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## COMPARATIVE HISTOLOGY OF HEALTHY AND PSOROSIS-AFFECTED TISSUES OF CITRUS SINENSIS<sup>1, 2</sup>

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### INTRODUCTION

THE GENERAL CHARACTERISTICS and effects of psorosis (scaly bark) have been described by Fawcett<sup>(18)</sup> and Fawcett and Lee.<sup>(21)</sup> The first evident expression of the disease is the cracking or rupturing of the outer bark, with the formation of raised scales, pustules, or pimples. As the disease progresses, the wood underlying the affected bark is also commonly involved. The bark symptoms constitute the most conspicuous form of the disease and suggested the name psorosis originally given it by Swingle and Webber.<sup>(53)</sup> In ensuing years other effects were occasionally noted on small twigs, water-sprouts, mature leaves, and rarely on fruit. More recently a mosaic-like symptom on young leaves has been discovered by Fawcett,<sup>(20)</sup> suggesting a virus disease. Most of the histological work of this paper was completed before the mosaic-like symptom was discovered, and considerable attention was given to searching for the presence of possible microorganisms in the diseased tissues. This paper deals especially with the differences in structure of normal and diseased bark and wood. Some work in comparing normal and diseased twig and leaf tissues is also included.

### MATERIAL AND METHODS

Specimens showing various stages of psorosis on Valencia orange trees nine years old were collected at different seasons of the year at the Citrus Experiment Station, Riverside, California. Through the

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courtesy of J. C. Perry, specimens of bark and wood from trunks of Valencia orange trees seven years old, affected by psorosis, were collected monthly for an entire year at East Highlands, California. Additional specimens of diseased Valencia orange wood and bark were obtained in San Diego and Orange counties. Specimens from psorosis-affected Washington Navel orange trees were collected at East Highlands. As far as possible, healthy specimens approximating the diseased specimens in age were collected from groves in which the diseased trees occur.

Much of the material was sectioned and studied while fresh. The monthly collections from East Highlands were preserved in lactophenol. The remaining specimens were killed in formalin-acetic-alcohol or chrom-acetic-formalin. Stains generally employed to show the presence of fungi in host tissues were largely used. These included cotton-blue (Linder<sup>(32)</sup>), safranin (Moore<sup>(38)</sup>), Haidenhain's hematoxylin (Chamberlain<sup>(6)</sup>), gentian-violet, thionin (Stoughton<sup>(52)</sup>), and the combinations used by Cartwright,<sup>(5)</sup> Vaughan,<sup>(56)</sup> and Dickson.<sup>(12)</sup> Microchemical tests were made for fats and oils with Sudan III, for starch with IKI, and for gum with orcinol-HCl and phloroglucin-HCl, as outlined by Eckerson.<sup>(15)</sup> The chitosan reaction was employed in testing for chitin.

### HEALTHY BARK

In this paper the term "bark" is used to designate those tissues outside the cambium. The literature pertaining to citrus bark as a whole is meager, the chief works being those of Moeller<sup>(37)</sup> and Penzig,<sup>(41)</sup> no reference to this genus being made by Mitlacher<sup>(35)</sup> in his discussion of rutaceous barks. There are, however, numerous references to special structures occurring within citrus bark, although many of these are made in connection with leaf anatomy. Mention of such works will be made as these particular structures are discussed.

The external appearance of the bark varies considerably as a stem increases in age. First-year shoots, which are angular at the apex and become rounded at the base, are smooth and glossy green throughout their length. On two-year-old shoots, slightly raised, vertically elongated lenticels begin to appear as light-gray streaks on a smooth, green background. In older stems, lenticels increase in number. At the age of five or six years, the bark is generally grayish or brownish with vertically elongated, slightly depressed green streaks. These green areas gradually decrease in number as the stem increases in age, until in time the bark is grayish or brownish over the entire stem. Throughout its life the bark remains smooth, except for very slightly raised, vertically elongated lenticels.

If a stem which has completed its first growing season is sectioned, the following primary permanent tissues included in bark may be observed to occur in centripetal order: epidermis, cortex merged with pericycle, and phloem (plate 1, figs. 1 and 2). In accordance with the observations of Moeller,<sup>(37)</sup> Penzig,<sup>(41)</sup> Douliot,<sup>(13)</sup> and Solereder<sup>(51)</sup> on *Citrus aurantium* and *C. limonum*, phellogen first appears immediately beneath the epidermis in stems several years of age. The phellogen produces phellem centrifugally and phelloderm centripetally; thus the periderm, which is persistent, is composed of these three layers. As has been previously pointed out by Moeller<sup>(37)</sup> and Damm,<sup>(10)</sup> the epidermis in *Citrus* commonly persists over at least a portion of the stem for many years (plate 3, fig. 1); hence, after the first two or three years the centripetal order of tissues comprising the bark is epidermis, periderm, primary cortex merged with pericycle, and phloem. The characteristics of these tissues in normal *Citrus sinensis* bark are described below.

*Epidermis*.—In surface view the ordinary epidermal cells are rather small, polygonal, with straight walls of variable thickness (plate 2, figs. 1–3). Over the internal oil glands the epidermis is commonly depressed and slightly modified. Here the cells are usually smaller, flatter, and concentrically disposed, as in the case of similar cells in citrus leaves figured by Penzig<sup>(41)</sup> and Tschirch and Oesterle.<sup>(54)</sup>

As may be seen from plate 2, figure 1, the epidermis is well provided with stomata. Although stomatal density is influenced considerably by age of the stem, for a given variety, the number per square millimeter on stems is probably always lower than that occurring on the lower side of the leaves (Reed and Hirano<sup>(46)</sup>). The guard cells are surrounded by accessory cells as in the case of stem stomata of *Citrus aurantium* figured by Penzig<sup>(41)</sup> (plate 2, figs. 1–2).

On first-year shoots, epidermal cells, with the exception of guard cells which contain chloroplasts, are mostly hyaline. However, toward the base of stems which have completed the first growing season and in the epidermis of older stems, cells with brown contents are to be found scattered singly or in small groups (plate 2). Frequently, the guard cells and accessory cells turn brown before the other epidermal cells.

*Periderm*.—Phellogen is first formed only in the layer of cortical cells immediately underlying groups of brown epidermal cells and brown cortical cells bordering the stomatal cavities (plate 2, figs. 4 and 5). The lateral extent of groups of phellogen cells in the early stages is frequently less than 12 cells. The cells are rectangular and radially flattened in transverse and radial sections, polygonal and approximately isodiametric in tangential section, and have dense granular protoplasm.

The phellogen soon gives rise to several layers of phellem, which



after a time rupture the epidermis by their growth. The cells of the phellem are radially arranged and readily traced back to the phellogen initials. At first they differ from the phellogen cells only in having greater radial diameters. Soon, however, small groups of cells in the phellem layers farthest from the phellogen become uniformly thick-walled (plate 2, fig. 5). Microchemical tests indicate that the thick walls of the phellem cells are lignified, while the thin-walled phellem cells are suberized. As the phellem increases in age, a notable increase in the relative abundance of lignified cells occurs until a lignified layer of greater radial depth than the suberized layer is produced. With continued production of phellem, alternating layers of lignified and suberized cells are produced (plate 1, figs. 3 and 4).

As the browning of the epidermis progresses, additional groups of phellogen cells are produced which give rise to phellem similar to that described above. In time, the isolated groups of phellogen are joined, and it becomes evident that phellem containing lignified cells is found only in lenticels. Because of the method of increase in lateral extent of the phellogen, several alternating layers of lignified and suberized cells are generally found near the center of a lenticel, while commonly but one lignified layer occurs at the borders of a lenticel. However, since the lignified layers of the lenticels are frequently attacked by various fungi (Peltier and Neal<sup>(40)</sup>), and subsequently by erosion, the number of these layers at the center of a lenticel may not greatly exceed that at the borders. The phellem produced between lenticels often develops without rupturing the epidermis. It consists solely of suberized cells similar to those found in the suberized layers of lenticels.

Phelloderm develops much more slowly than phellem. It is not visible in the early stages of phellem development but is found in limited amounts in stems possessing a phellogen which has been active for a considerable period of time (plate 3, fig. 1). The phelloderm cells are radially arranged and may be traced back to the phellogen layer without difficulty. They are parenchymatous, rectangular in transverse and radial sections, polygonal in tangential section, and contain chloroplasts.

*Primary Cortex and Pericycle.*—In current season's shoots the diameter of the primary cortex in transverse section is extremely variable. Near the apex where the stems are angular, the cortex is generally arched (plate 1, fig. 1). As the angular condition of the stem becomes lessened, the cortex loses its arched contour and forms a ring with approximately equal diameters (plate 1, fig. 2), a condition previously mentioned by Pitard.<sup>(44)</sup> Vesque<sup>(57)</sup> refers to the primary cortex as purely homogeneous. This term is not well chosen. Throughout its first year, the primary cortex generally is composed entirely of parenchyma,

but this shows considerable variation (plate 1, figs. 1 and 2), a fact referred to by Penzig.<sup>(41)</sup> Near the apex of such stems pericyclic fibers are scattered in small groups adjacent to the phloem. Near the base of first-year stems the pericyclic fibers often form a ring several cells wide (plate 1, figs. 1 and 2).

In the subepidermal layer of the primary cortex, crystal-bearing cells are developed in considerable numbers near the apex of first-year shoots. These apparently do not increase in number as the stem develops and hence become widely scattered as the stem increases in age. A fully developed crystal cell is considerably larger than other subepidermal cells, and further, differs from them in lacking chlorophyll and having thickened radial and inner walls to which a large, solitary calcium oxalate crystal surrounded by a membrane is attached (plate 2, fig. 2). With few exceptions, the long axes of subepidermal crystals are perpendicular to the epidermis. Crystal cells of this type were observed in citrus leaves by Payen<sup>(39)</sup> and Schacht.<sup>(47)</sup> Their developmental stages have been traced by Pfitzer,<sup>(42)</sup> von Guttenberg,<sup>(22)</sup> and Wittlin<sup>(60)</sup> in the lamina, and by Wakker<sup>(58)</sup> in the petioles of sour orange, *Citrus aurantium*, and by Kohl<sup>(29)</sup> in the petioles of sweet orange, *C. sinensis*, and grapefruit, *C. grandis*. The findings of these investigators are lacking in agreement.

With the exception of the crystal cells, the subepidermal layer is composed of thin-walled chlorenchyma which closely resembles the subjacent cortical tissue. The width of the chlorenchyma band is rather variable but generally exceeds six cells. Centripetally the cells become larger, thicker-walled, contain fewer chloroplasts, and show more pronounced tangential elongation. Between the chlorenchyma and pericyclic fibers, a band of colorless parenchyma tissue occurs (plate 1, figs. 1 and 2). At times some of the cells of this layer have irregularly thickened walls and probably should be referred to as weakly collenchymatous rather than parenchymatous. Many of the cells of this layer contain large, solitary calcium oxalate crystals which do not show definite orientation with respect to the periphery of the stem. In addition to calcium oxalate crystals, starch grains, oil droplets, and hesperidin (plate 7, fig. 4) were observed in primary cortical parenchyma cells.

In stems more than one year old, small irregular groups of stone cells begin to appear in the primary cortex, particularly in the colorless parenchyma zone (plate 1, fig. 3). Fully formed stone cells are characterized by much reduced lumina and thick, striated, lignified walls with numerous ramiform pits. In the development of stone cells from parenchyma cells, all cell dimensions, but especially the tangential diameters, are increased. Parenchyma cells bordering stone cells are accord-

ingly more or less crushed. In older stems, growth of the phelloderm and secondary phloem are also factors which doubtless result in partial or complete crushing of some of the cortical parenchyma cells.

Oil glands are formed very early in the development of the primary cortex (plate 1, figs. 1 and 2). They are close together near the stem apices but become rather widely separated in old stems. They commonly lie partly in the chlorenchyma and partly in the colorless parenchyma band. In form they are spherical or subspherical, their usual size in the material investigated being 90 to 210  $\mu$ . When fully formed a gland is commonly bordered by 2 to 6 concentric layers of epithelial cells with dense protoplasm and rich oil content. The interior of the gland is then characterized by fragments of cell walls and numerous oil droplets. Similar glands occurring in the leaves of various *Citrus* species have received the attention of numerous histologists. Such glands are regarded as lysigenous by Chatin,<sup>(7)</sup> von Höhnelt,<sup>(27)</sup> Moeller,<sup>(37)</sup> DeBary,<sup>(11)</sup> and Penzig;<sup>(41)</sup> while Martinet,<sup>(33)</sup> Van Tieghem,<sup>(55)</sup> and Leblois<sup>(31)</sup> hold that they are schizogenous. The investigations of Sieck<sup>(49)</sup> on a number of rutaceous species including *Citrus aurantium* show that in reality the glands originate schizogenously and later become lysigenous.

**Phloem.**—As Moeller<sup>(37)</sup> and Penzig<sup>(41)</sup> point out, secondary phloem in *Citrus* is characteristically banded (plate 4, figs. 1 and 2). In first-year stems the phloem is composed of sieve tubes, companion cells, and phloem parenchyma. In older stems, bands of phloem fibers alternate with bands composed of the other phloem elements. The rings of both thick and thin-walled elements are broken by phloem rays.

Phloem fibers are closely crowded. Their lumina are nearly obliterated, while their walls are thick, lignified, and sparsely pitted. In transverse section they are chiefly angular and vary in diameter from 8 to 22  $\mu$ . They are generally about 400 to 675  $\mu$  long. The ends of fibers are rather abruptly tapered, usually serrate, and occasionally forked. The bands of fibers are commonly 20 to 100  $\mu$  in radial thickness.

Phloem parenchyma is abundant, both crystal-bearing and storage types occurring in fairly well-marked tangential bands in old as well as young phloem. The parenchyma cells of both types form vertical strands.

The crystal-bearing parenchyma borders the bands of phloem fibers and usually forms bands but one cell layer wide. Its cells are nearly cubical or somewhat vertically elongated, the usual diameter being 8 to 16  $\mu$ . Each cell contains a large, solitary calcium oxalate crystal. The cell walls are irregularly thickened.

Bands of storage parenchyma are usually one to four cells wide (plate 4, fig. 1). They occur adjacent to the bands of crystal-bearing paren-

chyma which border the bands of phloem fibers and also between such bands. The storage parenchyma cells are thin-walled and contain an abundance of starch grains and oil droplets. Usually they are 6 to 10  $\mu$  in radial diameter, 16 to 20  $\mu$  in tangential diameter, and 65 to 95  $\mu$  high.

The other bands of phloem tissue are composed of sieve tubes, companion cells, and scattered parenchyma cells of both types described above. In the band nearest the cambium, sieve-tube elements may be easily distinguished from parenchyma cells by means of their large central vacuoles, greater radial diameters, sieve plates, and accompanying companion cells (plate 4, fig. 1). The sieve tubes, companion cells, and scattered parenchyma cells in the sieve-tube bands soon undergo more or less radial crushing. Consequently in old phloem the lumina of all cells in such bands are practically obliterated, and protoplasts disappear, making it difficult to identify the various elements. Active sieve-tube elements are commonly 15 to 27  $\mu$  in tangential diameter, about 12 to 15  $\mu$  in radial diameter, and 110 to 160  $\mu$  long. Their end walls are horizontal or slightly oblique. Solitary sieve plates are confined to the end walls when these are horizontal, but five or more may occur in scalariform arrangement on the radial walls when the end walls are oblique. Companion cells are triangular or oblong in transverse section and vary greatly in size. A companion cell may lie across the entire radial wall of a sieve-tube element or it may border one corner of a sieve-tube element.

Phloem rays are homogeneous, uniseriate or multiseriate (plate 4, fig. 3). The uniseriate rays are 10 to 22  $\mu$  wide; 1 to 10 cells, 22 to 160  $\mu$  high. Multiseriate rays are 2 to 5 cells, 22 to 65  $\mu$  wide; and 4 to 27 cells, 55 to 375  $\mu$  high. The ray cells are chiefly radially elongated, oblong in transverse and radial sections, and circular in tangential section. In size they are generally about 11 to 19  $\mu$  in vertical and tangential diameters and 16 to 33  $\mu$  in radial diameter. The walls of the ray cells are thin and have numerous simple pits. Large calcium oxalate crystals, starch grains, and oil droplets were observed in the lumina of ray cells.

#### DISEASED BARK

*External Appearance.*—The earliest external symptom of psorosis on the bark is a roughening of the surface or exfoliating of small scales of outer bark over very limited areas of the trunk or large limbs. Such areas very gradually increase in size until the entire circumference of the trunk or limb is completely encircled. As the disease progresses the scales often become somewhat larger and involve the deeper layers of bark. Exudation of gum from affected areas may or may not accompany the scaling away of the bark.

*Pathological Anatomy.*—When bark showing the beginning stages of psorosis is sectioned, it exhibits differences from normal bark only in localized areas underlying the roughened surface. The striking histological feature of such bark is the occurrence of yellow to brown contents in the parenchyma cells of phelloderm and primary cortex underlying the affected surface (plate 5, figs. 1, 3, and 5). The cells with brown contents commonly occur in tangentially elongated groups (plate 5, fig. 3). Near the surface such groups may be rather extensive, but toward the interior of the primary cortex, they generally do not exceed three cells in the radial and vertical directions and two to four cells in the tangential direction, and frequently are only one cell wide and one cell high (plate 5, figs. 1 and 3). In some sections, isolated, brown cells are visible in the primary cortex. Brown contents may be observed in parenchyma cells which retain their normal form, but are more frequently met with in cells that are more or less crushed (plate 5, fig. 6).

Very soon after a group of brown cells is formed at the periphery, a subjacent phellogen layer extending to the normal phellogen is formed in the parenchyma of the primary cortex or phelloderm (plate 5, figs. 4 and 5). This produces phellem centrifugally and phelloderm centripetally. After a time the brown cells cut off by the corky layer are exfoliated in the form of a bark scale (plate 5, fig. 2).

The phellem is not unlike that which is normally produced. Generally it consists entirely of suberized cells (plate 3, fig. 2, and plate 5, fig. 2), but may be partly composed of lignified cells. However, phelloderm produced in bark affected by psorosis is commonly much more abundant than that normally formed in healthy bark. Moreover, it frequently contains in addition to parenchyma, broken tangential bands of stone cells (plate 3, figs. 2 and 3). These differ from the stone cells in healthy bark in that they are little, if any, larger than the parenchyma cells from which they are derived and are radially arranged within the groups.

As the disease progresses, additional groups of brown cells develop in the original phelloderm and cortex and in the newly formed phelloderm. These groups of brown parenchyma cells and any groups of stone cells which they may surround are soon cut off by subjacent periderm which develops as described above. After the tissues of the primary cortex are exfoliated, browning commonly continues to occur in the last-formed phelloderm layer. In severe cases it may extend to living portions of the phloem; when this occurs, subjacent phloem parenchyma subsequently gives rise to phellogen (plate 5, fig. 4).

Since browning of cell contents and subsequent periderm formation do not occur simultaneously throughout any given ring of cells, the phellogen ring becomes arched as the disease progresses (plate 5, fig. 4).



The arched contour of the phellogen, together with the abnormally large amount of phelloderm produced subjacent to brownish areas, doubtless creates abnormal pressure conditions in the underlying tissues. Hence, it is not surprising to find more or less distortion within such tissues.

In numerous parenchyma cells scattered from phelloderm to phloem, unusual contents were observed in one bark specimen collected in December and killed in chrom-acetic-formalin. A similar specimen collected from the same tree at the same time and killed in formalin-acetic-alcohol shows such contents to a far lesser extent. Such cell contents differ from the normal in including one to ten spherical, ovoid, or somewhat irregular-shaped masses varying in diameter from 2.5 to 11  $\mu$ . Such masses are deeply stained by thionin and gentian violet and become yellow when treated with potassium bichromate; they remain unstained, however, after treatment with Sudan III or phloroglucin and HCl. Because of the range of size which these bodies exhibit and the fact that each is apparently surrounded by a thin membrane, J. Dufrénoy has suggested that they represent vacuolar phenolic precipitates. It seems probable that this condition may represent an early stage in the development of brown-cell contents, for Dufrénoy<sup>(14)</sup> points out that a gentle excitation of any nature may be expected to induce the normally single vacuole of a healthy citrus cell to break into many smaller ones, while a more severe shock results in greater changes of vacuolar contents, which, in some cases, may be evinced by browning. A limited number of microchemical tests have indicated that the contents of brown cells in psorosis-affected tissues undergo a series of changes. In living material, such contents are frequently stained violet-red by neutral-red, and usually give a dark-green reaction with ferric chloride, indicating the presence of phenolic compounds. In some sections, Sudan III indicates the presence of some fatty substances. Very rarely, gum may be detected by means of phloroglucin-HCl or orcinol-HCl reactions. In killed material, the contents of brown cells usually show an affinity for stains which color lignin, but at times are impervious to stain.

In some instances, small gum pockets develop in the unusually thick phelloderm (plate 3, fig. 3). Such gum pockets involve only parenchyma tissue and evidently are schizolysigenous in origin. Contents of many of the cells bordering the cavity, as well as those of the cavity, give the reaction of gum upon treatment with phloroglucin-HCl or orcinol-HCl. Within some cells bordering the cavity or close to its margins, peculiar bodies stained by gentian violet are visible. Such bodies are chiefly spherical, about 4.75 to 9.50  $\mu$  in diameter, are bound by what appears to be a membrane about 0.5 to 1.2  $\mu$  thick, and commonly con-

tain a smaller globular structure. Generally, but one such body is present within a protoplast, but as many as three may occur.

In one badly diseased bark specimen from San Diego County, small groups of wood cells surrounded by cambium occur within phelloderm which has replaced the entire primary cortex and most of the phloem. These woody bodies resemble those described by Küster<sup>(30)</sup> in that they consist very largely of tracheids. However, occasionally they contain a few vessels.

### HEALTHY WOOD<sup>5</sup>

Citrus wood has been described in more or less detail by Moeller,<sup>(36)</sup> Solereder,<sup>(50)</sup> Penzig,<sup>(41)</sup> Piccioli,<sup>(43)</sup> and Burgerstein.<sup>(2)</sup> From the descriptions of these authors, it may be concluded that structural differences between the woods of various species of *Citrus* are not well marked, since those that are pointed out are of a nature now known to be influenced by environment.

The *Citrus sinensis* wood studied is pale yellow, diffuse porous but with visible growth rings, hard, and of fine texture, the pores and rays being barely visible without a lens. With the aid of a lens the pores are seen to be fairly uniformly distributed throughout a growth ring, chiefly solitary or in radial multiples of 2 to 5, but occasionally in irregular or circular clusters of 3 to 5. Wood parenchyma is moderately abundant, chiefly paratracheal and metatracheal, but partly diffuse. Libriform wood fibers are the dominant element of the wood. Rays are commonly narrower than the pores, straight, or somewhat curved, and light colored, their distance apart being 1 to 3 pore widths. The minute structure of the various elements is described below.

Pores are chiefly circular to radially elongated; elliptic when solitary; and radially shortened, elliptic to angular when grouped. They vary in tangential diameter from 16 to 90  $\mu$ , the average diameter varying greatly in different specimens. The number of pores per square millimeter is also exceedingly variable in different specimens (plate 6, figs. 1 and 2), the observed range being 11 to 83. Vessel members are chiefly cylindrical, 34 to 285, mostly about 170  $\mu$  long. Perforations are simple, the plates horizontal, or slightly oblique. The lateral walls of vessels of secondary xylem are copiously pitted and lack spiral thickenings. Intervascular pit-pairs have roundish borders about 3 to 4  $\mu$  in diameter and included, slit-like apertures.

Metatracheal parenchyma bands are 2 to 6 cells wide. Both paratracheal and metatracheal parenchyma cells frequently contain stored

<sup>5</sup> Terms used in describing wood are those proposed by the Committee on Nomenclature, International Association of Wood Anatomists.<sup>(28)</sup>

food. They are about 10 to 15  $\mu$  in radial and tangential diameter, 60 to 135  $\mu$  high, and occur in strands. Their walls are thin and copiously pitted. Diffuse wood parenchyma strands are composed of 4 to 8 nearly cubical or somewhat vertically elongated cells about 22 to 43  $\mu$  high, each of which contains a large calcium oxalate crystal, which fills the lumen and is embedded in the irregularly thickened wall.

Libriform wood fibers are cylindrical in the central portion, tapering gradually, or sometimes abruptly at first, to smooth, saw-toothed, or rarely forked ends. Their usual diameter at the middle is about 10 to 16  $\mu$ , while their length varies from 250 to 900  $\mu$ , being chiefly about 500  $\mu$ . Their walls are about 4  $\mu$  thick with moderately numerous simple pits.

Both uniseriate and multiseriate rays are present (plate 6, fig. 10). The uniseriate rays are 7 to 11  $\mu$  wide, 1 to 13 cells (20 to 170  $\mu$ ) high, and are homogeneous. Multiseriate rays are chiefly homogeneous, but occasionally slightly heterogeneous with upright cells restricted to the margins of the ray. They are 2 to 4 cells (17 to 45  $\mu$ ) wide, 4 to 37 cells (54 to 435  $\mu$ ) high, usually spindle-shaped, occasionally with uniseriate ends, rarely connected vertically. Both procumbent and upright cells have thin walls with numerous pits and commonly contain starch and oil. Procumbent cells are roundish to angular in tangential section, radially elongated, oblong in transverse and radial sections. Upright cells are conical to vertically elongated oblong in tangential section, squarish in transverse and radial sections.

### DISEASED WOOD

Macroscopically, wood affected by psorosis differs from healthy wood in showing general discoloration or discolored concentric laminae from which gum may ooze when such wood is first cut. Often, affected wood is also gnarly.

Microscopically, the wood which is generally discolored is characterized by an abundance of gum in the vessel lumina. On transverse section, pores are often completely filled with gum (plate 6, fig. 6). Longitudinal sections show that, as a rule, this is due to the accumulation of gum in the vicinity of the perforation plates rather than to complete filling of the vessel lumina by gum.

Discolored laminae in the wood are due to the presence of traumatic gum ducts (plate 6, fig. 7). As in cases of gum-pocket formation in citrus wood described by Butler,<sup>(4)</sup> embryonic wood cells are involved. Accordingly, when present, gum ducts mark the beginning of successive growth rings, but they do not always completely encircle the stem. The distance between complete or partial rings of gum ducts is highly va-

riable, the observed range in one specimen being 27 to 1,350  $\mu$ . The gum ducts are apparently schizolysigenous in origin and vary considerably in size. Generally, they involve only cells between the rays (plate 6, fig. 11), extending vertically for considerable distances, tangentially from a few cells to the distance between rays, and radially from 30 to 165  $\mu$ .

Frequently the vertically elongated cells bordering the gum ducts are more or less completely filled with gum, but ray cells between gum ducts rarely contain gum. Occasionally, however, such cells contain abnormal globular or yeast-shaped masses (plate 6, fig. 8).

The tissues produced by the cambium subsequent to those involved in gum-duct formation are often normal in all respects. Not infrequently, however, some of the elements may become filled with gum, and at times patches of abnormal wood are formed. Such abnormal wood is homogeneous and lacking in elements of the form found in normal wood (plate 6, fig. 5). Its cells are nearly isodiametric, about 17 to 50  $\mu$  in diameter, with thin, lignified walls. In general aspect they resemble wood parenchyma, but the occurrence of weakly bordered pits in their walls indicates that they are of tracheid nature. They probably should be designated as parenchymatous tracheids, which, according to Küster,<sup>(30)</sup> are of frequent occurrence in wound wood. Some of these cells are completely filled with gum. Others contain globular or yeast-shaped bodies similar to those occasionally found in ray cells bordering gum ducts (plate 6, fig. 9).

In gnarly portions of the stem, all elements found in normal wood occur, but they assume somewhat altered forms and are arranged in different planes (plate 6, fig. 4). Such changes are doubtless correlated with changed planes of division in the cambium (plate 6, fig. 3), resulting from altered pressure conditions.

### HEALTHY LEAVES

The leaves of *Citrus sinensis* are unifoliolate compound. Their structure is in general similar to that of citrus leaves described by Penzig,<sup>(41)</sup> Tschirch and Oesterle,<sup>(54)</sup> and Schulze.<sup>(48)</sup> The blade is bifacial, pinnately veined, glabrous, deep glossy green on the upper surface, and somewhat paler and duller on the lower surface. Oil glands appear as numerous translucent dots when the blade is held to the light. Hirano<sup>(28)</sup> gives the average area of full-grown leaves as 38.7 sq. cm in Valencia orange and 41.1 sq. cm in Washington Navel orange.

The upper epidermis is without stomata. Its cells are tabular with long axes parallel to the surface. The epidermal walls are straight and thick, the outer with a thick cuticle and the lateral with cutinized wedges

extending about half their depth. The cell contents are sparsely granular and hyaline. Over oil glands the epidermis commonly dips inward and the cells are concentrically arranged, often smaller and generally thinner-walled than the surrounding cells. According to the investigations of von Höhnelt<sup>(27)</sup> and Haberlandt<sup>(24)</sup> on the leaves of sweet orange, *Citrus sinensis*, such modified structure of epidermal cells over oil glands permits emptying of the glands. Occasionally, crystal-bearing cells are found in the upper epidermis, but as von Gattenberg<sup>(22)</sup> has shown, these are of subepidermal origin and reach the epidermal layer through gliding growth. According to Butler<sup>(3)</sup> the upper epidermis often splits during development and is then replaced from the mesophyll.

The lower epidermis differs from the upper chiefly in that it possesses stomata, although the ordinary epidermal cells tend to be slightly larger, less angular, and more irregular in shape than those of the upper epidermis. Stomata are chiefly circular in surface view and are surrounded by accessory cells as in the case of citrus leaf stomata described by Schulze<sup>(48)</sup> and figured by Tschirch and Oesterle.<sup>(54)</sup> The usual diameter of stomata in the material studied is about 13 to 16  $\mu$ , but Bahgat<sup>6</sup> reports that stomatal size is influenced by environment. Stomata are less numerous in the vicinity of oil glands and large veins. Their density has been shown to be influenced by leaf size and age (Reed and Hirano<sup>(46)</sup>) as well as by environment (Bahgat). For mature *Citrus sinensis* leaves grown in full sunlight, Hirano<sup>(26)</sup> reports the average number of stomata per square millimeter in areas free from oil glands and large veins to vary from  $402 \pm 2.5$  in the Lue Gim Gong orange to  $533 \pm 2.5$  in the Ruby Blood orange, the numbers in Washington Navel orange and Valencia orange being respectively  $458 \pm 2.7$  and  $504 \pm 2.7$ . In section, the stomata are seen to have prominent outer cuticular ridges and weakly developed inner cuticular ridges. Specific differences in the development of cuticular ridges of citrus stomata have been found by McLean.<sup>(34)</sup>

In very young *Citrus sinensis* leaves, the chlorenchyma shows little differentiation (plate 7, fig. 2); but in mature leaves, palisade and spongy parenchyma are distinct (plate 7, fig. 6). Halma<sup>(25)</sup> reports that leaves collected from the north and south sides of the tree, and those taken from upper and lower branches failed to show any differences in the degree of palisade development, but that leaves from the dense interior portion of the tree were markedly below the average in the de-

<sup>6</sup> Bahgat, M. M. A study of the structure and distribution of stomata in the different species of *Citrus*. Thesis for the degree of Master of Science, University of California, 1923. (Typewritten.) Copy on file in the University of California Library, Berkeley.



velopment of palisade tissue. He finds that the depth of palisade tissue is  $23.8 \pm 0.008$  per cent of leaf thickness in Valencia orange, and  $22.8 \pm 0.12$  per cent in Washington Navel orange. Usually, the palisade tissue consists of two rows of elongated cells, but at times a third row may be partially developed. The spongy parenchyma is rather dense. Its cells are fairly regular in shape; those adjoining the palisade tissue are generally circular in cross section, while those in the remaining layers are chiefly somewhat elongated parallel to the leaf surface.

Spherical or subspherical schizolysigenous oil glands (plate 7, fig. 2) similar to those found in the primary cortex are formed before palisade and spongy parenchyma are well differentiated. In mature leaves they occur in both types of chlorenchyma. They usually lie subjacent to or within a few cells of the epidermis. Cells containing solitary calcium oxalate crystals are very numerous (plate 7, figs. 1, 6, and 7). As in the case of stems, those occurring subjacent to the epidermis or pushed into the epidermal layer by gliding growth are characterized by strongly but irregularly thickened inner and radial walls which are attached to the crystal in fully developed leaves. Cells of this type are larger and somewhat more frequent in occurrence in the palisade than in the spongy parenchyma. In addition to occurring subepidermally, large calcium oxalate crystals are also scattered in the spongy parenchyma, particularly in the vicinity of large veins. Starch grains and hesperidin also occur in the mesophyll.

With the exception of the midrib, none of the veins project on the upper side of the leaf. On the lower side of the leaf, the midrib projects considerably and the major lateral veins slightly. Whether a correlation between size of vein islets and leaf maturity found by Ensign<sup>(16)</sup> in *Citrus grandis* also occurs in this species has not been determined. In section, two collateral vascular bundles are seen to pass through the central portion of the midrib (plate 7, fig. 1), while but one such vascular bundle is present at the apex of the midrib and in smaller veins. The lower vascular bundle of the midrib, which alone extends to the apex of the lamina, is crescent-shaped, and like those in smaller veins has dorsal phloem. The upper vascular bundle of the midrib has ventral phloem and toward the base of the lamina nearly closes the opening in the crescent-shaped lower bundle. At the base of the lamina the two collateral vascular bundles unite to form a single amphicribal vascular bundle. Rays are developed in the xylem portion of both upper and lower vascular bundles of the midrib. A narrow band of thin-walled fibers borders the phloem. Collenchyma extends from the band of fibers to the chlorenchyma, which is considerably reduced in the midrib.

## DISEASED LEAVES

The first symptom of psorosis on leaves is the appearance of mosaic-like spots on rapidly growing young leaf blades. The mosaic effect is distributed over the entire lamina or only certain portions of it and is due to numerous elongated, light-colored areas 1 to 3 mm in length in the region of the smallest veinlets. The pale-green areas producing the mosaic effect commonly disappear or become masked as the leaf matures. Mature leaves may show few or many circular to irregular light-yellow to orange-colored areas varying in diameter from 0.5 to 10.0 mm. Frequently the discolored areas take the form of complete or partial narrow rings 2 to 7 mm in diameter. Raised, brown, corky areas are often present in the center of the yellow spots and also occur in the form of complete or partial rings of the same diameters as the yellow rings. Such corky areas occur on both upper and lower sides of the lamina and occasionally some of those on the two surfaces correspond in position.

Usually the tissues of mosaic-like areas of young leaves closely resemble those of healthy leaves of the same age except in chemical composition of cell contents as shown by staining reactions (plate 7, figs. 2 and 3). In leaves showing the mosaic effect, groups of epidermal and mesophyll cells with contents that stain heavily with safranin are far commoner than similar dark-staining cell groups in healthy leaves. In one diseased young leaf, a gum pocket was found in the mesophyll (plate 7, fig. 8).

When sections are made through the yellowish areas of mature leaves, ordinarily no departures from normal cell size, shape, or arrangement are evident. At this stage of the disease usually the only visible effect in the leaves is the yellowing or browning of contents of epidermal and, to some extent, of mesophyll cells in areas corresponding to the macroscopically discolored areas. In some instances, cells subjacent to those with darkened contents divide parallel to the leaf surface.

Sections through the corky areas of mature leaves show the presence of abnormal tissues at such points (plate 7, fig. 7). The cork on the upper surface of the leaf is produced by phellogen layers of limited extent produced in the palisade tissue, while that on the lower surface is formed by phellogen originating in the spongy parenchyma. Such phellogen layers may form in the mesophyll layers subjacent to the epidermis or at a depth of several cells in the spongy parenchyma but always originate subjacent to cells with brown contents. Towards the exterior the phellogen produces a phellem of tabular suberized cells, while towards the interior it forms a limited number of tabular parenchyma cells. At

about the time of periderm formation some of the cells underlying the periderm frequently divide. Such divisions are usually approximately parallel to the leaf surface. Scattered groups of brown cells are at times found in the mesophyll beneath the periderm. Not infrequently the leaf tissue external to the phellem is attacked by fungi of various kinds.

It is noteworthy that the histology of corky rings of *Citrus sinensis* leaves affected by psorosis corresponds closely to that of lesions attributable to other causes, indicating that as in cases cited by Butler,<sup>(3)</sup> similar reactions may result from different stimuli. Corky lesions of irregular form and unknown cause on orange leaves figured by Penzig<sup>(41)</sup> show similar arrangement of tissues in section. Penzig points out that browning of epidermal cells precedes the formation of such corky areas. Sections through lesions produced by *Sphaceloma fawcetti* Jenkins on citrus leaves are also similar (Cunningham,<sup>(9)</sup> Butler<sup>(3)</sup>). In citrus leaves wounded by mechanical means, Cunningham reports that a cicatrice is formed some distance from the edge of the wound, the intervening cells being dead and filled with a dense granular substance resembling tannin.

Although cork formation also occurs in citrus leaves from boron-deficient cultures, such leaves exhibit anatomical differences from leaves affected by psorosis. Haas and Klotz<sup>(23)</sup> have shown that in boron-deficient citrus leaves cork production is confined to the palisade tissue and veins.

## DISCUSSION

A histological study of tissues affected by psorosis shows that the characteristics of the disease are: (1) the abnormal browning of contents of parenchyma cells, (2) abnormal periderm production, and (3) sometimes gum production. It is significant that both normal periderm formation in healthy stems and abnormal periderm formation in stems and leaves affected by psorosis occur subjacent to cells with contents that have turned brown. A similar restriction of periderm formation to tissues bordering browned cells has previously been reported in other genera (Küster,<sup>(30)</sup> Priestley and Woffenden<sup>(45)</sup>). Küster suggests that in such cases "some products of disintegration" or "unknown chemical combinations" produced in the brown cells incite cork formation in adjacent healthy tissue. Priestley and Woffenden consider that the essential antecedent to phellogen formation is the blocking of a parenchymatous surface, usually by a deposit of suberin or cutin which may occur in mixture with other substances around brown cells. Their experiments have shown that the development of phellogen amidst parenchyma follows the accumulation of sap at such a blocked surface.

Since abnormal browning of primary cortical parenchyma cells is the first visible symptom of psorosis in the bark of trunks, and a similar browning of epidermal and mesophyll cells is the first sign of psorosis in mature leaves, the determination of the nature of this browning is important in an understanding of the histology of the disease. The finding of mosaic-like symptoms and the transmission of the disease by budding and rooted cuttings suggest a virus as the possible initiating cause (Fawcett<sup>(19, 20)</sup>). This suggestion is supported by the failure to find a microscopic causal organism, although the usual differential stains for fungi and the chitosan test were employed in examining affected tissue showing various stages of the disease, collected at different localities and at different times of the year. It is also supported by the striking similarity of some of the internal changes with those found in connection with many virus diseases; for example, the browning attended by hyperplasia in adjacent tissue is not unlike that accompanying definitely known virus effects.

Although the changes in the tissue bringing about the scaly condition of the bark are probably initiated by a virus, certain environmental conditions appear to influence these changes. As Fawcett<sup>(18)</sup> points out, in the majority of cases the apparent activity on the bark is quiescent during the winter and early spring and most pronounced during the summer and early fall.

That increased light intensity may be a factor accelerating the initial browning of cell contents in the cortex and leaves of citrus affected by psorosis is suggested by the fact that Cook<sup>(8)</sup> attributes localized browning in tomatoes to the pathological condition resulting from sunburn. That increased temperature, directly or indirectly through its influence on rate of transpiration, may be involved in the rate of browning of cells is suggested by the findings of Willison<sup>(59)</sup> and Priestley and Woffenden.<sup>(45)</sup> Willison<sup>(59)</sup> reports that browning of parenchymatous cells in wood and bark is influenced by temperature and moisture conditions. Priestley and Woffenden<sup>(45)</sup> indicate that the rate of blocking of a parenchymatous surface preceding cork formation is positively correlated with transpiration rate. As discussed above, in the case of citrus cortex and leaves, the browning of parenchymatous cells evidently represents such a surface blocking.

There is some evidence that factors increasing the transpiration rate may also be conducive to the formation of gum, which is often present in trees affected by psorosis. Fawcett<sup>(17)</sup> has shown that partial desiccation of tissues is not a necessary condition to the initiation of gum formation in citrus, but that it is one of the factors which accelerates gum formation in *Pythiacystis* gummosis. Bartholomew<sup>(1)</sup> indicates that

the water deficit in tissues resulting from excessive transpiration is also an important factor in gum production in endoxerosis of lemons. Since excessive transpiration is known to increase gum production in other diseases of *Citrus*, it is possible that it may be operative in accelerating gum formation in psorosis.

### SUMMARY

In a healthy one-year-old stem of *Citrus sinensis*, epidermis, primary cortex and pericycle, phloem, cambium, xylem, and pith occur in centripetal order. Since the bark is persistent the order of tissues remains the same in later years except for the addition of periderm and loss of epidermis over parts of the stem.

Periderm formation commonly begins in the second year with the production of patches of phellogen subjacent to groups of epidermal cells with darkened contents. A continuous phellogen ring ordinarily does not form until several years later. Centripetally the phellogen produces a very small amount of parenchymatous phelloderm. Centrifugally it produces alternating layers of suberized and lignified cells in lenticels and suberized cells between lenticels.

In a psorosis-affected stem the first visible symptom of the disease is the abnormal darkening of contents of small, usually tangentially elongated groups of parenchyma cells of the primary cortex. This is followed by the production of a phellogen layer subjacent to the darkened cells. This phellogen produces phellem similar to healthy phellem centrifugally and phelloderm centripetally. The phelloderm is much more abundant than that produced by the phellogen of healthy stems, and at times contains radially arranged groups of small stone cells in addition to parenchyma similar to that of normal phelloderm. This abnormal production of tissue results in the formation of small, macroscopically visible eruptions on the bark surface. As the disease progresses, groups of parenchyma cells nearer the center of the stem become darkened and phellogen is formed subjacent to such groups. In time the tissues external to the abnormal phellem are sloughed off in scales which are the most conspicuous symptom of the disease on stems.

Gum which is often externally visible on psorosis-affected stems is commonly formed in the xylem and occasionally occurs in gum pockets formed in the abnormally thick phelloderm of such stems. Diseased xylem is characterized by concentric rings or partial rings of vertical gum ducts between the rays, and by scattered vessels partially plugged with gum.

In healthy, young leaves, oil glands and subepidermal crystal cells are differentiated before palisade and spongy parenchyma tissues be-



come distinct. In psorosis-affected leaves in which the mesophyll is not yet completely differentiated, a mosaic-like effect due to small light-colored areas in the lamina is macroscopically visible. Sections of such leaves differ from those of normal leaves in their staining reactions and are characterized by groups of epidermal and mesophyll cells which stain heavily with safranin. A gum pocket was observed in the mesophyll of one psorosis-affected leaf approaching maturity.

Mature leaves are distinctly bifacial, having stomata confined to the lower surface and a well-developed palisade layer commonly two or three cells in depth. In psorosis-affected, mature *Citrus sinensis* leaves, round to irregular discolored and corky areas, often in the form of complete or partial rings about 2 to 7 mm in diameter, are present in variable numbers. Sections through the discolored areas show an abnormal darkening of epidermal and occasionally mesophyll cells, but they usually otherwise closely resemble those of healthy mature leaves. At times, mesophyll cells subjacent to those with darkened contents may divide parallel to the leaf surface. Sections through corky areas of psorosis-affected mature leaves show that cork is produced by a phellogen formed subjacent to epidermal or mesophyll cells with darkened contents.

The apparent absence of a microscopic causal organism, together with the mosaic-like effect seen in young leaves and the browning of cells attended by hyperplasia in adjacent tissue, suggests that the disease may be caused by a virus. There is some evidence that its development may be accelerated by environmental factors.

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## PLATES 1 TO 7

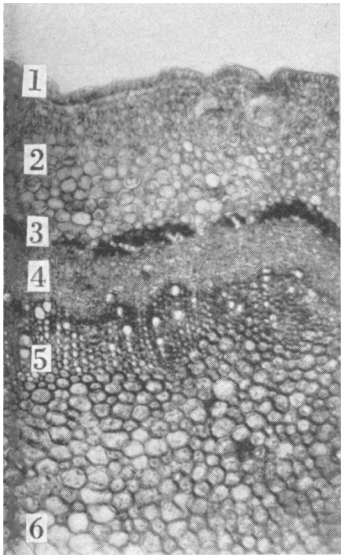
## PLATE 1

Fig. 1.—Transverse section taken near the apex of a healthy one-year-old Valencia orange stem showing epidermis (1), primary cortex (2), pericyclic fibers (3), phloem (4), cambium and xylem (5), and pith (6). ( $\times 87$ .)

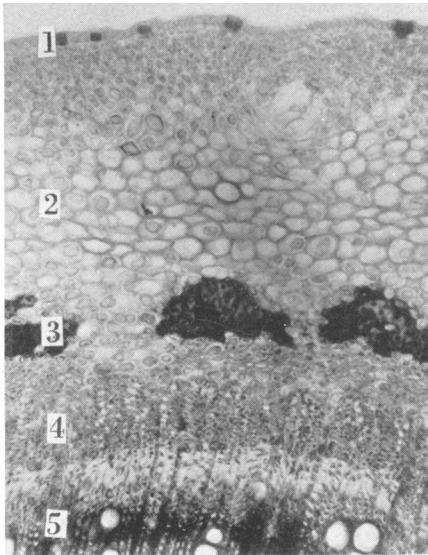
Fig. 2.—Transverse section taken near the base of a healthy one-year-old Valencia orange stem showing epidermis (1), primary cortex (2), pericyclic fibers (3), phloem (4), cambium and xylem (5). ( $\times 87$ .)

Fig. 3.—Transverse section of a healthy three-year-old Valencia orange stem showing periderm (1), stone cells in primary cortex (2), pericyclic fibers (3), and phloem fibers (4). ( $\times 87$ .)

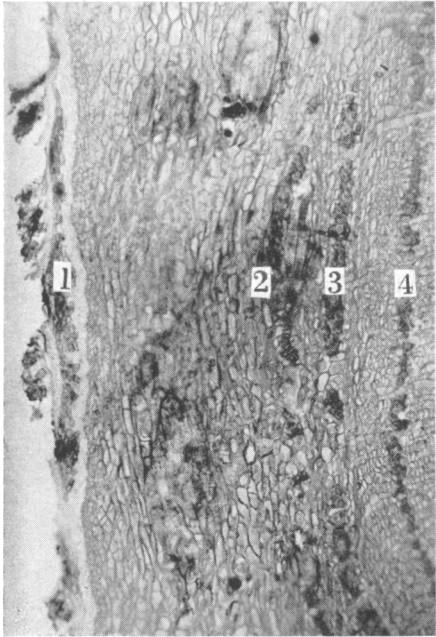
Fig. 4.—Radial section of lenticel and subjacent cortex (3) of a healthy nine-year-old Valencia orange trunk showing narrow bands of suberized cells (1) alternating with bands of lignified cells (2). ( $\times 87$ .)



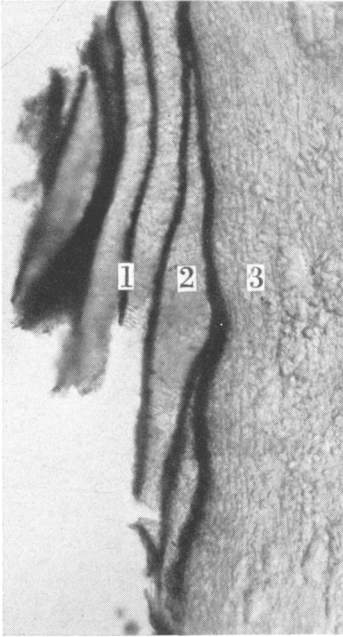
1



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## PLATE 2

Key to Symbols: 1, ordinary epidermal cell; 2, stoma; 3, sub-epidermal crystal cell; 4, cortical parenchyma; 5, suberized phellem; 6, lignified phellem.

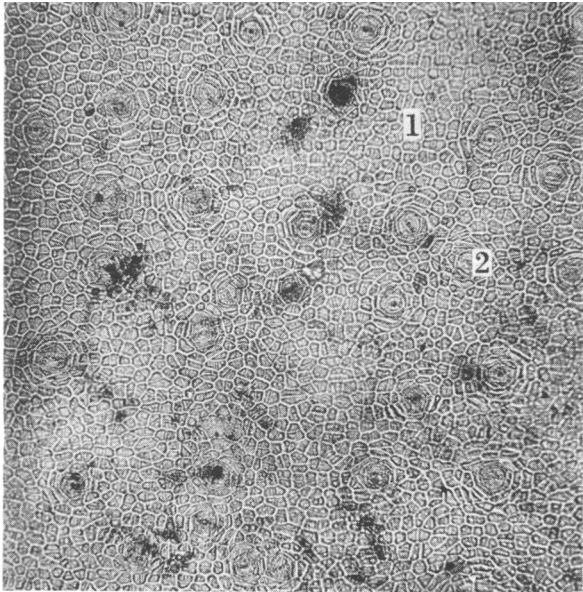
Fig. 1.—Surface view of epidermis from a healthy two-year-old Valencia orange stem showing distribution of ordinary epidermal and guard cells with darkened contents. ( $\times 120$ .)

Fig. 2.—Transverse section of epidermis and subjacent tissue of a healthy one-year-old Valencia orange stem showing sub-epidermal crystal cell and stomatal cavity. ( $\times 420$ .)

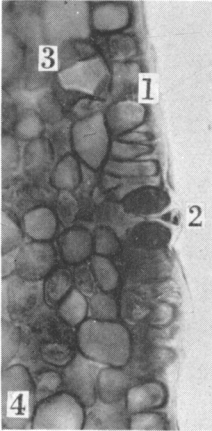
Fig. 3.—Transverse section of epidermis and subjacent tissue of a healthy two-year-old Valencia orange stem showing a group of cells with darkened contents. ( $\times 420$ .)

Fig. 4.—Transverse section of epidermis and subjacent tissue of a healthy two-year-old Valencia orange stem showing initial development of phellogen subjacent to a group of epidermal cells with darkened contents. ( $\times 420$ .)

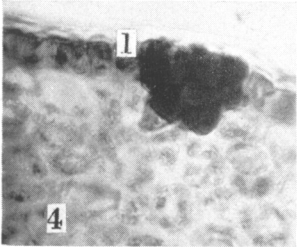
Fig. 5.—Transverse section of epidermis and subjacent tissue of a healthy two-year-old Valencia orange showing a slightly more advanced stage of phellem development than in figure 4. ( $\times 420$ .)



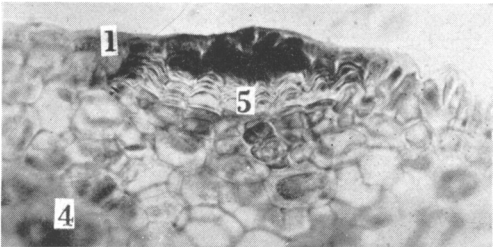
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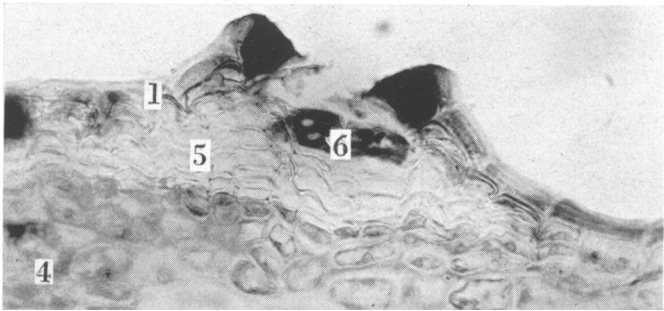
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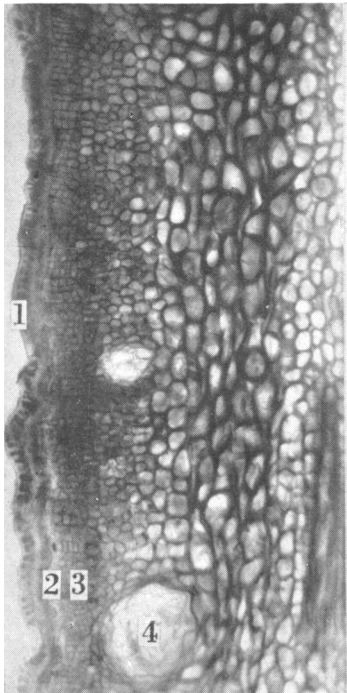
### PLATE 3

Key to Symbols: 1, epidermis; 2, phellem; 3, phelloderm; 4, oil gland in the cortex; 5, stone cells; 6, gum pocket.

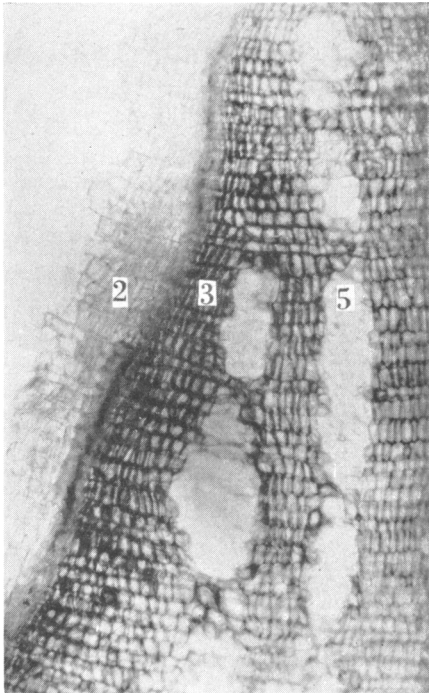
Fig. 1.—Radial section of outer bark of a healthy Valencia orange trunk showing persistent epidermis and periderm. (×120.)

Fig. 2.—Transverse section of abnormal periderm in psorosis lesion on trunk of a nine-year-old Valencia orange. (×120.)

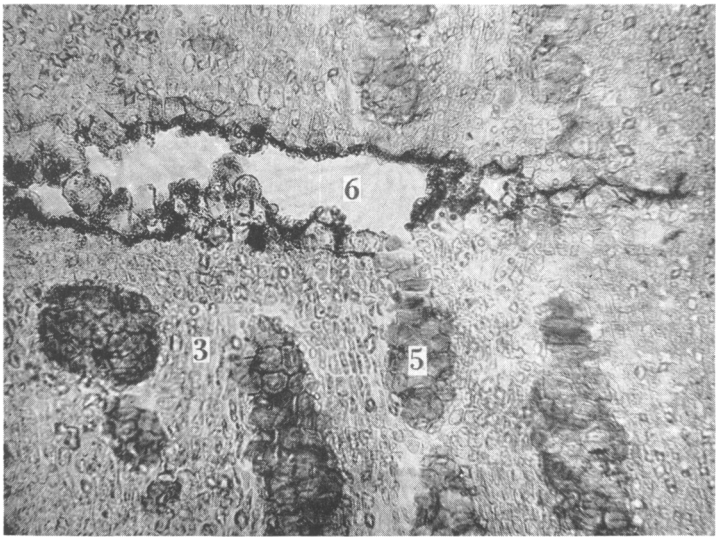
Fig. 3.—Transverse section of a gum pocket in phelloderm of a psorosis lesion on the trunk of a nine-year-old Valencia orange tree. (×120.)



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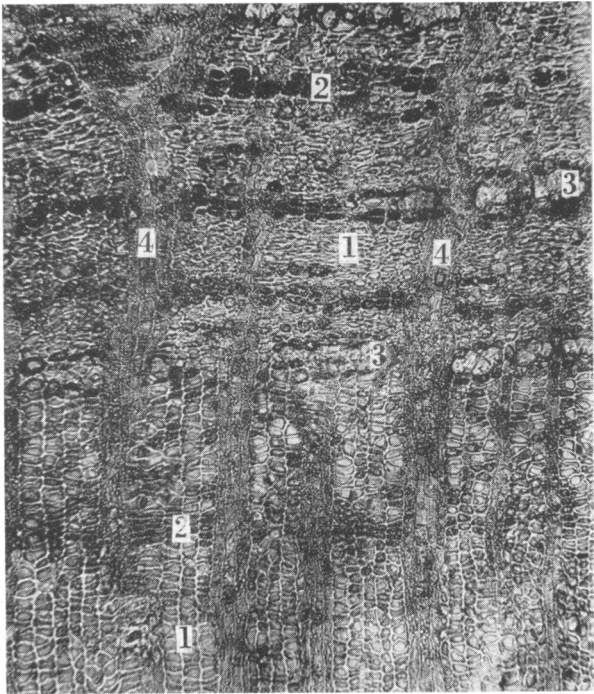
#### PLATE 4

Key to Symbols: 1, sieve tubes and companion cells; 2, phloem parenchyma; 3, phloem fibers; 4, phloem ray.

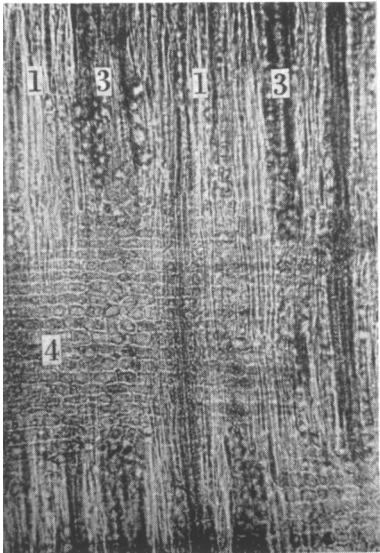
Fig. 1.—Transverse section of the inner portion of the phloem in a healthy nine-year-old Valencia orange trunk showing occurrence of various tissues in tangential bands. ( $\times 120$ .)

Fig. 2.—Radial section of the inner phloem of a healthy nine-year-old Valencia orange trunk. ( $\times 120$ .)

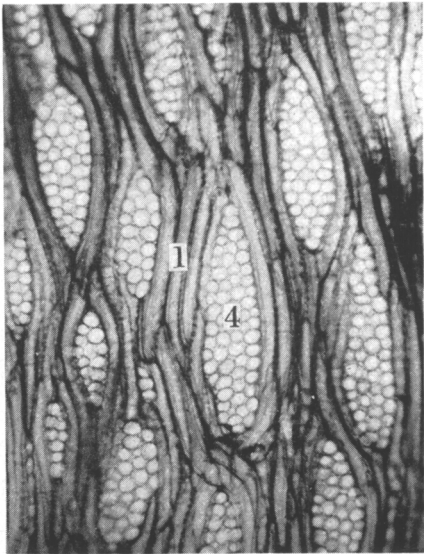
Fig. 3.—Tangential section of active phloem of healthy nine-year-old Valencia orange trunk. ( $\times 120$ .)



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## PLATE 5

Key to Symbols: 1, tissue with abnormal brownish cell contents; 2, abnormal periderm; 3, stone cells; 4, xylem.

Fig. 1.—Radial section of a young psorosis lesion on the trunk of a nine-year-old Valencia orange tree showing groups of parenchyma cells with darkened contents. ( $\times 90$ .)

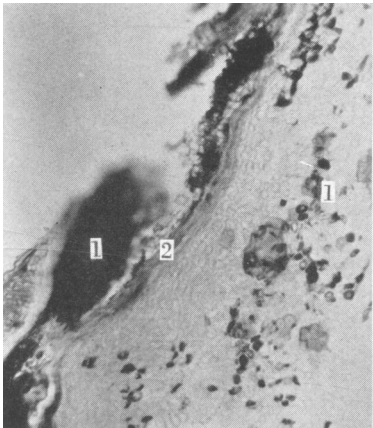
Fig. 2.—Transverse section of a young psorosis lesion on the trunk of a nine-year-old Valencia orange tree showing a portion of a small bark scale. ( $\times 90$ .)

Fig. 3.—Transverse section of a young psorosis lesion on the trunk of a nine-year-old Valencia orange tree showing tangentially elongated groups of parenchyma cells with darkened contents. ( $\times 90$ .)

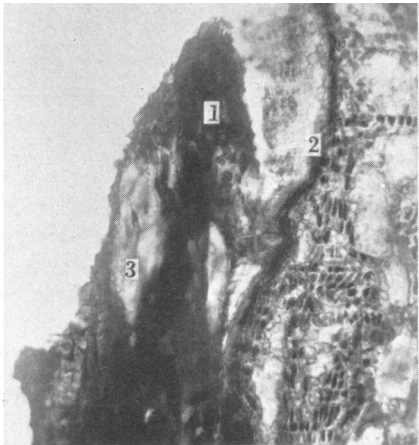
Fig. 4.—Transverse section of a psorosis-affected Washington Navel orange twig showing abnormal periderm extending through the primary cortex to the xylem. ( $\times 90$ .)

Fig. 5.—Transverse section of a psorosis-affected Washington Navel orange twig showing abnormal periderm formed in the cortex and small groups of cortical parenchyma cells with darkened contents. ( $\times 90$ .)

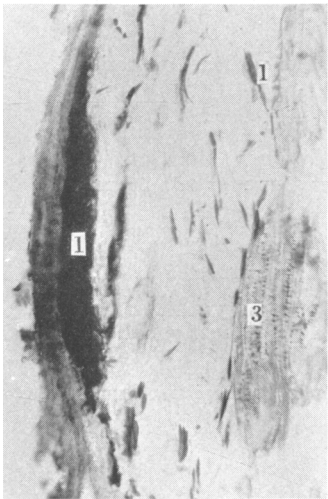
Fig. 6.—Macerated cortical parenchyma cells with darkened contents from the trunk of a nine-year-old Valencia orange tree affected with psorosis. ( $\times 469$ .)



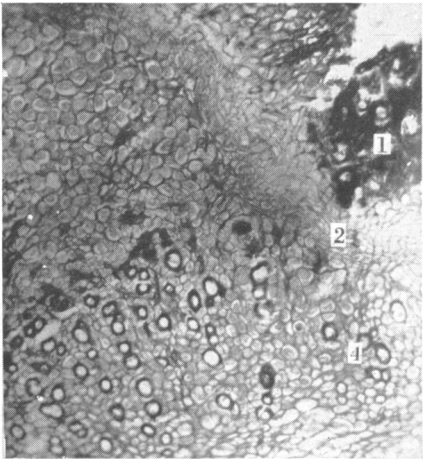
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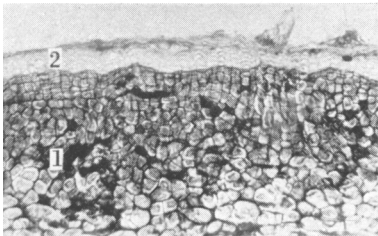
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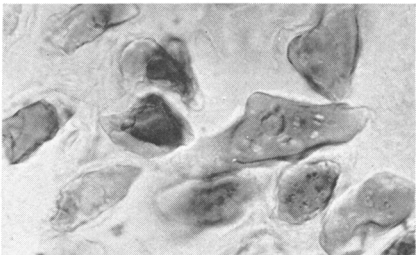
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## PLATE 6

Key to Symbols: 1, cambium; 2, pore or vessel member; 3, ray; 4, gum duct; 5, abnormal parenchymatous tracheid; all figures, Valencia orange.

Fig. 1.—Transverse section of cambium and subjacent xylem with few pores in a healthy trunk. ( $\times 80$ .)

Fig. 2.—Transverse section of cambium and subjacent xylem with numerous pores in a healthy large limb. ( $\times 80$ .)

Fig. 3.—Transverse section of cambium and subjacent xylem in a psorosis-affected branch showing irregular arrangement of tissues. ( $\times 80$ .)

Fig. 4.—Transverse section of xylem in a psorosis-affected branch showing irregular orientation of wood elements. ( $\times 80$ .)

Fig. 5.—Transverse section of xylem in a psorosis-affected branch showing a group of gum ducts and abnormal parenchymatous tracheids. ( $\times 80$ .)

Fig. 6.—Transverse section of discolored wood in a psorosis-affected branch showing gum in some of the vessels. ( $\times 80$ .)

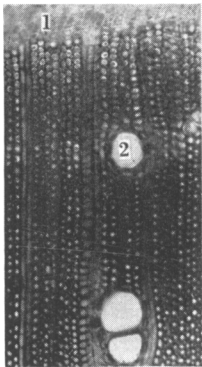
Fig. 7.—Transverse section of xylem in a psorosis-affected branch showing gum ducts. ( $\times 80$ .)

Fig. 8.—Abnormal cell contents in the xylem rays of a branch affected by psorosis. ( $\times 427$ .)

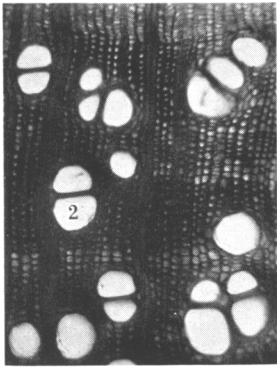
Fig. 9.—Parenchymatous tracheid in abnormal xylem produced subsequent to a gum pocket in a psorosis-affected branch. ( $\times 427$ .)

Fig. 10.—Tangential section of xylem in a healthy branch. ( $\times 80$ .)

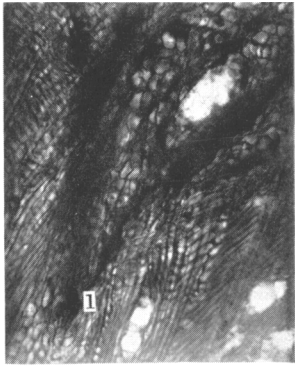
Fig. 11.—Tangential section of xylem in the region of gum ducts in a psorosis-affected branch. ( $\times 80$ .)



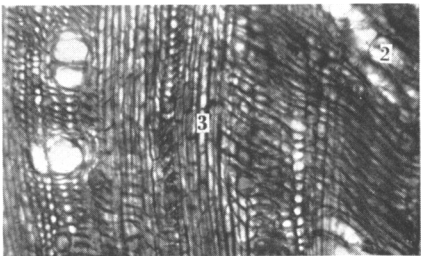
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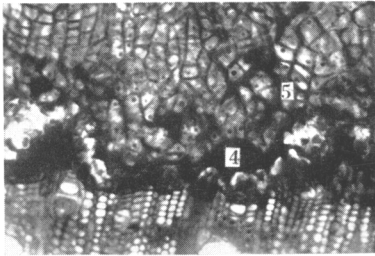
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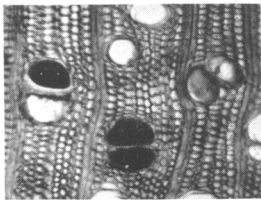
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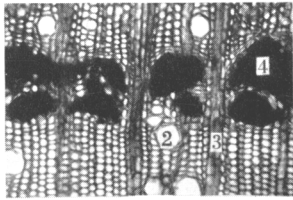
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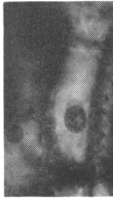
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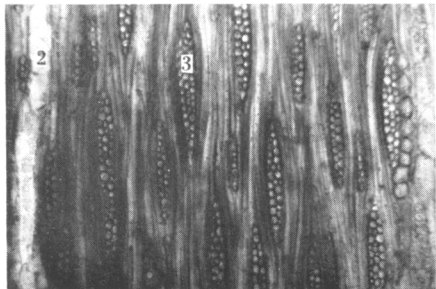
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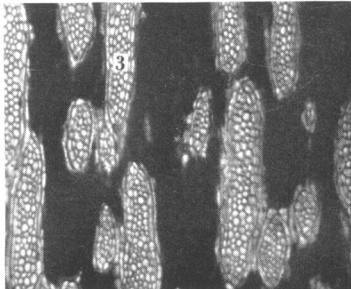
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## PLATE 7

Key to Symbols: 1, oil gland; 2, subepidermal crystal cell; 3, tissue with abnormal brownish cell contents; 4, abnormal phellem; 5, abnormal mesophyll cells.

Fig. 1.—Transverse section of the midrib taken at about the midpoint of a healthy mature Valencia orange leaf. ( $\times 90$ .)

Fig. 2.—Transverse section of a healthy young Valencia orange leaf. ( $\times 90$ .)

Fig. 3.—Transverse section of a psorosis-affected young Valencia orange leaf showing a group of mesophyll and epidermal cells with heavily stained contents. ( $\times 90$ .)

Fig. 4.—Hesperidin crystals in cortical parenchyma cells of a healthy one-year-old Valencia orange stem. ( $\times 469$ .)

Fig. 5.—Transverse section of a psorosis-affected mature Valencia orange leaf showing abnormal mesophyll subjacent to epidermal and palisade cells with darkened contents. ( $\times 90$ .)

Fig. 6.—Transverse section of a healthy mature Valencia orange leaf. ( $\times 90$ .)

Fig. 7.—Transverse section of a psorosis-affected mature Washington Navel orange leaf showing cork produced subjacent to epidermal cells with darkened contents. ( $\times 90$ .)

Fig. 8.—Transverse section of a psorosis-affected immature Valencia orange lamina showing a gum pocket in the mesophyll. ( $\times 90$ .)

