HISTOLOGICAL STUDY OF TISSUES FROM GREENHOUSE TOMATOES AFFECTED BY BLOTCHY RIPENING[1]

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INTRODUCTION

The appearance and quality of greenhouse tomatoes (*Lycopersicon esculentum*) maturing in late spring and early summer are often impaired by red and colorless markings, commonly called blotchy ripening. In some cases the percentage of irregularly ripened fruits is less than 1 percent, while in others it may be as high as 50 percent. Investigations as to the nature of the disorder and methods for its control are being conducted at the Michigan Agricultural Experiment Station. This paper presents, as a part of these investigations, the results of a histological study of the tissues from blotchy-ripened fruits.

EXTERNAL APPEARANCE OF BLOTCHY RIPENING

Blotchy ripening is primarily a disorder of the spring crop of greenhouse tomatoes maturing in May, June, and July and is of little consequence to the fall crop maturing from October to January. Throughout the North Central States it rarely occurs under field conditions, although a few fruits showing all the characteristics of the disorder were observed during the period of the severe drought of 1934.

In affected fruits areas of the outer wall[3] (pericarp) fail to develop and color normally. The individual blotch may be relatively large, involving from 25 to 50 percent of the entire surface of the fruit, or may be so small that it is not readily distinguishable. A fruit may show only one small blotch or several large blotches; large and small blotches may be formed on the same specimen. No sharp line of demarcation separates the green or white areas from the normal red portions; they merge gradually. Though these areas may appear on any portion of the fruit, they generally radiate from the pedicel attachment. Blotchy fruits in which all portions of the fruits are involved are shown in plate 1. As the fruits approach maturity these areas remain hard and green; and as ripening proceeds further, they assume a waxy or glassy appearance which may be accompanied by a sunken or pitted condition.

The vascular bundles lying beneath these clear, glassy blotches invariably appear to be brown or black and necrotic. This condition may be observed through the epidermis in many fruits. An affected area may be confined to one of the furrows formed above the interlocular walls of the fruit; such areas have been frequently observed immediately above the main bundle of a carpel. Transverse cuts made through a blotchy fruit (pl. 2, *A*) show that only the outer wall is affected. Usually there are small discolored regions in the center

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[3] The term "outer wall" as used in this paper does not include the partitions between the locules.

of the blotch which have the appearance of necrotic vascular bundles. In severe cases cavities may be associated with the affected tissues. The discolored portions are found only in the distinct blotches and do not occur in the normally ripened portions. Longitudinal cuts (pl. 2, *B*) reveal the apparently necrotic bundles and associated tissues even more strikingly than do the transverse ones. As shown in the longitudinal cuts this appearance of broken-down tissues is confined entirely to the blotchy areas.

The disorder is apparently restricted to practically mature fruits. Fruits in all stages of development have been dissected and examined for evidences of blotchiness. No immature fruit has shown any detectable signs of developing into blotchy fruit. The first evidences of blotchiness have been observed only after the fruit begins to develop color, which is usually from 2 to 5 days before it is ready to harvest.

LITERATURE REVIEW

Bewley and White (*2*)[4] attempted to dissect tomato fruits so as to expose the vascular system, but "owing to the delicate nature of the individual strands", abandoned this method and adopted clearing methods. They carefully removed the skin of a half-ripe fruit, scraped away the superficial tissue, and exposed the external portion of the vascular system. They presented drawings showing that the veins radiate from the stem end, and that in the proximal half of the fruit there are few cross connections, while in the distal half the veins anastomose to form an intricate network. By clearing a fruit thus prepared in xylol following alcohol they obtained "a good idea of the vascular system of the entire fruit."

Their examinations revealed certain differences between the vascular bundles of blotchy fruits and those of healthy fruits. "The bundles of blotchy fruits seemed somewhat thicker than those of healthy fruits, owing to the spongy nature of the cells immediately surrounding them. Necrosis of the bundles frequently occurs" (*2, p. 325*). Drawings are shown of necrotic bundles appearing beneath distinct blotches. In another illustration they showed an affected bundle with an adjacent group of "corky cells" and stated that "such cells occur frequently in blotchy fruits." By means of a hand lens they observed "the presence of gaps or canals in the parenchyma bordering the necrotic bundles." The walls of these cells were brown and necrotic. Although no mention is made of the fact, their drawings indicate that plugging of the tracheae accompanies the necrosis.

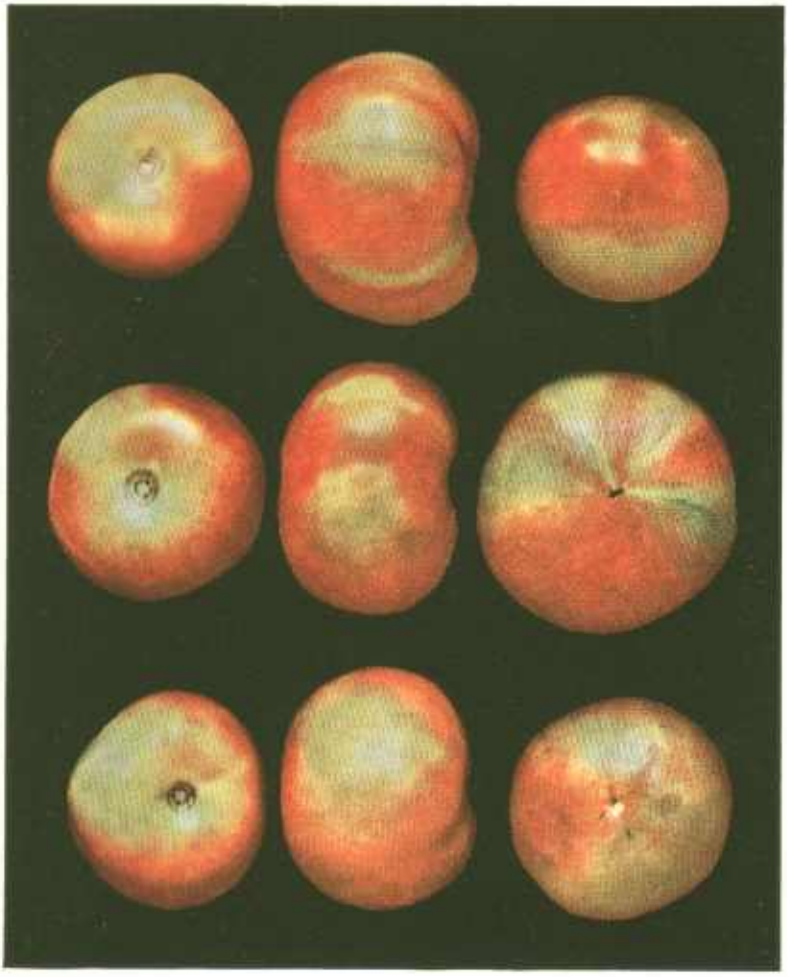
Bewley and White (*2, p. 337*) from their results over a 5-year period (1921–25) concluded that "blotchy ripening of tomato fruits is the result of malnutrition in respect of potash and nitrogen", and "may be reduced to less than 1 percent. by suitable applications of sulphate of potash and sulphate of ammonia." However, they did not attempt to connect "the necrosis of the bundles" with these nutrient deficiencies.

Seaton's investigations of the disorder [5] (*12*) indicate that blotchy ripening is not a nutritional disorder arising from soil conditions. He has advanced the hypothesis that the withdrawal of water from the

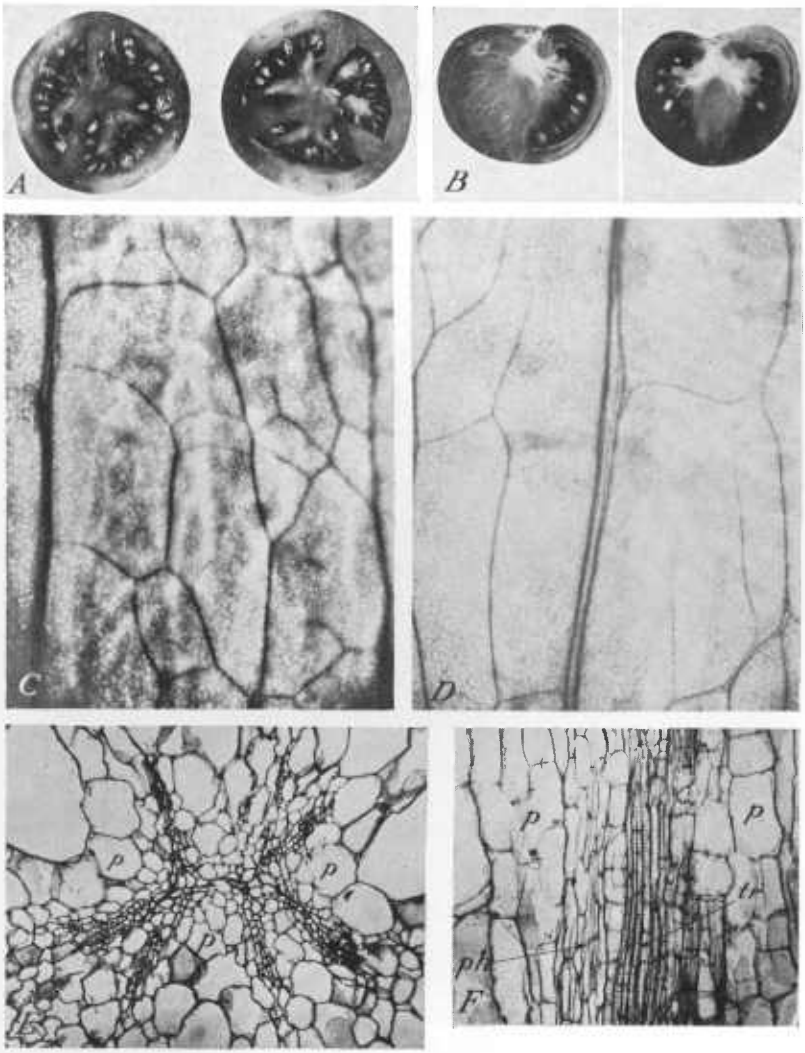
[4] Reference is made by number (italic) to Literature Cited, p. 224.

[5] SEATON, H. L. INVESTIGATIONS ON BLOTCHY RIPENING OF GREENHOUSE TOMATOES. 1933. (Unpublished thesis, Mich. State Col.).

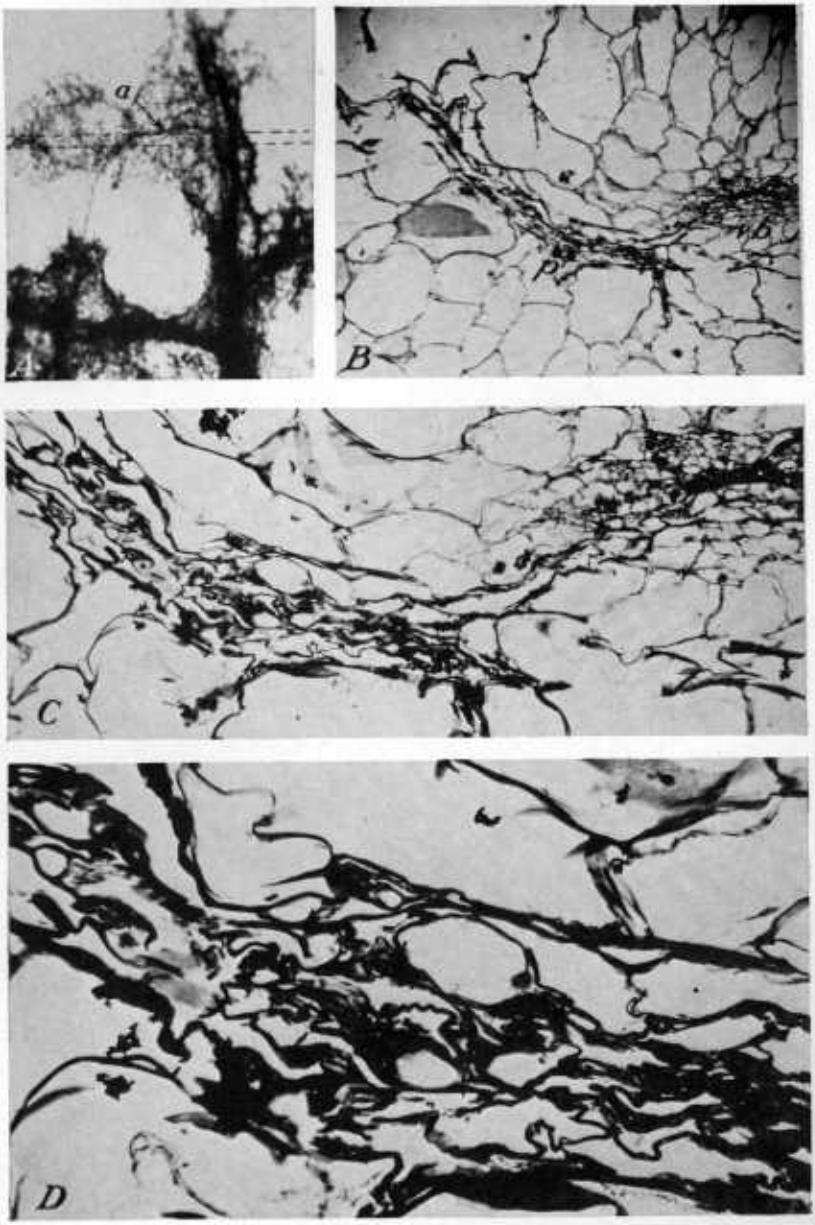
Greenhouse Tomatoes Affected by Blotchy Ripening PLATE 1



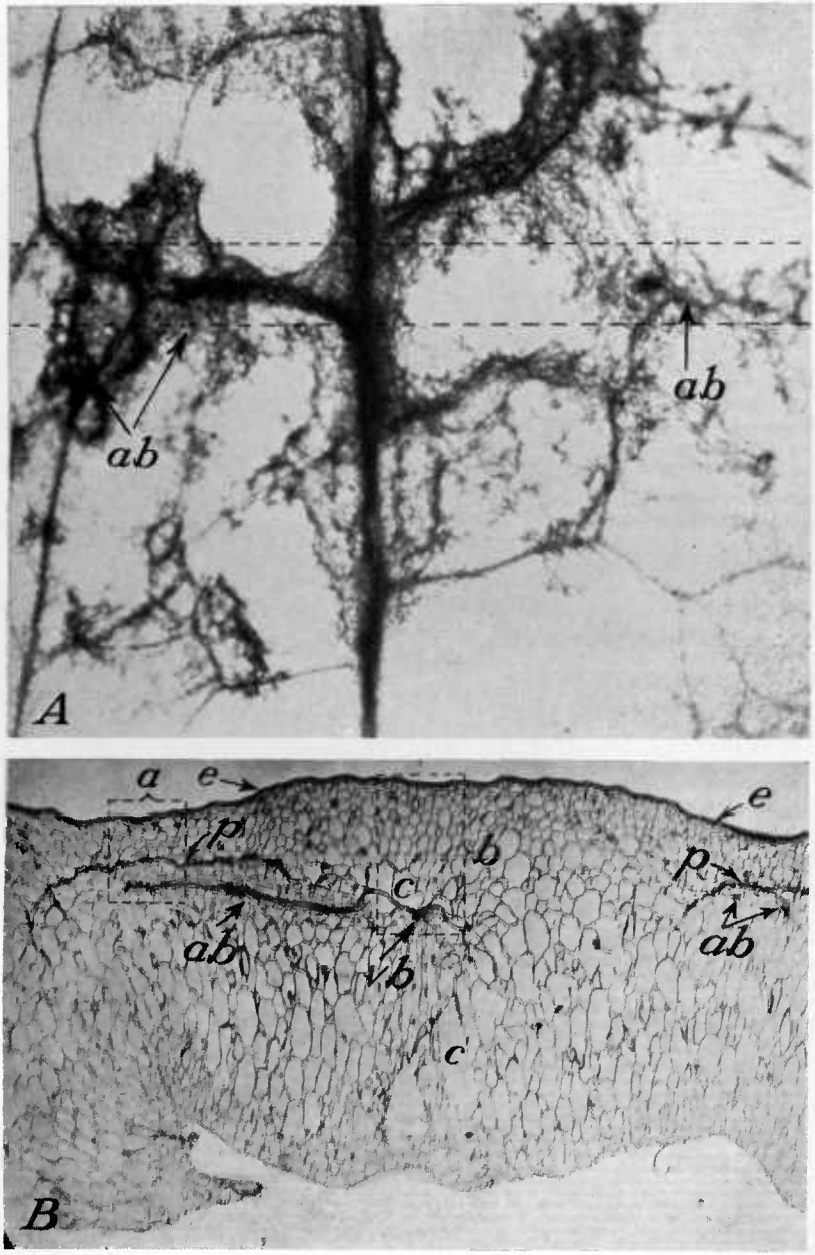
Tomatoes showing blotchy ripening. The glassy areas appear on all parts of the fruit but are less abundant in the stylar region. Some of the blotchy areas show a sunken or pitted condition, whereas dark, discolored tissues adjacent to the bundles appear in others.



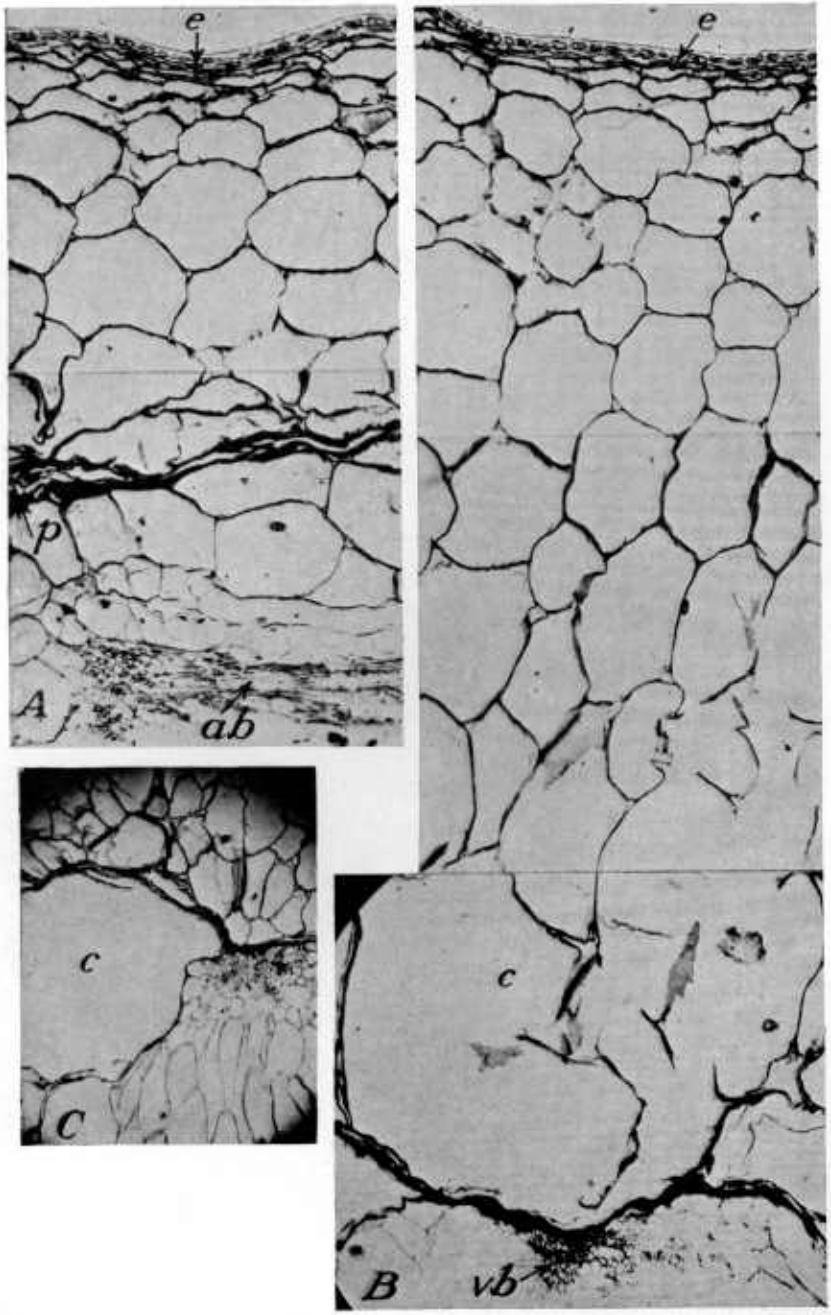
A, Blotchy ripened fruits cut transversely. Only the outer fruit wall is involved. The small dark areas in the blotches are affected tissues adjacent to the vessels. × ½. *B*, Fruits cut longitudinally to show the position of the affected tissues in the blotchy areas. No discolored tissues are apparent in the normal pericarp. × ½. *C*, A cleared section from a normal fruit wall near the stylar region. One large carpellary bundle and numerous small anastomosing veins are shown. × 5. *D*, Same as *C*, from an area near the stem end. The anastomosing veins are less numerous in this region. × 5. *E*, Transverse section of a large carpellary bundle from a normal pericarp. This bicollateral bundle is typical. Note the large parenchyma cells (*p*) of the vascular ray. × 125. *F*, Longitudinal section of a bundle from an unaffected fruit wall. The spiral thickened tracheae (*tr*), the adjacent phloem (*ph*), and the surrounding parenchyma (*p*) are shown. × 125.



A, External view through the epidermis of a blotchy fruit. The discolored tissues appear to surround and involve the large bundle and the anastomosing veins. The broken lines (*a*) indicate the position of the section shown in *B*. × 10. *B*, Transverse section from area indicated in *A*, *a*. Note the large vascular bundle (*vb*) and the broken down parenchyma tissue (*p*) which lies between the anastomosing bundle shown in *A* and the epidermis. × 50. *C*, Identical with *B*. The vessels of the bundle appear unaffected and the discolored areas are collapsed parenchyma. × 145. *D*, Identical with *C*. The distorted cell walls and cell contents which make up the dark areas are shown. × 450.



A, View through epidermis of a blotchy fruit taken in the region of a carpellary bundle. Normal areas may be seen among the discolored portions which surround the anastomosing bundles (*ab*). The broken lines indicate the position of the cross section shown in *B*. × 10. *B*, Transverse seotion of region indicated in *A*. Note the wavy appearance of the epidermis (*e*) with sunken portions above regions where the underlying parenchyma (*p*) has collapsed, while above the unaffected areas and where cavities (*c*) appear it is unaltered. The dark collapsed parenchyma tissues (*p*) are located between the epidermis (*e*) and the bundles (*ab* and *vb*). See plate 5 for details of the marked portions *a* and *b*. × 10.



A, Region indicated as *a* in plate 4, *B*. The epidermal cells (*e*) and the several underlying layers appear normal with the dark hand resulting from the collapse of several layers of parenchyma (*p*) immediately above the anastomosing bundle (*ab*). Tbe bundles show no evidences of necrosis or plugging, and apparently the cells subjected to break-down lie between the bundles and tbe epidermis. × 75. *B*, Region indicated as *b* in plate 4, *B*. Compare the thickness of this area with tbat shown in *A*, wbere a collapse of cells is apparent. Tbe large cavity (*c*) seems to be made up of dismembered cell walls, some of which bave collected around the vessels of the bundle. As in *A* tbe broken-down tissues are located between tbe epidermis (*e*) and the hundle (*vb*). × 75. *C*, Same bundle as sbown in lower portion of *B*, but from a section taken above that shown in *B*. The vessels are unaffected and the dark areas are made up of distorted walls and cell contents of tbe parencbyma which once filled the cavity (*c*). × 75.

fruits during periods of excessive transpiration, 3 to 5 days before the fruit ripens, results in the break-down of the tissues involved in the blotchy areas.

MATERIALS AND METHODS

The normal and blotchy-ripened fruits which furnished the material for this investigation were grown in the experiment station greenhouses at East Lansing in 1933 and 1934. Samples were collected each year in June and were about equally divided between fruits of the Grand Rapids variety and fourth- and fifth-generation hybrids between Ailsa Craig and Marglobe. In 1933 comparatively small portions of the outer fruit wall from distinct blotches were excised from freshly harvested material; but in 1934 much larger portions were taken, in some cases as much as one-fourth of the entire outer wall being used. The epidermis was removed from some samples and allowed to remain intact on others. In 1933 the material was killed and fixed in alcohol-formalin-acetic acid killing solution, embedded in paraffin, sectioned, and stained with Delafield's haematoxylin. In 1934 the samples were handled in the same manner, except that the large sections, after being cleared in xylol, were photographed with transmitted light in that liquid in an especially designed cell. After the gross photographs (pls. 2, *C* and *D*; 4, *A*; and 6, *A*), at a magnification of 5 and 10 diameters, were examined, the portions indicated in the plates were dissected from the cleared samples, embedded in paraffin, sectioned, and stained in the same manner as the 1933 material.

STRUCTURE AND APPEARANCE OF THE PERICARP

THE PERICARP FROM NORMAL FRUITS

When the outer fruit walls are cleared in xylol following alcohol, the vascular anatomy of the pericarp may be followed easily. Several large carpellary bundles radiate from the corky abscission layer, extend around the fruit, and converge again at the stylar scar. Relatively large branches from the main carpellary bundle are found in the furrows outside the interlocular walls and smaller anastomosing veins from these extend into these walls (pl. 2, *B*). In the outer carpellary walls other branches of the main bundle appear and extend with it to the stylar scar. In the pericarp near the pedicel attachment and extending to the region of the greatest diameter of the fruit few connecting veins are present between the main bundle and the large branches (pl. 2, *D*). However, from the region of the greatest diameter to the stylar scar the bundles anastomose freely and form an intricate network of connecting veins (pl. 2, *C*). Thus the areas between the bundles and veins are larger, and more of their parenchymatous cells are further removed from bundles in the lower half of the ovary wall than in the upper half. These observations are, in general, in agreement with those of Bewley and White (*2*) and the observations by Cooper (*4*) on the anatomy and development of the tomato flower.

Histological examinations of the pericarp from mature fruits (pls. 4, *B*; and 5, *A* and *B*) show that the outer epidermis is made up of small, heavily cutinized polygonal cells. The inner epidermis is more delicate than the outer and shows little or no cutinization. Only the

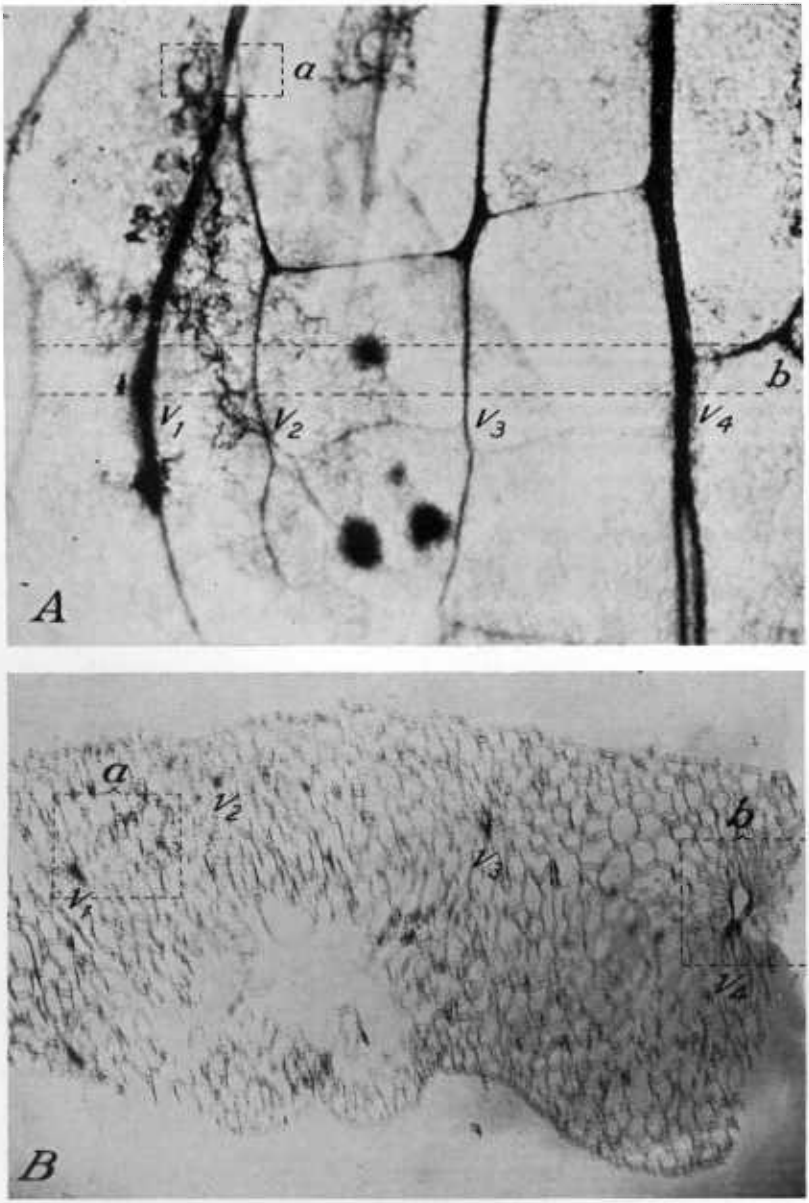
outer and the inner epidermis and the fleshy layer between the two are distinct. The several layers of parenchyma cells constituting the fleshy layer adjoining the epidermal layers are smaller and have slightly thicker walls than those of the center, where the cells are greatly extended and the walls are excessively thin and delicate at maturity. Intercellular spaces of any appreciable size are not present. Throughout the center of the fleshy layer, bicollateral vascular bundles, dissected with vascular rays of large, spongy parenchyma occur (pl. 2, *E*). In longitudinal section the tracheae of these bundles are seen to be the spirally thickened type (pl. 2, *F*).

THE PERICARP FROM BLOTCHY FRUITS

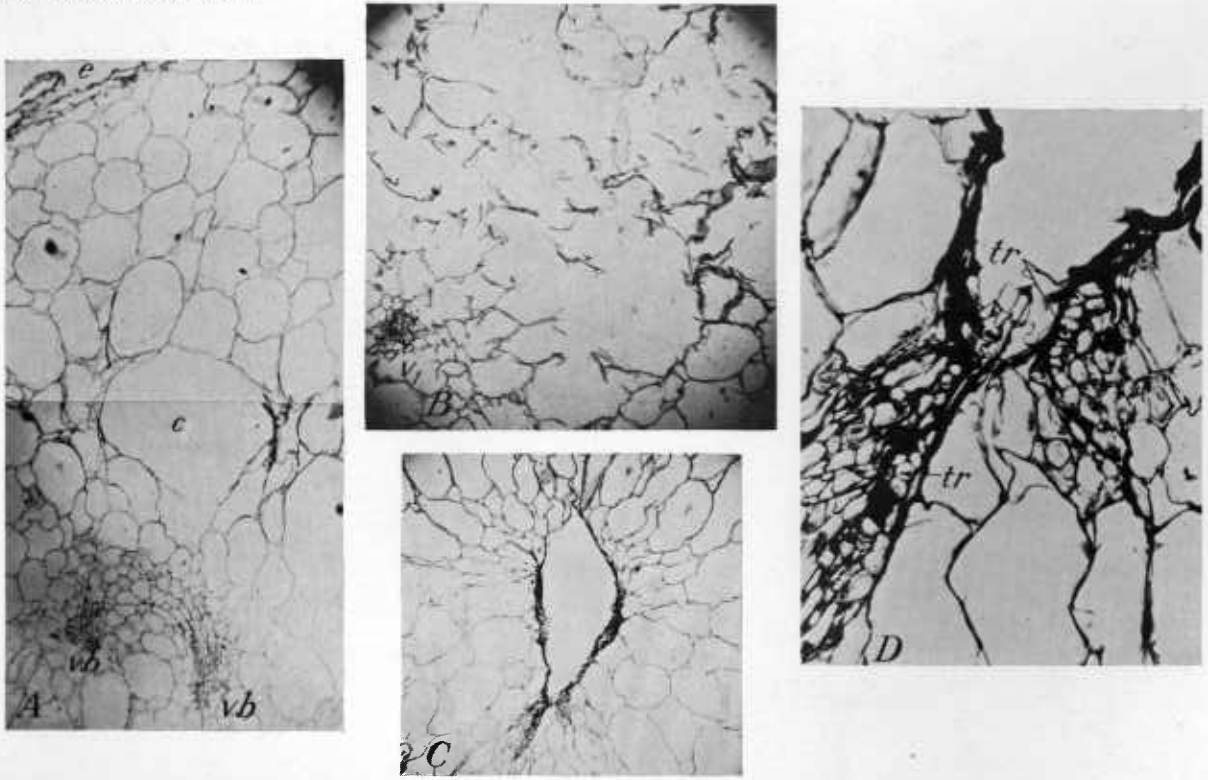
In cleared sections from blotchy fruits large dark areas attendant to the bundles and their branches are apparent, while less dense, slightly diffused areas of similarly affected tissues appear between the bundles (pls. 4, *A* and 6, *A*). Under low magnification the bundles in blotchy regions seem to be enlarged throughout the extent of the blotch and give the appearance of being necrotic and functionless, as Bewley and White (*2*) reported from their observations with a hand lens. However, when carefully prepared sections are examined under higher magnification, the actual conditions of the vascular elements and surrounding tissues appear quite different.

An external view through the epidermis of a blotchy fruit (pl. 3, *A*) illustrates the deceptive appearance of the necrotic and enlarged bundle and the anastomosing veins surrounded by affected tissue. In a transverse section of this same area (pl. 3, *B*) at higher magnification, the large bundle appears to the right of the field and the band of discolored tissue in the center is from immediately below the anastomosing bundle. The elements which appeared plugged at lower magnification are in reality open and unaffected, with some broken-down vascular ray parenchyma between them. The band of dense material, shown under high power (pl. 3, *C* and *D*), is clearly composed of collapsed parenchyma cell walls and the cell contents from the center of the fleshy layer of the ovary wall. The arrangement of the collapsed cells seems to indicate that they were subjected to mechanical stresses.

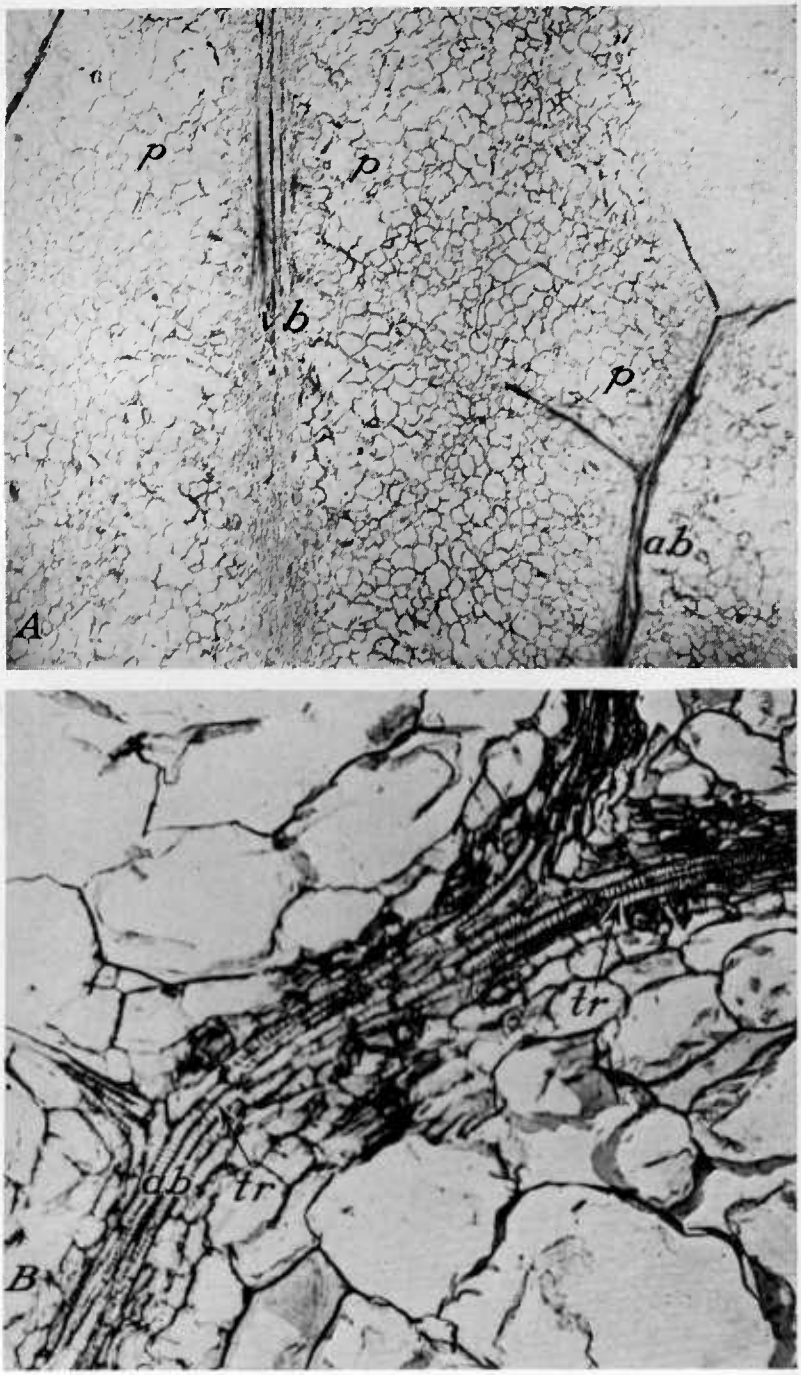
An interesting picture of affected portions of the pericarp and their positions relative to the epidermis and vascular bundles is shown in the transverse section in plate 4, *B*. The epidermis is wavy, being sunken above portions where the underlying parenchyma has collapsed, and unaltered above normal areas and in regions where cavities occur. The dense bands of broken-down cells occur between the outer epidermis and the bundles. In the parts where the epidermis is sunken (pl. 5, *A*), the debris of cell walls and cell contents appears to be forced together; while in the portion where the large cavity appears above the bundle (pl. 5, *B*), fragments of debris have collected around the tracheae and dismembered cell walls are found in the resulting cavity. A similar cavity intermediate between the epidermis and a point near the union of two normal bundles, which are surrounded by unaffected parenchyma, is shown in plate 7, *A*. The accumulation of the dense cellular material between the epidermal layer and the bundles may account for the misconception that the bundles are involved.



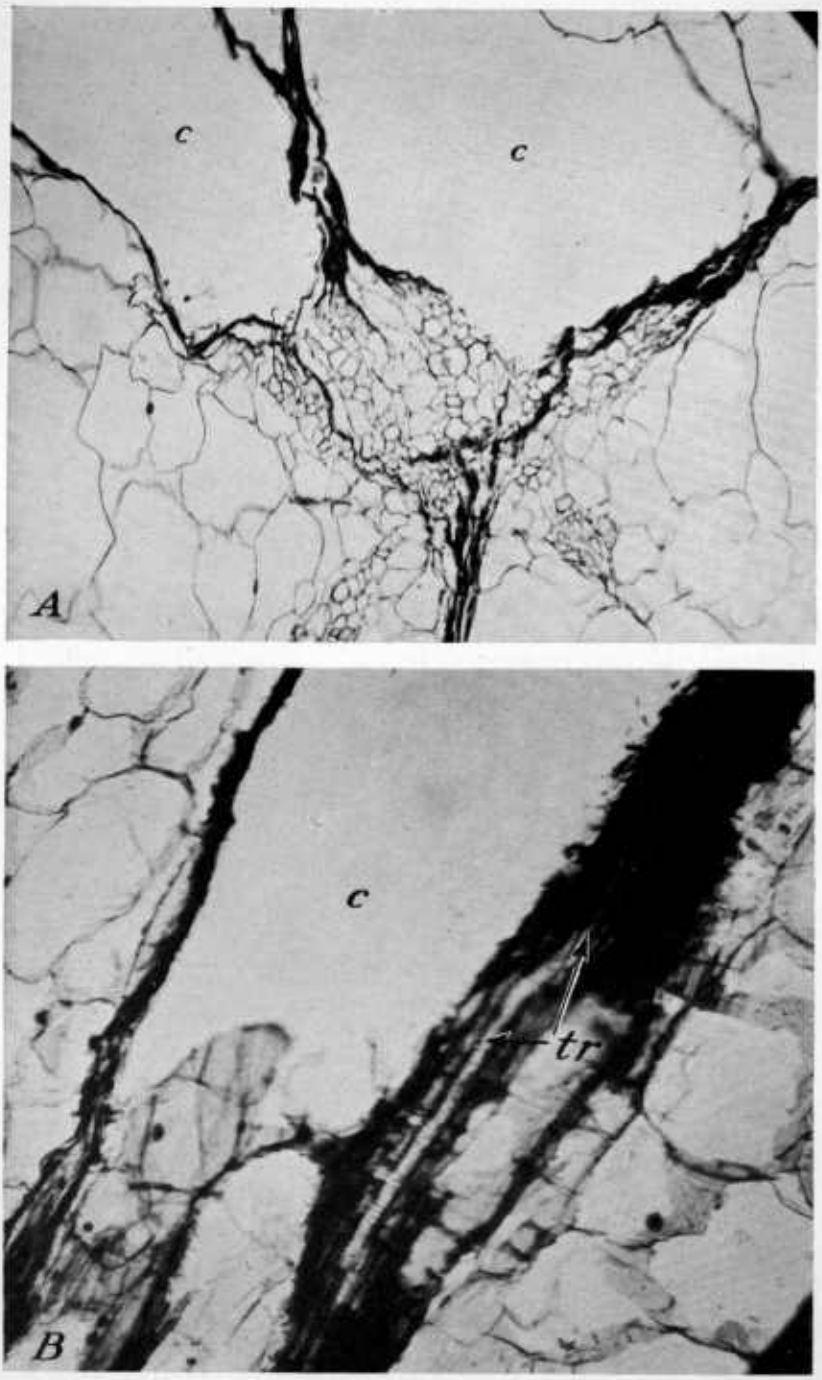
A, Seemingly enlarged and discolored bundles with connecting veins and associated tissues as they appear in a cleared wall from a blotchy fruit. The small area (*a*) is shown in plate 7, *A*, and the larger central portion (*b*) is shown in *B*. × 10. *B*, Transverse section of fruit wall shown in *A*, *b*. Note the distribution of the bundles (v_1, v_2, v_3, v_4,) and their relation to the broken-down tissues. The large cavity in the center is through the middle of the dark area shown in *A*. It is the result of rupture during removal of the outer epidermis. See plate 7 for details of the marked areas *a* and *b*. × 10.



A, Transverse section designated in the upper left, (*a*) of plate 6, *A*, taken in the region of tbe union of the two hundles. The epidermis (*e*) is shown to the upper left, with a large cavity (*c*) and dark tissues between it and the normal bundles (*vb*). × 50. *B*, Section from area *a* in plate 6, *B*, between the two small bundles (v_1 and v_2). The deteriorated cell material between these bundles has not been compressed as in plate 5, *A*. × 33. *C*. Large cavity shown at *b* in plate 6, *B*, with a margin of discolored and broken-down cell material. Ohserved with the naked eye or a hand lens, tbe whole cavity and margin would appear to he an enlarged hundle. See *D* for details. × 33. *D*, Lower portion of cavity shown in *C*. Ohserve the accumulation of cell debris around the large open tracbeae (*tr*) wbich form the rigid framework for tbe distorted material. Compare with normal hundle (pl. 2, *E*). × 300.



A, A longitudinal tangential section through the outer wall of a blotchy fruit. Note the broken-down parenchyma (*p*) to either side of the large bundle (*vb*) and between the branches of the anastomosing bundle (*ab*). × 9. *B*, The anastomosing bundle (*ab*) shown in *A* where it seems to be necrotic. At this magnification the spiral thickened tracheae (*tr*) appear normal. × 150.



A, Transverse section through a large bundle with adjacent cavities (c). The radiating strands of cell debris appear to have been draped over the strands of tracheary tissue. Note that the parenchyma of the vascular rays found in a normal bundle (pl. 2, *E*) are included in the amassed material. × 250. *B*, Longitudinal view of an adjacent portion of the bundle shown in *A*. The large cavity (c) is bordered at the left by distorted cell material, which also covers the tracheae (*tr*) to the right of the cavity. × 250.

Where small, diffused spots appear between the bundles, a different condition exists than in areas where dense accumulations of cellular material occur. The diffused spots are usually made up of broken-down cells which have not been forced together into a dense mass, but are scattered individually throughout the space they formerly occupied (pl. 7, *B*). This scattered arrangement of dismembered cells almost always occurs midway between two bundles (pls. 6, *B* and 7, *B*) and may be considered as a stage intermediate between the normal and the condition where bands of dense material are formed. The bundles associated with the disintegrated parenchyma have been found to be unaffected in almost every case (pls. 7, *B* and 8, *B*). Longitudinal tangential sections of blotchy fruits show this relationship of the bundles to the broken-down parenchyma quite clearly (pl. 8, *A*).

In severe cases of blotchy ripening, large, dense masses of dead cellular material are found to occur in the bundles in such manner that even the tracheae appear affected (pls. 6, *B;* 7, *C* and *D;* and 9, *A* and *B*). Usually, well-defined cavities are present within the necrotic bundle, and the whole mass may give the appearance of the complete distortion of all the elements of the bundle. Nevertheless, under high power one finds the radiating strands of cell debris have been pulled in around the strands of tracheae, which form the framework on which the amassed material is draped. The cells that are actually affected include, for the greater part, the thin-walled parenchyma of the vascular rays, while the tracheae are uninjured and appear to have functioned normally in the areas beyond the blotch (pls. 8, *B* and 9, *A*).

DISCUSSION

The histological observations reported here, as well as data from other investigations of the disorder, substantiate the hypothesis advanced by Seaton [6] (*12*) that blotchy ripening is due primarily to conditions resulting from the withdrawal of water from the fruit during periods of excessive transpiration occurring 2 to 5 days before the fruit ripens, and indicate that deficiencies of potassium and nitrogen, as suggested by Bewley and White (*2*), are probably secondary and occasional. It is evident that blotchy ripening is closely associated with the break-down of the parenchyma near and adjacent to the vascular bundles of the maturing ovary walls. That some physical force is operative in bringing about the conditions antecedent to blotchy ripening is also strongly suggested. Moreover, the very location of the affected tissues indicates that a strong pull, exerted through the vascular system upon the normally large, turgid, thin-walled, delicate parenchyma cells between the bundles and connecting veins of the fleshy layer, results in their rupture and distortion. Indeed, areas similar to that shown in plates 4, *B* and 5, *A* suggest a cleavage of tissue such as might result from loss of turgor, the upper portion being supported by the denser tissues of the outer portion of the pericarp, while the portion below lacks such support and is pulled away.

MacDougal (*8*) has shown by the use of an auxograph that the daily accretion in size of tomato fruits is connected with temperature and

[6] SEATON, H. L. See footnote 5.

water relations. As the temperature of the fruit attached to the plant rose from 12° or 14° to 26° or 28° C., the volume increased to a point where the increased temperature caused an excessive water loss by transpiration which overbalanced the gain by hydration. The midday shrinkage could not be prevented by watering the plants abundantly. His data show that a water deficit may exist in the fruits because of excessive transpiration regardless of the moisture content of the soil. Seaton,[7] using an aniline dye under greenhouse conditions favoring excessive transpiration, has followed the movement of water from the fruits to the transpiring leaves. On bright, warm days in July the dye appeared in the upper leaves in from 1 to 1½ hours after it entered the fruit, while on rainy or cloudy days 4 to 8 hours elapsed before it could be detected in the fruit pedicel.

Similar changes in the direction of the water stream have been advanced as explanations for similar physiological disturbances, such as the blossom-end rot of tomatoes (*3*), the internal decline in lemons (*1*), bitter pit of apples (*7*), the dropping of blossoms in the tomato (*9*), and the shedding of unopened bolls in cotton (*6*).

In the development of some fruits, according to Eames and MacDaniels (*5*), the cells which later form the flesh of the ovary wall are formed during the early development, and development to the mature condition does not involve cell division. The growth consists mostly of the radial enlargement of cells, and in some fruits the formation of intercellular spaces. Thus, in the tomato, ripening involves, histologically, increase in cell size and change in cell shape, the cells becoming turgid with fluid and the walls excessively thin and delicate. According to Sando (*11*), Rosa (*10*), and others, during the ripening processes there is an increase in the percentages of moisture, acids, and sugars, and a decrease in solids, nitrogen, starch, pentosans, crude fiber, and ash. Consequently, the parenchymatous cells of the outer fleshy wall, where the greatest increase in size and the changes in chemical composition occur, become more susceptible to injury as maturity is approached. Since the climatic conditions which usually prevail during the ripening period of the spring crop of greenhouse tomatoes are conducive to excessive transpiration, it is logical to expect the greatest losses from blotchy ripening to occur intermittently during that season.

In the red areas of blotchy fruits the normal ripening and coloring are not retarded, and the processes are completed. However, with the break-down of the parenchymatous cells near and adjacent to the bundles in the blotchy areas, the connections which the outlying cells have for the transfer of elaborated foods and water are severed, and they are deprived of the materials which are essential for normal ripening. Consequently, these areas remain hard and develop the colorless or glassy appearance characteristic of the disorder.

SUMMARY

A histological study of tissues of greenhouse tomatoes affected by blotchy ripening is reported.

This disorder, which affects greenhouse tomatoes that ripen in May, June, and July, is characterized by a failure of areas of the outer fruit wall to develop and color normally. As the fruit approaches maturity, these areas remain hard and green; and as ripening proceeds further,

[7] SEATON, H. L. See footnote 5.

they assume a waxy or glassy appearance. The vascular bundles lying beneath the blotches invariably appear brown and necrotic, and in severe cases cavities may appear adjacent to them. The disorder is restricted to practically mature fruits.

Anatomically, the vascular system of the normal fruit wall consists of large carpellary bundles, their branches, and anastomosing veins. The outer fruit wall is made up of the outer epidermis, the fleshy layer of large parenchyma cells, and the inner epidermis. The bundles are bicollateral, dissected with vascular rays of parenchyma, and with spirally thickened tracheae.

In cleared sections of blotchy fruit walls, large dense areas attendant to the bundles are apparent, while less dense, slightly diffused areas appear between them. Cavities frequently occur in the bundles in severe cases. Histological examination reveals that the discolored tissues are in all cases parenchyma of the fleshy layer and that the bundles are not involved. Bands of discolored cellular material appear between the epidermis and the bundles, which produce the impression that the bundles are affected when viewed through the epidermis. The cavities found in blotchy portions are the result of a collapse of the parenchyma which originally occupied these areas. The diffused spots are composed of dismembered cells from the fleshy layer. Cavities in the bundles result from a collapse of the vascular ray parenchyma which is pulled in around the unaffected tracheae.

The break down of the parenchymatous cells near and adjacent to the bundles in the blotchy areas severs the connections of the outlying cells for a transfer of elaborated materials and water, and normal ripening is inhibited.

The histological observations reported substantiate an earlier hypothesis advanced by the senior author, that blotchy ripening is primarily due to conditions which result from the withdrawal of water from the fruits during periods of excessive transpiration, occurring 2 to 5 days before the fruit ripens.

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