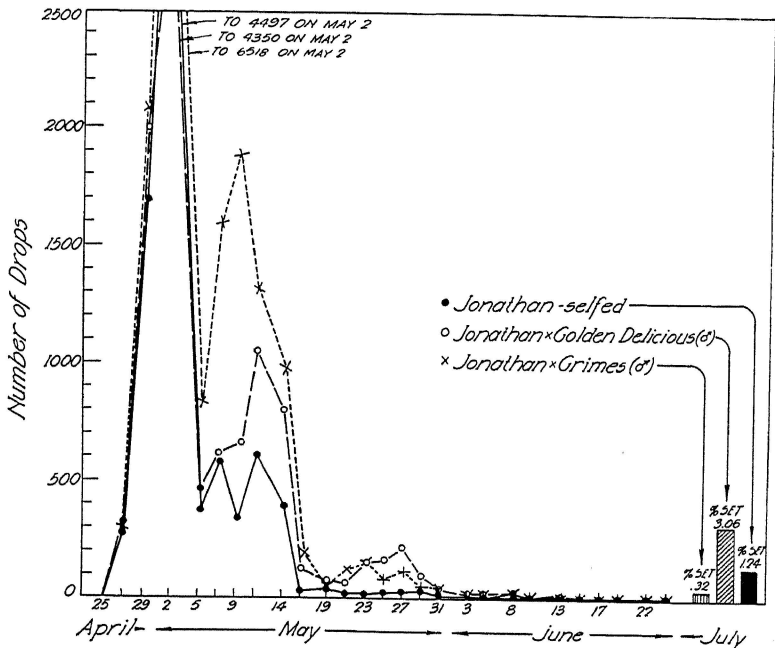


Fig. 17.—Distribution of drops from three separate trees of the Jonathan variety when self-pollinated and pollinated with Golden Delicious and Grimes. See table 6, C, D and E.

An even more striking second drop was exhibited by Ben Davis when the flowers were cross-pollinated. The two trees under consideration behaved identically in this respect, though a different pollen was used in each instance. (Figs. 18-19 and Tables 7, B and D). When self-pollinated, both trees produced a strikingly larger first drop and the second was reduced correspondingly (Figs. 18 and 19, Tables 7, A and C). The third and fourth waves of shedding were not important.

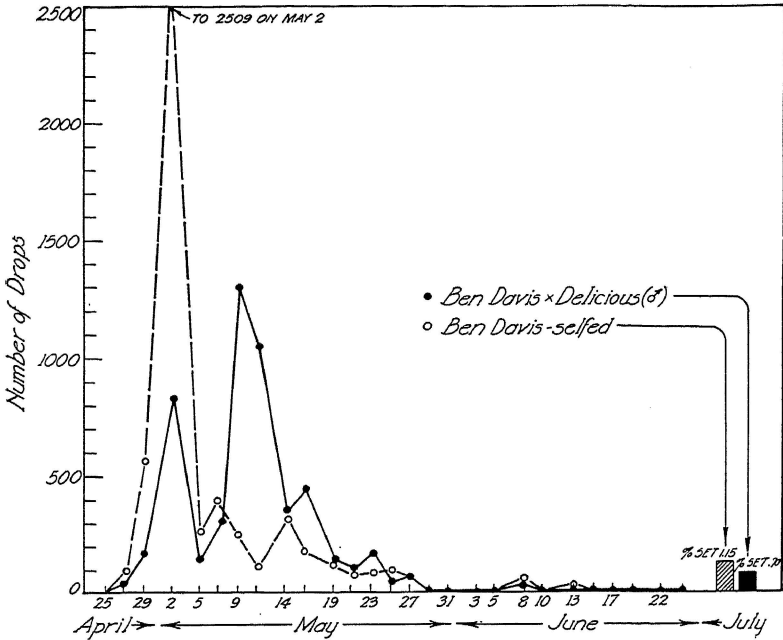


Fig. 18.—Distribution of drops of the Ben Davis variety when self-pollinated and pollinated with Delicious. See table 7, A and B.

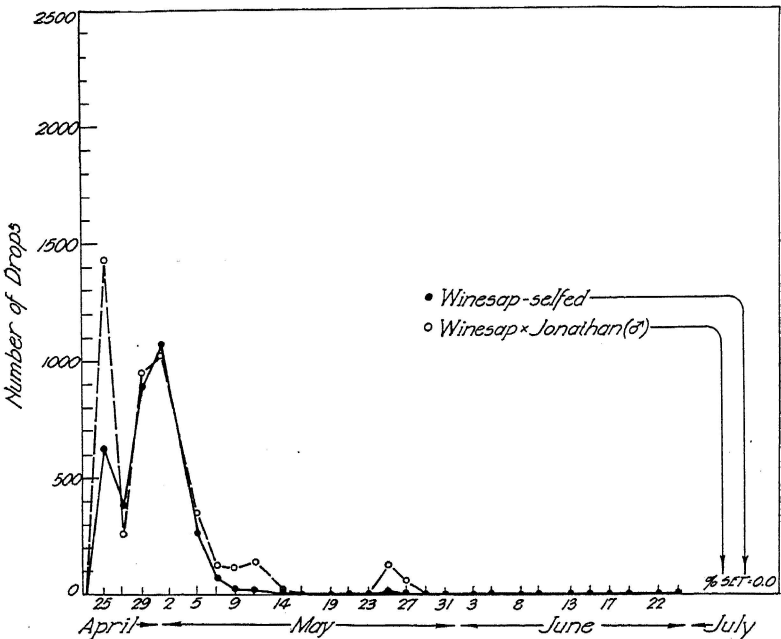


Fig. 19.—Distribution of drops of the Ben Davis variety when self-pollinated and pollinated with Golden Delicious. See table 7, C and D.

TABLE 7.—FRUIT SHEDDING RECORDS IN "ON" YEAR OF THE *Ben Davis* VARIETY WHEN SELF-POLLINATED AND CROSS-POLLINATED WITH KNOWN POLLEN.

Date of collection of drops	A Self-pollinated	B Pollinated with Delicious	C Self-pollinated	D Pollinated with Golden Delicious
April 25	---	---	---	---
April 27	88	39	68	77
April 29	554	170	655	290
May 2	2509	828	2126	622
May 5	252	148	185	68
May 7	388	291	286	57
May 9	236	1294	210	733
May 11	103	1043	0	1215
May 14	310	349	63	375
May 16	179	434	56	261
May 19	116	127	48	91
May 21	72	94	53	126
May 23	79	153	89	164
May 25	91	49	121	100
May 27	65	67	120	112
May 29	3	8	12	8
May 31	10	7	17	18
June 3	5	4	17	15
June 5	6	1	11	11
June 8	51	21	82	42
June 10	9	4	12	5
June 13	17	5	26	18
June 15	1	1	4	4
June 17	5	3	7	6
June 19	4	3	3	3
June 22	0	3	0	0
June 25	4	0	0	1
June 29	0	0	0	2
July 2	0	0	0	0

In general, then, it is quite evident that distinct varietal traits are exhibited by apples in the abscission of their immature fruit (1, 2, 12). Most likely, the behavior is determined by the genetic constitution of the clone and hence is deep-seated and hereditary. Some varieties have a characteristic heavy first drop with but few fruits shedding thereafter, while others have a second drop which is very pronounced. These varietal differences become less marked in case of the last two waves of shedding but, considering the reduced numbers of fruit present on the trees at that time, they may be equally important from an economic consideration.

Relation to Type of Pollination.—There is a popular idea among growers that when apple flowers are not properly pollinated, the young fruit will be shed prematurely and abundantly. In other words, there will be a dangerously heavy so-called "first drop". What evidence do we have in our records that this might be true? A review of all the charts will show unmistakably that, in all varieties considered, the first drop was more abundant and other drops smaller when the flowers were self-pollinated. Cross-pollinated ones, therefore, "stick tighter" and remain longer on the spurs. This illustrates clearly the effects produced by gametes of another variety.

If foreign pollen has a beneficial influence on fruit setting, then there may be even a noticeable difference in the dropping performance of the same variety when a very good or only a mediocre pollenizer is

used. Unfortunately, our records are not extensive enough to answer this question definitely. It is probable, however, that such generally effective pollenizers as Delicious, Jonathan, and Ben Davis (13, 14) may have a more marked influence than comparatively poor pollenizers on the character and rate of shedding of immature apples. This may be anticipated, probably, due to a more efficient fertilization and more rapid embryo development with some pollen than with others. Jonathan, Delicious, and Ben Davis have been found to be more desirable pollenizers than other varieties if the results are measured by an increased yield of fruits (13, 14).

Relation to Permanent Set.—Does a heavy “June drop” (third and fourth drops) usually mean a reduced yield of fruit at maturity? This is often thought to be the case. Almost all of our charts give the permanent or July set of fruit (as percentage of flowers set). An examination of the graphs will make it evident that no close relationship can be established between the last two waves of abscission and the final set. In most instances a high percentage set was preceded by comparatively heavy third and fourth drops. Thus, if correct, our results are negative. A more extensive survey, however, may possibly show a closer correlation between these two factors.

Drops in “On” and “Off” Years.—In many apple varieties the “off” year is characterized by an almost total absence of flowers. Other varieties may carry an appreciable number of blossoms. Naturally, trees in the latter condition only may be used for a study of drops in “off” years. In respect to their bearing habit, most of the standard varieties in our orchard have a gregarious behavior. The years 1930 and 1932 were “off” years. However, a number of trees flowered enough to permit an analysis of their fruit-shedding performance.

It was thought desirable to ascertain whether some of the more important varieties dropped their non-setting flowers and immature fruits differently in the “on” and “off” years. Though having sometimes a fairly good bloom, they may or may not set well in an “off” year. In other instances the relative percentage of flowers which develop fruits to maturity may be high in a normal “non-bearing” year. It has been found (2) that when trees are exposed to open pollination the natural sequence of drops seems to be more or less the same in “on” and “off” years. But because of great differences in numbers of fruit that absciss in the respective years, interpretation of records is not always certain.

Our methods of pollination permit a ready comparison of the seasonal abscission of flowers and fruits under self- and cross-pollination, the source of pollen being known in each case. The study was limited to three varieties—Delicious, Jonathan and Grimes.

The results obtained with Delicious are presented in Figures 20 and 21 and Tables 1-C, 8-A, 1-B, 8-B. Whether self- or cross-pollinated, the first three drops are distinguishable in the "off" year. The fourth drop was usually absent. It is rather interesting to note that, excepting when self-pollinated, the percentage of flowers on the Delicious trees that set fruit permanently was higher in the "on" year. When pollinated with Grimes the set was in "on" year

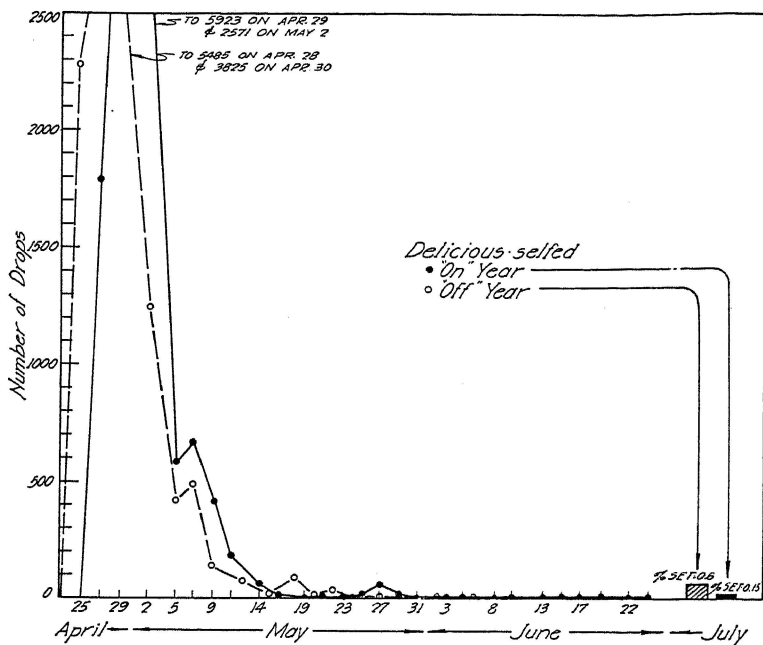


Fig. 20.—Distribution of drops of the Delicious variety in "on" and "off" years when self-pollinated. See tables 1, C and 8, A.

TABLE 8.—FRUIT SHEDDING RECORDS IN "OFF" YEAR OF *Delicious* VARIETY WHEN SELF-POLLINATED AND CROSS-POLLINATED WITH JONATHAN.

Date of collection of drops	A Self-pollinated	B Pollinated with Jonathan
April 25	2274	2096
April 28	5485	3381
April 30	3825	1645
May 2	1244	465
May 5	413	268
May 7	485	206
May 9	140	77
May 12	73	51
May 15	16	31
May 18	86	26
May 20	14	15
May 22	32	6
May 24	3	5
May 27	1	0
May 29	1	1
June 2	0	0
June 6	0	0

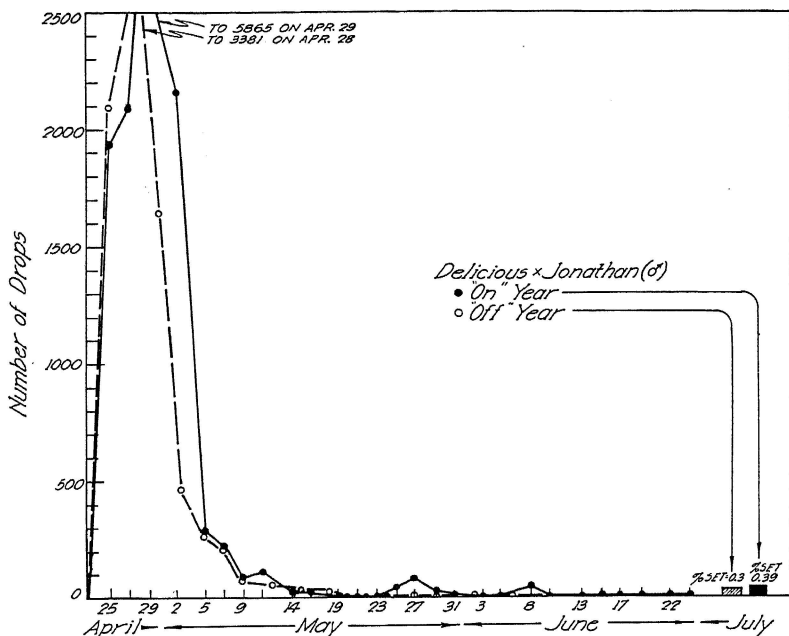


Fig. 21.—Distribution of drops of the Delicious variety in "on" and "off" years when pollinated with Jonathan. See tables 1, B and 8, B.

2.34%, "off" year 0.3% ; with Ben Davis, "on" year 2.0%, "off" year 0.3%. In this respect, Delicious seems to differ from Jonathan and Grimes, the latter varieties producing a better set in the "off" year.

The fruit-setting performance of the Jonathan, when self-pollinated and when exposed to Delicious pollen, is given in Figures 22 and 23 and Tables 6-C, 9-A, 6-A, 9-B. Both trees in the "off" year

TABLE 9.—FRUIT SHEDDING RECORDS IN "OFF" YEAR OF THE *Jonathan* VARIETY WHEN SELF-POLLINATED AND CROSS-POLLINATED WITH DELICIOUS.

Date of collection of drops	A Self-pollinated	B Pollinated with Delicious
April 25	589	415
April 28	1067	1320
April 30	1512	2137
May 2	723	901
May 5	544	466
May 7	341	508
May 9	93	293
May 12	57	82
May 15	84	34
May 18	54	113
May 20	13	14
May 22	12	39
May 24	4	12
May 27	16	7
May 29	3	4
June 2	1	5
June 6	3	3

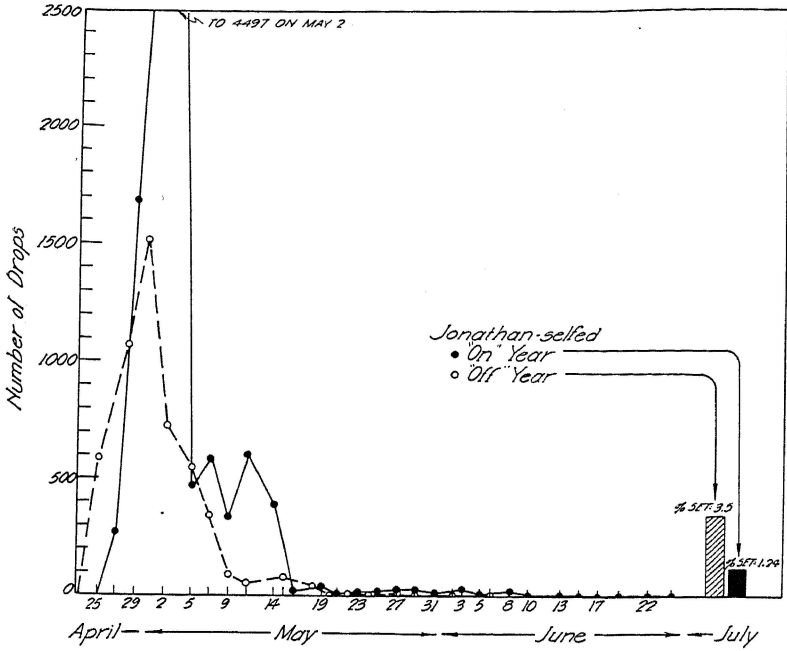


Fig. 22.—Distribution of drops of the Jonathan variety in "on" and "off" years when self-pollinated. See tables 6, C and 9, A.

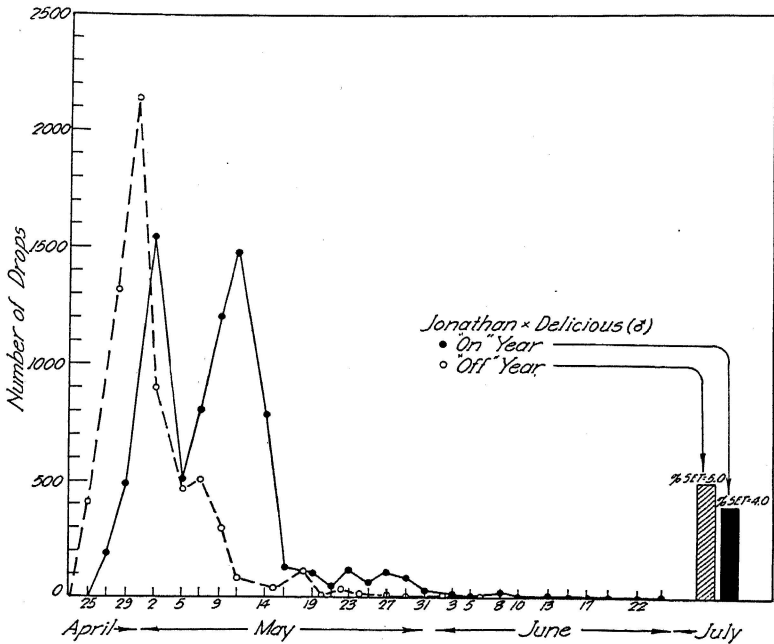


Fig. 23.—Distribution of drops of the Jonathan variety in "on" and "off" years when pollinated with Delicious. See tables 6, A and 9, B.

flowered fairly well. Again, the first three drops in this year are observable in the records, but they occurred somewhat earlier than in the "on" year. The fruit set, determined in July, was considerably higher in the "off" year than in the "on" year. The nature of abscission of immature Grimes apples in the "off" year was very much like that of the Jonathan (Figs. 24 and 25 and Tables 5-A, 10-A, 5-B, 10-B). The final percentage set of fruits was relatively high in both years.

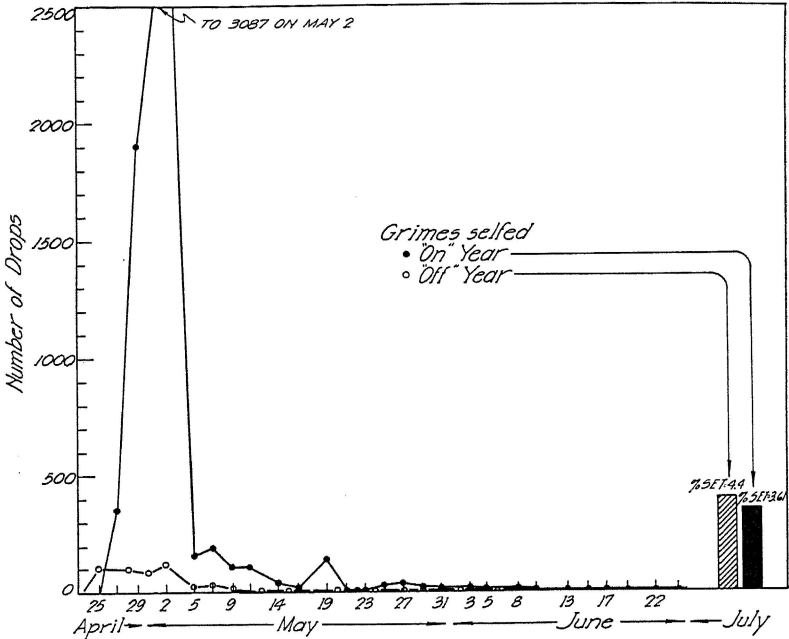


Fig. 24.—Distribution of drops of the Grimes variety in "on" and "off" years when self-pollinated. See tables 5, A and 10, A.

TABLE 10.—FRUIT SHEDDING RECORDS IN "OFF" YEAR OF THE Grimes VARIETY WHEN SELF-POLLINATED AND CROSS-POLLINATED WITH JONATHAN.

Date of collection of drops	A Self-pollinated	B Pollinated with Jonathan
April 25	105	503
April 28	104	320
April 30	84	483
May 2	122	202
May 5	29	47
May 7	30	111
May 9	16	59
May 12	9	9
May 15	7	7
May 18	17	22
May 20	1	14
May 22	1	2
May 24	1	2
May 27	0	1
May 29	0	1
June 2	1	0
June 6	1	2

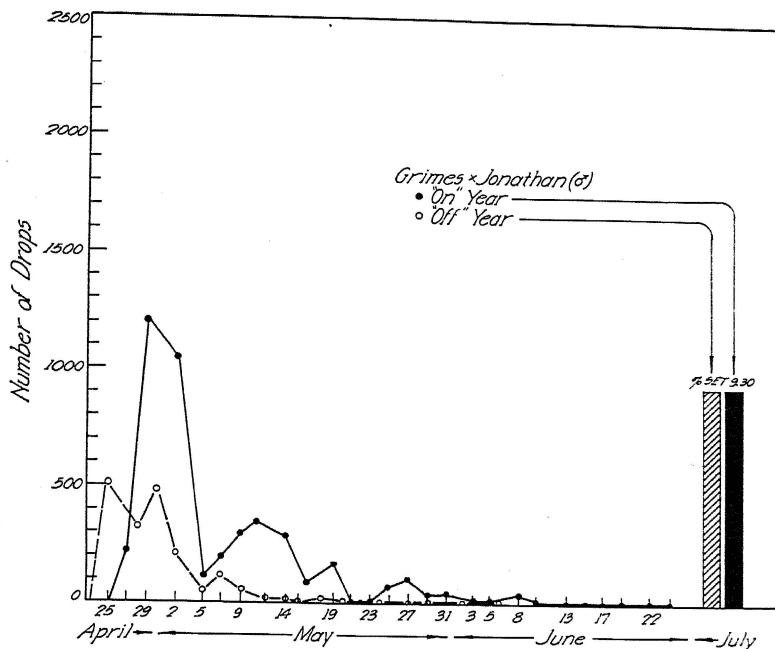


Fig. 25.—Distribution of drops of the Grimes variety in "on" and "off" years when pollinated with Jonathan. See tables 5, B and 10, B.

DISCUSSION

Any deliberation on the nature of abscission of immature apples must be guided by a recognition of the fact that our present knowledge of the subject is very limited. Further experimentation must be done and additional records have to be accumulated before a final decision can be made on the character and causes of this phenomenon.

The present investigation seems to have been extensive enough to show that four quite definite waves of shedding of young fruits occur in the cultivated apple. The first drop is usually very voluminous and often very protracted, thus leading one to suspect that not all the non-setting flowers (fruit) abscise as a result of the same cause. It is probable that a vast majority of the specimens in this, and possibly some of the second drop, consist of blossoms that have not been pollinated or in which fertilization did not take place. The idea that the whole fruit drop consists of such flowers is not tenable, in view of recent histological studies, which show the presence of embryos in at least some of these fruits (1, 20). Hence here, as in the case of other drops, embryo abortion is linked with the abscission of non-setting apples. But is embryo abortion the primary

cause of even a part of this drop? What stops these embryos in their further development? Is it a question of constitutional genetic differences as the main factors involved? If so, wherein lie these differences?

It is more than probable that a large and varying proportion of the first drop specimens are made up of abortive flowers. On older, but especially weaker trees, one may observe most any year blossoms that are subnormal in respect to the development of the whole or parts of the essential sexual organs, chiefly the pistils. It is doubtful whether such flowers are capable of participating successfully in fertilization and fruit setting. It has been found that various abnormalities and retardations exist in the development of the macro-gametophyte of weak apple blossoms (18, 4). Most probably in many of them gametic union does not take place and they drop promptly.* Here should be considered also a number of varieties, notably those of the Winesap group, in which disturbances exist during reduction division, leading to formation of non-functional gametes of both sexes. Such varieties often have a conspicuously heavy first wave of shedding of non-setting flowers (Tables 2, C and D, and 3, A, B, C, and D).

These observations tend to show that, considering the various possible causes of the first wave of shedding of apples, the drops may be separated into several (at least three) groups: (a) Structurally and functionally abnormal flowers, (b) Unpollinated or unfertilized flowers, and (c) Fertilized flowers (fruits) in which embryos abort early.

Fruits that abscise during the second wave of shedding show a slight development of the torus, thus suggesting that the flowers from which they arose may have been stimulated by fertilization or at least pollination (10). Whether all individuals of this drop contain embryos can be decided only by an extensive histological study. In the same variety and from the same tree, the second drop is practically always more extensive when the flowers are cross-pollinated than when selfed (Figs. 6, 7, 9, 11, 13, 14, 15, 17, 18, 19). Should this be considered as a circumstantial evidence that this drop is not caused by lack of fertilization but is of physiological origin?

The period of flowering, fruit setting and its development is in many ways a "critical time" in the yearly cycle of an apple tree. It is a time when "things happen." Really tremendous amounts of nutrient substances are required for the growth of various organs associated directly or indirectly with sexual reproduction (11). Moreover, vegetative development is also at its maximum then. Consequently one may anticipate that, under conditions of excessive fecundity, a shortage of some limiting substances may result

*Parthenocarpic fruits do not seem to occur as often in the apple as it was once believed.

leading to excessive competition among the young apples and a resultant drop.

Are the later drops, the third and the fourth, likewise caused primarily by competition among the fruits for the general or local food supply? Almost all of the specimens that abscise when they are 1 centimeter or more in diameter contain embryos in various stages of development (9, 1). As a rule, however, such embryos are smaller and fewer in drops (19) than in apples that remain on the tree. Therefore, they may be overlooked by the casual observer (15). With equally favorable positions on the spurs, in competition for nutrients and other indispensable environmental (both external and internal) factors, fruits with few and weak embryos most likely do succumb first. But how much more unfavorable an environment will it take to cause an apple, which has many and large embryos, to abscise, when one poorly supplied with "good" seeds will reach maturity? That the food supply, particularly nitrogenous, has a decided bearing on the fruit set, of this we have on record numerous positive results, but it has yet to be proven that the normal order of fruit shedding, its wave-like character, can be altered thereby.

Thinking of the sequence of the various waves of fruit shedding, the question naturally arises why do they occur with such striking regularity in all varieties and under all types of pollination. It has been shown that environmental factors can alter this normal trend but little, if at all (2). Evidently, then, the periodicity in abscission of the main drops is connected in some way with the seasonal development of the tree or parts of it. At the time of fruit setting and immediately thereafter other major organs (leaves, shoots, roots, etc.) of the apple grow rapidly. Does a correlation exist between the development of certain vegetative parts and fruit abscission? Of interest in this connection are the observations that very similar, regular, wave-like drops take place in the plum and other fruits (3, 1, 2).

It is very likely, of course, that the periodicity in fruit shedding is regulated by the various stages of the development of the fruit itself or of its embryos. Although being part of the "mother sporophyte," the apple fruit is a more or less independent organ with its own structural development. Are there particular "critical periods" in its growth during which certain environmental factors, largely of internal physiological origin, may cause it to drop? Similar vulnerable stages may exist in the life of the embryos—young sporophytes of varied genetic constitution but considerable similarity in their development. Naturally, the fate of the fruit is closely linked with that of the embryo.

Of the ten or more potential embryos in an apple not all are regularly initiated. And if produced, there is usually a difference

in the time of their conception and their growth rate. One will be easily convinced of this variability by dissecting carefully the seeds of very young apples. If some of the drops are controlled primarily by embryo development, then the circumstances are very diverse indeed. Particularly so due to the fact that each embryo undoubtedly has a different genetic constitution and possible inherent capacity for development. Brave volunteers are required to launch upon this uncharted "deep and dark sea," with genes of unknown character lurking everywhere.

Referring to the popular conception of the "first drop" and "June drop" in the apple, it is quite evident that in either instance these definitions are very loose and ambiguous. By "first drop" are commonly understood the first and second waves of shedding, which result from several distinctly different causes. Either the third or fourth drops, or both, are usually designated as the "June drop." While the first two waves of shedding are numerically high and incomparably more important, they do not loom so large in the minds of most fruit growers. This undoubtedly results from the fact that these drops are not conspicuous on the ground and disappear shortly. On the contrary, the comparatively large specimens that are shed in May and early June, making up the third and fourth drops, are very noticeable by their presence under the trees, where they remain for a number of days. They are "impressive," and thus one speaks of and writes about and emphasizes the "June drop."

The writer does not wish to be misunderstood by being considered unmindful of the fact that in some varieties (Wealthy, Duchess, Ben Davis, etc.) and in some years (favorable for a heavy set) the third and fourth drops may be very pronounced. Then, too, even a moderately small shedding of fruit late in the season may be often disastrous, considering the actual number of fruits then present on the tree. But, by and large, in most standard winter varieties of apples, the so-called "June drop" is not nearly so important as it is thought. If the percentage of flowers or fruits that absciss during the first two drops is not abnormally large, then, despite a heavy third or fourth drop, a good yield is usually assured.

SUMMARY

1. The cultivated apple exhibits four waves of abscission of non-setting flowers and immature fruits. They seem to occur at intervals of approximately 12-14 days and appear to be governed primarily by internal hereditary factors.

2. The first drop is usually the largest and possibly of a compound character. Frequently it overlaps with the second drop, which follows it in close succession. These two constitute what is commonly called the "first drop" of apples. They appear in all varieties and under all conditions of pollination.

3. The third and fourth waves of shedding of apples may be fairly pronounced or almost lacking. Fruits that absciss during these drops are of considerable size. Though numerically smaller than those of the early drops, they make their presence on the ground conspicuous and are popularly emphasized as the "June drop".

4. Some varieties, notably Delicious and those of the Wine-sap group, show a characteristic and pronounced early abscission of flowers and fruits, while others (Duchess, Wealthy, etc.) have more noticeable later drops of immature apples.

5. Under self-pollination, the first wave of abscission is usually very heavy and the others correspondingly lighter. Cross-pollination augments the second and third drops and may affect the fourth one also. The variety of the pollen does not seem to have any characteristic influence on the nature of shedding of apples.

6. No relationship appears to exist between the intensity of the last two drops ("June drop") and the final set of apples. A high yield of fruits may be produced though there be comparatively heavy late drops.

7. Apple varieties that flower in the "off" year show the same natural sequence of shedding as in the "on" year. There is, of course, a great difference in number of specimens that absciss in the respective years, making interpretation of records somewhat difficult.

8. A discussion is presented regarding the probable causes of the various drops. The diverse factors that may be responsible for the first shedding of apples are emphasized. Embryo abortion is thought to be the chief cause of abscission of the already enlarging fruit.

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