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The Low-Temperature Hazard to Set of Fruit in the Apple

By M. J. DORSEY

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The Low-Temperature Hazard to Set Of Fruit in the Apple

By M. J. DORSEY, Chief in Pomology

IN THE LATITUDE in which the main apple plantings of Illinois are situated, low temperatures during the normal period of bloom in early spring months are common. The frosts and freezes that occur then cause concern to apple growers year after year, since it is at this time that the succulent flower parts of fruit trees are particularly susceptible to injury. Little has been known, however, concerning the precise character of the injury which is caused when low temperatures occur.

The present study was therefore undertaken as part of the thinning investigations that have been under way at the University of Illinois for several years. Its purpose was first to determine the type and extent of the injury that may occur to the flower buds and flower parts during the dormant season as well as in the early spring; and second, to ascertain the extent to which the tissues recover from injury, particularly the tissues of the flower parts, pistil, and young fruit. It is hoped that the facts which the study has developed will enable growers to evaluate soon afterwards the effect of a freeze upon the set.

ORCHARD OBSERVATIONS IN OTHER STATES

Frost injury to the apple is a matter of frequent comment among fruit growers when the injury results in russet markings of various patterns on the fruit (Fig. 1). Typical cases of russetting are described in the reports of Jones,^{8*} Dorsey,^{4*} Howlett,^{7*} MacDaniels and Heinicke,^{9*} and others. In this connection, however, three references are of special interest because they deal with the injury which occurs in early spring.

Referring to the condition of the apple a week after being frozen, the writer, in a paper read before the Minnesota State Horticultural Society in 1918,^{4*} said:

"The pistils, seeds and core were brown—that is killed—and the skin separated from the young apple in patches or entirely. There were some variations found in the degree of killing. In some cases the pistils were not killed and in

*Thruout this bulletin these numbers refer to literature citations on page 170.

others the seeds were not. In all cases where the pistil, seeds and core were killed, the apple fell a few days afterward. Where these were not killed, and the skin only was affected by being broken away, these apples 'set' and matured. The skin being killed entirely or only part way around soon dried and turned brown, and with further growth of the apple, was torn away, leaving the surface underneath exposed. It was now necessary to form a new surface to this area left bare by the removal of the skin or epidermis."

These observations were made at the Fruit Breeding Farm near Excelsior, Minnesota, following a temperature of 27° F. on the night of May 12, 1918, when apples generally were "at or a few days past full bloom."

FIG. 1.—EFFECT OF A FREEZE UPON YELLOW TRANSPARENT

Some of the seeds were killed. The russet rings indicate incomplete mending.

A similar condition was reported by MacDaniels and Heinicke^{9*} in New York after a temperature of 24° F. had occurred on May 14, 1928, when about half of the apple flowers were open. These investigators said: "In many cases in trying to remove the petals the outer layer or layers of cells on the entire ovary and upper part of the pedicel

slipped off, adhering to the perianth." This freeze affected the flowers of all the varieties examined but the stigmas and ovules were uninjured. "It seemed as if sufficient injury had taken place almost to eliminate the crop" but a good crop was "harvested with most varieties."

More recently Rosen^{10*} reported as follows regarding the injury to apples in Arkansas after the freeze of April 2 and 3, 1936, during which the temperature fell as low as 20° F.

"... A peculiar type of frost injury to apple blossom buds observed shortly after the injury occurred may be worth recording. This consisted of a severance or disjunction of the outermost five to seven layers of cells of receptacles and pedicels from the remainder of the tissues, appearing as a cleavage line when the material was sectioned, and allowing the peeling of these outer layers as one would peel a banana. Evidently the peripheral injury to the buds had not extended deeper than these outer layers. Even here the injury in many instances was so slight that at least some of the protoplasts remained alive and functioned in producing new cells or enlarging those present so that within one to two weeks after the cleavage, the outer layers in many instances apparently had grown and become connected to the underlying tissues. In those blossoms which had not suffered injury to the pistils and which had not abscised shortly after the frosts, those outer receptacle and pedicel layers which had been loosened at first could no longer be peeled from the underlying parts."

A crop followed the injury observed by Rosen.

After the first observations upon this type of injury by the writer in 1918, an opportunity arose in 1923 to study the same phenomenon during the freeze of May 9 to 11 in the orchards in the vicinity of Martinsburg and Inwood, West Virginia. In this instance snow fell and the temperature was near the freezing point while the apple trees were in full bloom. The temperature varied in different locations from 26° to 30° F. during the greater part of these two days. A number of the important commercial varieties were examined immediately after the freeze and on all of them the receptacle could be lifted out of the skin. From the rather limited observations on this occasion it was assumed, since the injury appeared so severe, that the crop which followed was made up for the most part of those flowers which were either not injured or only slightly so.

ILLINOIS ORCHARD OBSERVATIONS

Freeze of 1936

When the freeze of 1936 came on in Illinois it seemed an opportune time to check again the general effect of freezing temperatures upon the apple during the early succulent stages. The official temperatures for April 3 and 4 at Urbana were 20° and 22° F. respectively.* This cold spell was followed by another one in Illinois in a little over two weeks during which the temperature at Urbana fell to 26° F. on April 22 and to 29° F. on April 23 (see table on page 166). When the first cold wave came, the earliest buds were showing pink; at the beginning of the second cold spell the most advanced flowers were just about to open.

Examination of a number of the more important commercial varieties on the morning of April 22, after the tissues had thawed, disclosed not a single flower in which the outer cell layers of the stem, receptacle, and calyx lobes had not been separated from the tissues below by the ice masses. After this fact and also the extent of injury which occurred to the ovules and other parts of the pistil were noted, interest centered around the way in which the apple had recovered.

It will be evident at once that if there is a crop following an early spring cold spell such as the ones just mentioned, there are two possible reasons for it: either sufficient flowers escaped injury to account for the crop, or a sufficient number must have recovered. It is of course conceivable that in a slight freeze or in a "settling out" freeze, injury may be more severe in some parts of a tree than in others, particularly in the lower part, or in the lower areas of the orchard;^b but after the freeze of April 22-23, 1936, not a single flower could be found in the Station orchard, either in the tops of the trees or on trees in the higher parts of the orchard, in which the "skin" had not been "frozen loose." In spite of this, however, there was a heavy crop in 1936.

Interestingly enough, Rosen^{10} was making his observations in Arkansas after this same freeze.

^bThe difference in injury to the upper and lower parts of a tree during a "settling out" freeze was shown in a fortunate test made on a peach tree in the orchard of W. S. Perrine near Centralia during the freeze of April 26, 1937. A registered thermometer was placed in the top and another in the bottom of a tree. The temperature on the night of the 26th fell to 26° F. The peach crop was killed about 3 feet up on the bearing surface but was uninjured on the upper part of the tree. At 5 o'clock the next morning the readings on the two thermometers showed a difference of less than half a degree.

Freeze of 1938

The separation of the tissues was again observed during the freeze that reached Urbana on the night of April 2, 1938. During this cold wave the temperature fell as low as 22° F. in some sections of the state, altho a minimum of 24° to 26° F. was more frequently reported by orchardists.^a The official minimum reading at Urbana was 26° F. for the night of April 2 and following the freeze the temperature was unusually low for the next ten days, ranging between 30° and 38° F. The freeze of April 2-3 was followed by still another in some areas in the western part of the state on April 9, during which the temperature again fell as low as 22° to 26° F.

During the April 9 freeze the apple trees were in various stages of advancement, from prepink up to the pink stage, in different parts of the state. At Urbana the most advanced clusters were not as yet showing the petals (full bloom did not occur until April 17 to 26). In the southern part of the state however some varieties were in full bloom. The danger point would therefore be somewhat higher there than at Urbana.

When the cold wave of April 2-3 was predicted it was decided to collect flowers from Jonathan during the morning of the 2d, before the cold wave reached Urbana, and examine them to see how far the mending process from previous freezes had progressed. This was done. Then at 9 a.m. on April 3, after a thawing temperature had been reached, flowers were collected from the same limb to determine the extent and type of injury from the freeze the night before.

The sectioned pistils showed that the break in the outer cell layers, which had occurred earlier, had almost mended before the freeze of April 3, but that during the freeze the typical break in the tissues appeared again. The mending process after this freeze was well under way by April 14. This instance is typical of what may be expected in recurring spring freezes and shows that mending once started may be broken, only to occur again when growing conditions are restored.

As always happens after such low temperatures, growers were interested in estimating the damage to the crop. A number of them noted the separated epidermis, since attention had been called to this type of injury at some of the horticultural meetings. The reports showed that wherever the temperature fell as low as 22° to 24° F.

^aIn order to check the local readings, some of the thermometers were compared with a registered instrument. The comparisons showed the local readings to be approximately correct.

there was serious injury. At Mt. Sterling, where the temperature was 24° F. between 10:30 and 11:00 on the evening of April 2, Mr. O. G. Jones^a estimated the killing in Delicious to be 90 percent, Jonathan 60 percent, Golden Delicious 30 percent, and Grimes 25 percent. The damage in the southern part of the state was extensive in the lower orchards at somewhat higher temperatures than at Mt. Sterling, because the bloom was further along.

As the season developed there was an exceptionally heavy second drop over the state, so heavy in fact that there was a light crop on many varieties. The differences among varieties in their ability to withstand the 1938 freeze were approximately as follows: The early varieties—Duchess, Yellow Transparent, and Wealthy—came thru the freeze in best condition. Willow, Golden Delicious, and King David ranked next. Grimes, Jonathan, Stayman, and Gano came next, with Delicious generally proving most susceptible to this type of injury.

Since snow and sleet sometimes accompany the cold spells, as was the case in early April, 1938, a word might be added concerning their effect upon apple bloom. Neither snow nor ice, as such, seem to do much damage aside from the breaking of limbs. The real cause of the injury is the low temperature reached. In 1938 apple bloom, and peach bloom as well, over a large area in the state, was packed in a thick ice coating for nearly 24 hours on April 9, with no apparent injury attributable to the ice. When sleet is accompanied by killing temperatures, it is tempting to ascribe the injury to the ice coating rather than to the low temperature because the ice coating is more conspicuous and unusual; but the temperature reached rather than the sleet is the cause of the injury.

CONTROLLED FREEZING TESTS

The freezes in 1936 and 1938, reported above, were typical of those which may be expected in Illinois in April and sometimes as late as May (see table on page 166). Temperatures are often low enough to injure the pistils but not low enough to kill the pistil or the ovules. Since the orchard observations showed that all flowers might be injured during a freeze, it seemed necessary to determine whether some of them might escape injury if subjected to temperatures above the actual killing point.

It was therefore decided to determine experimentally the approxi-

^aPersonal letter to Dr. V. W. Kelley under date of April 9, 1938.

mate temperature at which ice forms in the succulent apple tissues at the prebloom stage; and with this information at hand, to see whether all flowers are affected alike in temperatures approximating this level. This was the object of the following controlled experiments in storage rooms in the spring of 1936, in which, it will be seen, the drop in temperature was more gradual than is sometimes the case out of doors.

At the outset it should be recalled that in woody tissues ice crystals appear when the temperature reaches about 26.5° F. (Wiegand^{13*}) and in the peach fruit bud, at about 28° F. on longer exposures and at 27° F. on shorter ones (Dorsey^{4*}). Considering the many variables involved, such as variety, growth stage, previous weather conditions, etc., some slight differences may be expected in the temperature at which ice crystals form in the succulent flower parts of the apple. It seems likely, however, in the light of the orchard observations, that beyond a certain point, in spite of these variables, all flowers would be affected. This proved to be the case with flowers brought directly into the cold-storage room, to a temperature of 27° F., on April 25, two days after the 1936 freeze. At this time some of the pistils seemed somewhat withered, but the ice masses reappeared in the broken zone in spite of this. Of the hundreds examined, the ice masses were present in every one after two hours' exposure in a room at 27° F. This checked with the findings in the orchard, altho the temperature in the storage room was not quite so low and the exposure probably shorter.

This point was of sufficient interest to prompt further tests with older pistils. So on May 18, twenty-five days after the freeze of April 22-23, when there was no apparent evidence of its effect, limbs of Delicious, Grimes, and Jonathan were brought in for study. These limbs, loaded with fruit about half an inch in diameter, were placed with the freshly cut ends in water and run thru the following temperature changes:

4:00 p.m., limbs put in cold storage at 50° F., cooling system turned on.	7:00 a.m., temperature 40° F.
6:00 p.m., temperature 46° F.	8:40 a.m., temperature 37° F.
9:00 p.m., temperature 45° F.	11:00 a.m., temperature 38° F.
11:00 p.m., temperature 44° F.	1:00 p.m., temperature 37° F.
1:00 a.m., (on the 19th), temperature 42° F.	3:40 p.m., temperature 30° F.
5:00 a.m., temperature 41° F.	4:10 p.m., temperature 29° F.
	5:00 p.m., temperature $27\frac{1}{4}^{\circ}$ F.

When the temperature of the room reached 32° F., the young fruits were frequently examined for ice crystals. These were first in evidence about 5 p.m., when the room registered $27\frac{1}{4}^{\circ}$ F. The cooling

FIG. 2.—PHOTOMICROGRAPHS SHOWING INITIAL TISSUE BREAKS IN FRUIT AND IN LEAF RUDIMENTS OF THE APPLE RESULTING FROM FREEZING TEMPERATURES

- a. Initial break in artificially frozen Grimes, showing the separation of the cells.
- b. Tissue break in leaf rudiments in Jonathan during the first fall freeze, November 24-28, 1938.
- c. Separated outer cell layers of the flower bud in Delicious by the first fall freeze, 1938.
- d. Extent of tissue mending in Jonathan by March 20, 1936.
- e. Initial outgrowth of cells from the broken surface (Grimes).
- f. First steps in mending process three days after fruit was frozen (Jonathan).
- g. Extent of mending in separated surfaces of Grimes 10 days after freeze of April 22, 1936.
- h, i. Grimes 17 days after the freeze of April 22, 1936.
- j. Completion of the mending process in Grimes 27 days after freeze of April 22, 1936.

system for this room was cut off at this point, which allowed the room to warm up gradually. At 9 a.m. the next morning the thermometer stood at 44° F.

An attempt was then made to lower the temperature gradually to about 28° F. in order to determine whether or not all the fruits would be injured. Of the hundreds of apples on these limbs, not a single one escaped injury. The kind of rupture that was typical on these varieties is shown in Fig. 2, a; it will be seen that it extended entirely around the pistils. The ovules were not injured, altho the tissue under the skin had turned slightly brown to a depth of about $\frac{1}{16}$ of an inch.

After making this test it seemed desirable to repeat the experiment with still larger fruit. Accordingly one of the tubbed trees of Shackelford, bearing apples about $\frac{3}{4}$ inch in diameter, was placed in the following temperature changes: first, in the storage hallway at 40° F. for three hours; then directly into a storage room at 32° F.; and this room was then gradually lowered to 28° F. At the latter temperature ice formed in the outer tissues of the apples, as before, and the leaves appeared water-soaked and wilted. After a five-hour exposure to this temperature, the tree was moved into one of the storage rooms at 40° F., held there for about two hours, and then moved into a greenhouse where the temperature was held at 65° to 85° F. In the greenhouse the leaves soon regained their normal appearance and showed no external evidence of injury from the freezing temperatures to which they had been subjected. The skin of the fruit, however, was broken loose, tho there was still no apparent injury to the seeds in any of the twelve fruits cut open.

After being in the greenhouse for about five days, the same tree was again put into the freezing chambers as before. This time, however, the temperature was lowered to 25° F. and held at that point for four hours. At this temperature the fruit froze badly, disk-shaped crystals being formed all thru the inner tissues in addition to the palisade-like crystal layer immediately under the skin. The leaves were even more water-soaked in appearance than at the first exposure. The nature of the injury caused by the large ice masses in the tissues of the larger fruit can be seen in Fig. 3. All the apples remaining on the tree after the first exposure were killed.

The tree was removed from the low-temperature room in the same gradations as in the first instance; and when it was put back into the greenhouse, the leaves again regained their normal appearance. There was browning in the bark in the cambial area, but the tree and leaves made an apparently normal growth for the remainder of the season.

FIG. 3.—ARTIFICIALLY FROZEN APPLES

Note separated layers of "skin" cells and the ruptured flesh in the larger apples.

An interesting result from freezing the fruit as late as this was observed under the binocular microscope. In cutting thru the fruit it seemed at first that the skin was completely separated from the flesh beneath. But when the skin was pulled off from the wilted fruit, irregular strips of cells were found to connect it with the tissue below. These strands would, no doubt, serve as connecting tissue if mending were to take place after freezes at growth stages as late as this.

From these controlled freezing tests it may be concluded that the tissues of the young fruit are broken by the ice masses at approximately 28° F. The ovules, however, are not injured to any great extent at this temperature. In the freezing tests made at different stages in the fruit's development, the temperature at which the outer cell layers were separated did not seem to vary appreciably. It should be noted also that the orchard observations check closely with the results obtained in these controlled freezing tests.

TIME OF INJURY

The observations thus far reported were confined to relatively late stages in the early growth of the apple. It was realized during the winter of 1937-38, after the studies of the recovery of the tissue ruptures had been completed, that earlier observations would be highly important. On collecting material in January to study midwinter conditions in the tissues of the flower and leaf rudiments it was found that the typical separations had already taken place; so then it seemed necessary to determine whether or not these separations occurred during the first fall freeze.

Accordingly, when the first freezing temperatures occurred in the fall of 1938, material was collected for microscopic study. This freeze reached Urbana November 24 and lasted until the 28th. On November 25 the temperature fell to 11° F. Typical ruptures, which occurred in the tissues of the flower and leaf rudiments during the first fall freeze, are shown in Fig. 2, b and c. These photomicrographs of Jonathan and Delicious show the sharp line of separation between the outer cell layers and the deeper tissues. The same condition was present in Stayman and Grimes.

In 1936 flower buds had been examined about every three or four days during February and early March, and in this interval some mending was evidenced by the slight pushing out of the cells from the broken surfaces. By the latter part of March the cells had bridged the break (Fig. 2, d).

The persistence of the broken tissues might be expected in the winter in view of the low temperatures and the relative inactivity in growth. Even if partial or complete mending did take place during the winter, the tissues would again be broken with each successive cold spell.

The absence of mending in the tissue during the dormant season may be looked upon as an adaptation to fluctuating temperatures. It was surprising, tho, to find the outer cell layers of the flower buds and leaf rudiments broken away so early in the dormant period.

NATURE OF INJURY

The break in the tissue caused by freezing comes as the result of a cleavage between the cells, presumably at the middle lamella, rather than as a tearing or rupturing of the cell walls. The plane of the break can be seen clearly in many of the microphotographs in Fig. 2.

FIG. 4.—EFFECT OF A FREEZE UPON FLOWER CLUSTERS AND FIRST LEAVES
Note crinkled appearance of leaves and the small size (α) of some of the flowers that were killed. This freeze occurred April 2-4, 1936.

In the three varieties of apple studied most extensively—Grimes, Jonathan and Delicious—the cleavage line always occurred deeper on the stem than on the fruit or calyx lobes. In a large number of observations the typical separation was six to eight cells deep on the stem, three to five on the fruit, and two to three on the calyx lobes. There is some irregularity in the line of separation, as these figures indicate, but the above depths in terms of cell layers in the cross section are approximately correct.

The fruit looks plump and smooth while frozen and changes but little in external appearance when it is first thawed. In a few days, however, the severely injured pistils take on a yellowish cast and may undergo slight enlargement before dropping off about two weeks later. The loss of the pistil follows only a deeper, more severe freezing which has killed or severely injured the ovule or seed; if the fruit has not been severely injured it will recover.

The drying and withering of artificially frozen fruits can be seen in Fig. 3. Note particularly how the epidermal layers are broken away and separated in some of the smaller apples. Fruits like those illustrated here fall in large numbers within a week or 10 days after the freeze. The peculiar crinkled appearance of Jonathan leaves after the freeze of April 2-4, 1936, can be seen in Fig. 4. This type of leaf injury could easily be confused with spray burn.

When the flowers are frozen at full bloom or soon after, the receptacles, as noted previously, can be pulled out of their skin. As one grower expressed it, they “slip their skin.” Very few of the pistils, however, develop into russeted apples (Fig. 1) as a result of this degree of freezing. When the ovules are injured or fertilization is interfered with as the result of low temperatures, development is of course very seriously retarded in the pistil as a whole. The effect of frost injury upon the set, however, should not be confused with the effects of poor pollination or low vigor.

MENDING OF THE INJURY

What now is the ultimate effect of the type of injury that results so generally from freezing temperatures? If all the flowers are injured by a freeze and a crop follows, it is obvious that some of the flowers must have survived in spite of the injury. This was found to be the case in the reports reviewed.

In Fig. 2 the first evidence of healing in the tissue that has been broken by freezing is the outward growth of a few cells from the sepa-

rated surfaces. While there is somewhat more mending growth from the inner surface of the rupture, yet many instances can be found of the initial cell extension taking place from the outer surface. Some of the photomicrographs show a chain-like bridge from one surface to the other (Fig. 2, g, h, and i). After the first bridges are formed, others soon follow, and in two to three weeks the mending of the break is complete. The series can be followed in Fig. 2, e-j.

The cells which grow outward from the two separated surfaces of the break unite at the point of contact, where the surfaces are moist. There is probably some deposition of cementing material here, altho there is no evidence of an increase in the thickness of the wall as a result of the union. When the mending process is well under way the break does not appear conspicuous in cross section because there has been considerable gliding growth as the cells fit together. As the fruit enlarges, the lace-like structure of the cross section of the restored area soon becomes more compact and the outer cell layers undergo the usual differentiation in the formation of the skin.

After the freeze of April 22-23, 1936, the ruptured tissues showed evidences of mending in four to six days, the first evidence being the pushing out of occasional cells from the surfaces of the break or cleavage. The maximum daily temperature of the week following this freeze was as follows: 61°, 77°, 69°, 71°, 75°, 70°, ending with 75° F. on April 30.

A word should be added as to the relationship between injury to the ovule and the mending process. When the temperature falls to the point where all the ovules in the young fruit are killed, the mending process is of little consequence because the pistil will drop anyway. When only a part of the ovules are killed, however, the mending process continues and the fruits which set are characterized by a low seed content. Mending may seem to take place only in the more vigorous pistils, whereas in reality those pistils that survive become vigorous because of growth adjustment to them. When growth activity then is resumed after a freeze which has eliminated some of the fruits, competition between the surviving pistils is resumed. The type of parthenocarpic development in apples noted by Whipple^{12*} has not been observed in Illinois.

Since injurious temperatures are more likely to occur before bloom than during or after bloom, it is probable that ovule injury is an important factor some seasons in reducing the set or in reducing the seed content of the apples. It is a matter of frequent comment among horticulturists that more seeds are found in apples some seasons than

in others. The difference, however, is generally ascribed to conditions at the time of pollination and fertilization. While conditions at this time are of great importance, there is a possibility that part of the ovules might have been eliminated prior to the time of pollination and fertilization because they were killed by low temperatures.

From this analysis of the effect of a freeze upon the set of apples, and potentially upon yield and the thinning problem, it will be apparent that the mending process becomes an important factor in production. At higher temperature levels, when the ovules are not injured, the mending of the tissues is in itself of primary importance in the subsequent set of fruit. However, at lower temperature levels the extent of ovule injury becomes the dominant factor in the persistence of the fruit because it limits or conditions the mending process.

LEAF INJURY

The injury which the first leaves that come out with the flower cluster may suffer from freezing is much more conspicuous than injury to the flowers. The peculiar crinkled appearance of frozen leaves is shown in Fig. 4. Since these leaves were unsprayed, there can be no doubt about the condition illustrated being traceable directly to the freezing. As the injured leaves grow, breaks in the margins or along the veins occur frequently. In some varieties a peculiar bronze color develops on the leaf margins, as was observed with Jonathan and Delicious in 1938. The leaves of the fruit buds are somewhat more advanced than those in the leaf buds proper, and for that reason they seem to be affected most; but when the leaves of the leaf buds come on they assume an appearance similar to that of the injured fruit-bud leaves.

In the first leaves the ice masses separate the lower layers of surface cells over large areas. In some parts of the leaf the pocket thus formed can be seen readily with the unaided eye when a cut is made vertically thru the leaf. Generally, however, the break is most conspicuous along the veins and midrib. A leaf thus broken apart may not grow together again. Sometimes the lower surface is killed, in which case it turns brown and even sloughs off. Such leaves are easily injured by sprays. Fortunately the first leaves are soon left behind; and as the new growth pushes out, many of them, especially if injured, are shed. The appearance of the foliage thus soon changes because the first leaves are so definitely overshadowed by the new ones which come on in the early spring growth.

TEMPERATURE DANGER POINT

Apple growers will now be interested in the approximate point at which low temperatures at different times of the year or at different growth stages become a factor in fruit injury.

The data on the approximate killing point in the different parts of the apple flower have been summarized in the graph (Fig. 5) appearing on page 164.

The temperature at which ice forms in the flower rudiments has been found to be near 28° F. thruout the dormant season. This is about the point at which ice forms in the extracted juice of fruit-tree twigs (Chandler^{2*}). This point may vary slightly among varieties or under different growth conditions or at different times during the season, but it is above the temperature at which the tissues are killed. Since it is fairly constant, it is represented by a straight line drawn horizontally across the growth stages.

The curve showing the injury or killing point of the flower buds indicates that the apple will withstand very low temperatures during the early and midwinter months without being killed. Even the record temperatures of the winter of 1935-36, which reached as low as -25° F. in some places in Illinois, did not cause serious damage to the apple. The curve for low-temperature injury to the dormant bud has accordingly been started at -25° F. The danger point for each of the other growth stages is based on controlled freezing tests and orchard observations. With so many variables to reckon with, it is, of course, possible in drawing this curve only to approximate the killing point of the tissues. It is believed, however, that the minimum temperature which the flower parts will endure is about as represented by the solid line in Fig. 5.

The curve showing the approximate killing point of the ovule is drawn a few degrees below that for the flower parts and the young fruit. The crop is endangered when this point is reached. The initial growth stages of the ovule appear somewhat earlier than the beginning of this curve, but the observations as to its injury were limited for the most part to the later stages. The differential in the injury or killing point of the ovules and the receptacle sometimes appears greater than shown here, but the artificial freezing tests indicated that the curve as drawn is approximately correct.

When conditions prevail which injure the ovules, some damage may also be expected to occur to the pistils. In 1938 many flowers showed some pistil injury without the ovules being affected. When injury

FIG. 5.—TEMPERATURE DANGER POINTS DURING DIFFERENT STAGES IN THE GROWTH OF THE APPLE

This graph shows the approximate temperatures at which injury may be expected to occur. The buds will withstand very low temperatures during the early and midwinter months.

to the ovules and styles occurs at temperatures of 22° F. or below, both the ovules and styles tend to be killed as a unit. This condition was seen most frequently between the breaking of the buds and the cluster-bud stage. Since these structures all seem to possess about the same degree of hardiness, the curve for ovule injury only has been drawn in Fig. 5.

A curve for pollen or anther injury has not been included in Fig.

5 because it is difficult to get accurate data upon this point. Pollen develops somewhat earlier than the ovule, and at the prepink stage the grains have two nuclei and a fairly thick protective outer covering. When the temperature is low enough to kill the ovules at any stage before dehiscence, pollen development is interrupted because the flower as a whole is killed. About the time of dehiscence, however, the pollen is seldom injured when there is a complete kill in the flowers. The order of hardiness would then appear to be pollen, ovules, and receptacle.

FREQUENCY OF FREEZING HAZARD

With the approximate limits to the temperature endurance of the flower parts mapped, it will now be of interest to see how often injurious temperatures may be expected after the buds open in the spring. A summary of the blooming periods of the apple at Urbana during the years 1901-1940 inclusive and the number of times the temperature fell below 30° F. during April and May has been brought together in the accompanying table (page 166). Since the advance of the season north and south is about ten to twelve miles a day, blooming dates in other parts of the state can be estimated accordingly.

This summary shows that the apple usually blooms at Urbana during the latter half of April and the first half of May. Within these years the earliest bloom was in 1910, when the flowers opened April 2. The latest bloom was in 1920 and 1926, when the flowers opened on May 6. Thus there has been a range of more than a month at Urbana between the earliest bloom and the latest. The early bloom of 1910 was followed by a freeze on April 23 and 24 which resulted in a complete crop loss. Temperatures below 30° occurred only once in May: on May 1, 1903, when 26° F. was reached.

The increased hazard from freezes when the bloom is early will be apparent from a survey of the temperature records. The danger point from low temperatures shown in Fig. 5 should be studied in the light of the temperatures which may be expected during the spring months. In only seven years during the forty-year period (1907, '12, '13, '33, '34, '35, and '37) did the crop escape tissue injury during the critical growth stages of April and May. In the other thirty-three years there were temperatures of 28° F. some time during these two months, and consequently there was tissue injury or an interruption in the mending process. In only two years (1910 and 1929) were there temperatures low enough to cause tissue injury in the period following bloom.

Nineteen-ten was the only year when the crop was killed outright. However, in 1903, 1927, and 1929 the temperature during the blooming period fell to such a point that, while there was not a complete kill, the set was greatly reduced.

GENERAL DISCUSSION OF OBSERVATIONS AND EXPERIMENTAL FINDINGS

From the above analysis it is evident that in determining the effect which low temperatures during the formative period of the flowers of the apple have upon the apple fruit, temperatures above the killing point, as well as below it, have to be reckoned with. When a single flower or the flower cluster as a whole is killed by severe freezing in the dormant bud, the fact that suppression has taken place may be overlooked because the rudiments are so small at this time, altho Whipple^{12*} points out that when killing occurs early the cluster scar can be seen on the spur when the new growth has advanced far enough. Later on when the flower parts are larger, as at the prepink stage, the entire cluster in the more susceptible varieties is frequently killed by low temperatures. When killing occurs in this way, the dead parts are cut off in a group by abscission. If only a part of the flowers in the cluster are killed, those eliminated in this way abscise at the base of the pedicel. Outright killing at different growth stages thus sometimes occurs, but this phase of the low-temperature effect is not so serious with the apple as is injury at higher temperatures.

Loss of flowers or clusters from low temperatures should not be confused with the normal drops due to incomplete fertilization. That there has been confusion is due to the fact that abscission as the result of freezing may not occur until some time after the freeze and may coincide with abscission due to incomplete fertilization. Howlett,^{7*} for instance, found that when pistils were injured by a freeze which came on after the first drop, the frozen pistils did not fall until the beginning of the second drop. It is quite possible, however, that ovule injury is sometimes an important factor in the first drop, because in such flowers fertilization would be prevented and further development would thus stop at a fairly definite point without gametic fusion. The time of abscission of flowers or pistils killed by low temperatures would therefore be determined largely by their stage of development when killed.

Frost markings of various patterns can often be traced directly to the tissue breaks in the outer cell layers at temperatures above the killing point. These markings or russetting appear to be much more numerous some seasons than others. Sometimes the russetting on the

fruit is primarily toward the stem end; at other times it is more central or even localized about the calyx. In either case growth conditions during the mending process may be an important factor in the development of the russeted surface. It is probable also that recurring freezes which would interrupt the mending process would have a bearing upon the initiation of a corky surface layer. The studies of Bell^{1*} show the formation of cork cambium when the outer layers are killed. If it were not for the mending process, however, there would be a complete russet surface on the entire crop whenever the temperature fell low enough to break the outer tissues loose.

The possible confusion of this type of injury with the so-called "spray burn" has been discussed by MacDaniels and Heinicke.^{9*} It was pointed out by those investigators that russetting occurred on unsprayed trees. It is quite probable, however, that on sprayed trees the mending process may be disturbed by the spray applications. The early-spring spray schedule calls for sprays at a time when the freezing hazard is still great. Any tissue ruptures that might occur from the prepink stage onward would undergo a good part of the mending process during the time when the first three sprays are put on. With a broken layer only three cells or so thick over the young fruit, it is possible that the stomatal openings may even permit the entrance of toxic substances directly into the rupture and in this way interfere with the cell growth and union in the mending process. If, however, the mending is not interfered with, it is difficult to see how there could be much relationship between spray injury and the breaking away of the surface layers by freezing unless the epidermal cells are rendered more susceptible to injury by being separated.

Finally consideration should be given to the location of the break in the tissues. Why does it occur in the fruit three or four cell layers deep and not nearer the surface or still deeper?

The prevalence of intercellular spaces in the zone of the break is undoubtedly an important factor in the location of the break. The outer surface of the apple is, of course, exposed to the freezing temperature first; then as the water freezes out of the outer cells, it crystallizes in the outer intercellular spaces first. Once the process starts in this zone it seems to be added to from both directions. In the deeper tissues the ice masses are not continuous but are well distributed in the tissues, thus making a similar adjustment possible in local areas. The latter condition, however, occurs only with the larger fruits and is not found even at killing temperatures previous to full bloom or soon afterward. Size and intercellular spaces thus both in-

fluence the location of the ice masses. With these two factors operating, the masses first form where it is necessary for them to form—in the outer zone of intercellular spaces. The adjustment to freezing thus started in the tissues becomes continuous as the exposure to low temperatures is continued.

Freezing injury is thus found to have a bearing upon the thinning problem when the injury is severe enough to reduce the set to a point where thinning is unnecessary. The extent or severity of the injury can generally be determined immediately after a spring freeze by the brown appearance of the ovules, but the crop reduction cannot be evaluated for certain until after the second drop.

SUMMARY AND CONCLUSIONS

This study deals primarily with the recovery of the apple flower from injuries which occur when the temperatures are low enough to rupture certain tissues but not low enough to kill the ovules.

When orchard temperatures reach as low as about 28° F. during the dormant period or in early spring, ice masses appear in the tissues of the flower parts, the speed of their formation depending upon the precise temperature level reached. The cells are broken apart apparently at the middle lamella and are not often torn or ruptured.

The separation of the tissues in the leaf and flower rudiments occurs with the first fall freeze if the temperature reaches as low as 27° or 28° F. In the latitude of Urbana, where growing conditions seldom prevail during the winter months, the ruptures persist during the dormant season.

In the early spring, as conditions become favorable for growth, the tissues begin to mend. This process, however, is interrupted with each recurring freeze. When conditions finally become favorable, the mending process is completed within two or three weeks.

The breaking or rupturing of the epidermis of the pistil or young fruit does not necessarily reduce the set, for recovery from this degree of injury is rapid. When, however, the temperature is low enough to kill the ovules, the set may be greatly reduced.

If the mending process is interrupted, so that the skin does not unite completely with the inner tissues, various patterns of russetting may be formed on the new surface by the cork cambium. Since "spray burn" may also result in the killing of the epidermal cells, it is easy to confuse it with freezing as the cause of the russet surface that forms on frozen fruits. The uniformity with which the mending

process takes place will thus be seen to have an important bearing upon the finish of the fruit.

In the latitude of Urbana late freezing temperatures low enough to affect the set of fruit may be expected to occur during the bloom of apples about one year in three. The likelihood of damage from low temperatures is increased by an early bloom.

In evaluating the effect of a freeze in which the temperature reaches or falls below the killing point of the ovules, the grower should first make an examination of the ovules. If all the seeds are killed in a large proportion of the flowers, the set may be light, especially if the weather is unfavorable at the time of pollination. On the other hand, if only a part of the seeds are brown in most of the crop, the set may not be affected by the freeze. If there is only a separation of the skin from the young apple and no injury to the seeds, the crop will generally not be reduced because the injury will mend if there is favorable growth vigor in the tree.

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