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BARK STRUCTURE OF SOUTHERN UPLAND OAKS[1]

Elaine T. Howard
Associate Research Chemist
Southern Forest Experiment Station, USDA, Pineville, La. 71360

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ABSTRACT

Bark structure of eleven oak species commonly found on southern pine sites was examined and described. In inner bark (phloem), groups of thick-walled lignified fibers and sclereids are interspersed among thin-walled cellulosic elements (parenchyma, sieve tube members, and companion cells). These fibers and sclereids greatly influence the bark's density, hardness, and other physical and mechanical characteristics. The innermost periderm is the boundary between inner and outer bark. In outer bark (rhytidome), areas of collapsed, dead phloem are enclosed by periderm layers. Periderm shape and spacing vary greatly within species. Great differences in exterior roughness and bark thickness also occur within species.

Keywords: *Quercus* spp., anatomy, bark, oaks, phloem, periderm, rhytidome.

INTRODUCTION

Small hardwood trees growing on sites better suited to southern pine present a major forest utilization problem in the South today. Oaks comprise about 48% of the hardwood volume on such sites (Christopher et al. 1976), and their bark accounts for a considerable part of total volume. For example, on oaks 6 inches in dbh, bark represents about 17% of stem volume. Removing the bark usually presents a disposal problem and results in the waste of large quantities of material that should be utilized. A possible solution is utilization of these small hardwoods as whole-tree chips.

When wood with bark is processed, the bark characteristics peculiar to the species often determine the nature and magnitude of the problems encountered. Because bark properties are influenced by their structure, behavior of a bark under certain conditions may sometimes be predicted from a knowledge of bark anatomy. Thus, the types of cells present, their arrangement, relative amounts, and physical dimensions and proportions are all of major importance in utilization.

The objective of the present study was to observe, compare, and describe the bark structure of eleven upland oaks growing on southern pine sites. Species sampled are listed below:

Common name	Scientific name
Black oak	*Quercus velutina* Lam.
Blackjack oak	*Q. marilandica* Muenchh
Cherrybark oak	*Q. falcata* var. *pagodaefolia* Ell.
Laurel oak	*Q. laurifolia* Michx.
Northern red oak	*Q. rubra* L.
Post oak	*Q. stellata* Wangenh.
Scarlet oak	*Q. coccinea* Muenchh.
Shumard oak	*Q. shumardii* Buckl.
Southern red oak	*Q. falcata* Michx.
Water oak	*Q. nigra* L.
White oak	*Q. alba* L.

Of these, post and white oaks belong to the white oak group; all others are considered red oaks. Species comparisons involving quantitative data and statistical differences in bark cell morphology are currently under investigation at the Southern Forest Experiment Station.

PAST WORK

Although phloem has long been a favorite topic for research by numerous botanists (notable among them are Huber 1939; Holdheide 1951; Srivastava 1964; Esau

[1] The author thanks Dr. Floyd Manwiller, Southern Forest Experiment Station, who supplied the bark samples.

1965, 1969), few references are found that specifically describe the particular species included in this study. Descriptions of the outer bark are particularly sparse.

Chang (1954) described white oak and northern red oak barks and suggested a table of diagnostic features of oak barks according to two groups—subgenera *Erythrobalanus* Spach. (red oaks) and *Lepidobalanus* Endl. (white oaks). Martin (1963) included photos and brief descriptions of black and northern red oak barks in his dissertation on bark thermal properties and fire injury. No information was found on the structure of the other oak barks examined in the present study.

PROCEDURE

One tree of each species (5.5 to 6.5 inches in dbh, outside bark) was cut from each of ten locations throughout an eleven-state area from Virginia to Texas. Whole bark, microtome sections, and macerated bark (including phloem) were studied to determine cell types present, their arrangement, and possible species differences. Samples were generally extremely brittle whether embedded or not; therefore, the following procedure was developed to keep sections intact during handling:

1. Make preliminary microtome cut to smooth block surface.
2. Press cellophane tape firmly onto dry block surface; then make cut.
3. Coat the section with Parlodion[2] in acetone.
4. Soak tape in xylene to release tape from coated section.
5. Bleach section in ammoniated hydrogen peroxide solution (10 ml of 20 volume H_2O_2 and four drops concentrated NH_4OH).
6. Mount. (Spread albumen thinly on slide, press section down with coating side up. Flood with absolute alcohol, and blot firmly.)
7. Soak slide in acetone to remove Parlodion.
8. Proceed through the alcohol series to water, then stain with safranin and fast green.

[2] Mention of trade names is solely to identify materials used and does not imply endorsement by the U.S. Department of Agriculture.

ANATOMY

The vascular cambium surrounds the stem at the boundary of the wood and bark. It produces wood (xylem) to the interior and phloem (conducting and storage cells of the bark) to the exterior. The layer of phloem produced each year is only a fraction as thick as the annual layer of wood. Each new layer of phloem pushes the older phloem layers outward from the enlarging wood stem.

A new tissue—the phellogen or cork cambium—appears within various areas of the older phloem at some distance outside the vascular cambium. The phellogen is a layer of dividing cells that produce tangentially oriented layers of periderm. The impervious periderms protect the delicate phloem tissue from harmful external influences. Portions of older phloem are sealed off from supplies of nutrients and moisture by the periderm layers, and cells of these isolated areas of phloem subsequently die. Each periderm dies when a newer one is formed further inward. The tissues are pushed outward by each year's growth; when outer layers do not flake off as rapidly as interior ones are formed, a thick, rough bark eventually accumulates. Longitudinal cracks form to accommodate tangential stresses caused by growth in the tree's girth.

The term "bark" as used in this paper will refer to all tissues produced outside the vascular cambium. It consists of two portions—the light colored inner bark (living phloem) and the dark outer bark (rhytidome). The innermost periderm separates the two zones (Fig. 1). Oak bark tissues and cells are listed below:

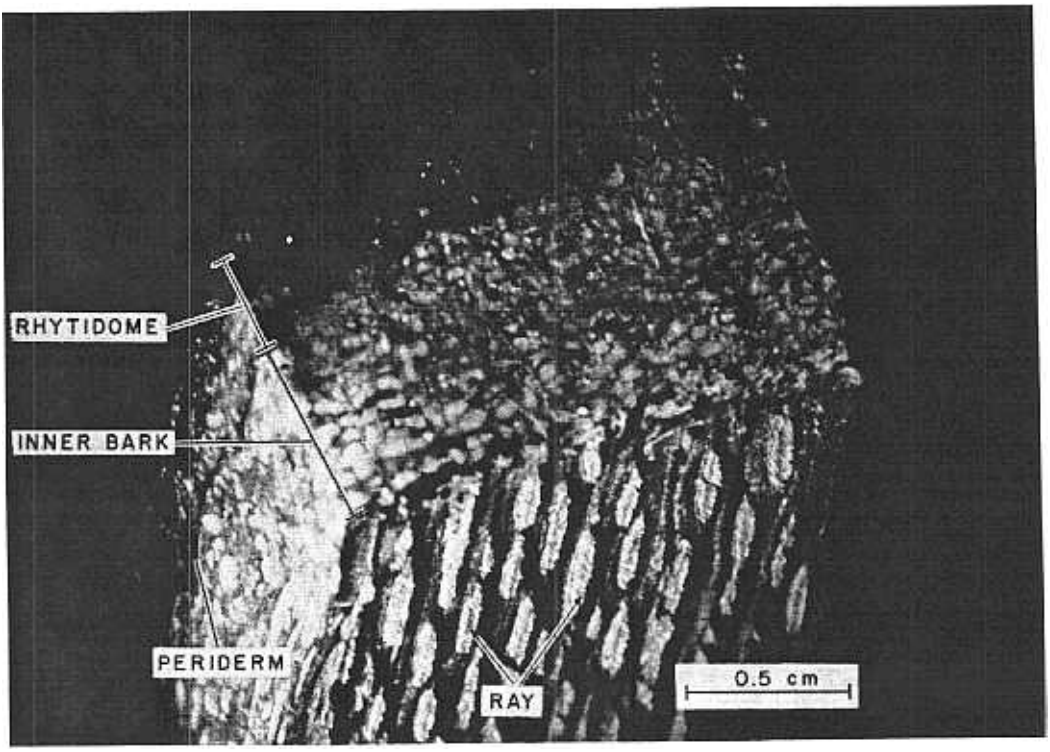

FIG. 1. Southern red oak bark, cross-sectional (top), radial (left), and tangential (foreground) views. Sclereid groups appear as white areas on cut surfaces. Rays protrude on surface next to cambium.

Inner bark (phloem)
- Sieve tube elements
- Fibers
- Sclereids
- Vertical parenchyma
- Ray parenchyma
- Companion cells

Outer bark (rhytidome)
- Old phloem
- Periderm
  - Phellogen
  - Phellem (cork)
  - Phelloderm

Phloem

The principal food-conducting tissue of the tree is the phloem, or inner bark, which transports substances manufactured in the crown downward to other parts of the tree. Oaks have a fairly thick inner bark, generally 3 to 7 mm, but only a narrow band (about 200 to 300 μm, according to Huber 1958) next to the cambium is active in conduction. When phloem ceases to function as conducting tissue, its structure becomes greatly modified. Thin-walled cells readily collapse and become distorted, their arrangement becomes disorganized, and the original tissue arrangement becomes indiscernible not far from the cambium. Most of the early collapse involves sieve-tube members and companion cells; parenchyma distortion occurs mainly after separation from the inner bark by a periderm. Only fibers and sclereids have rigid walls that resist distortion.

Sieve tubes.—Organic solutes are conducted primarily by the sieve tubes, which are comprised of individual sieve tube members joined end to end in longitudinal series. Only those in a narrow zone next to the cambium actively conduct solutes,

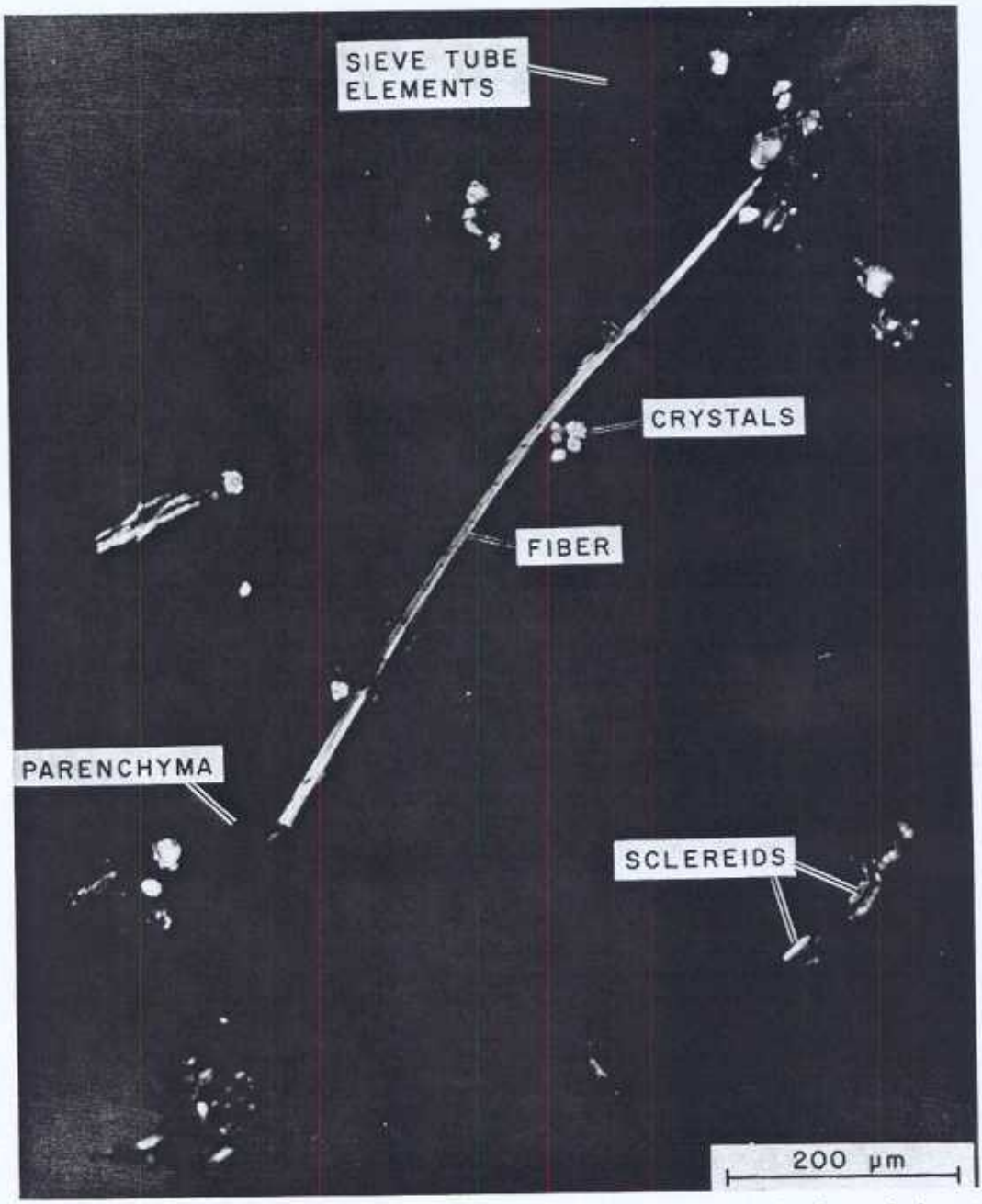

FIG. 2. Macerated bark from southern red oak. Fibers are the only greatly elongated elements in bark.

for most sieve tubes function one season only. Sieve tubes occur scattered singly, in groups, or in interrupted tangential bands. They rarely occur in actual contact with fibers or sclereids but are usually separated from them by parenchyma or companion cells (Zahur 1959).

Sieve tube members have thin, mainly

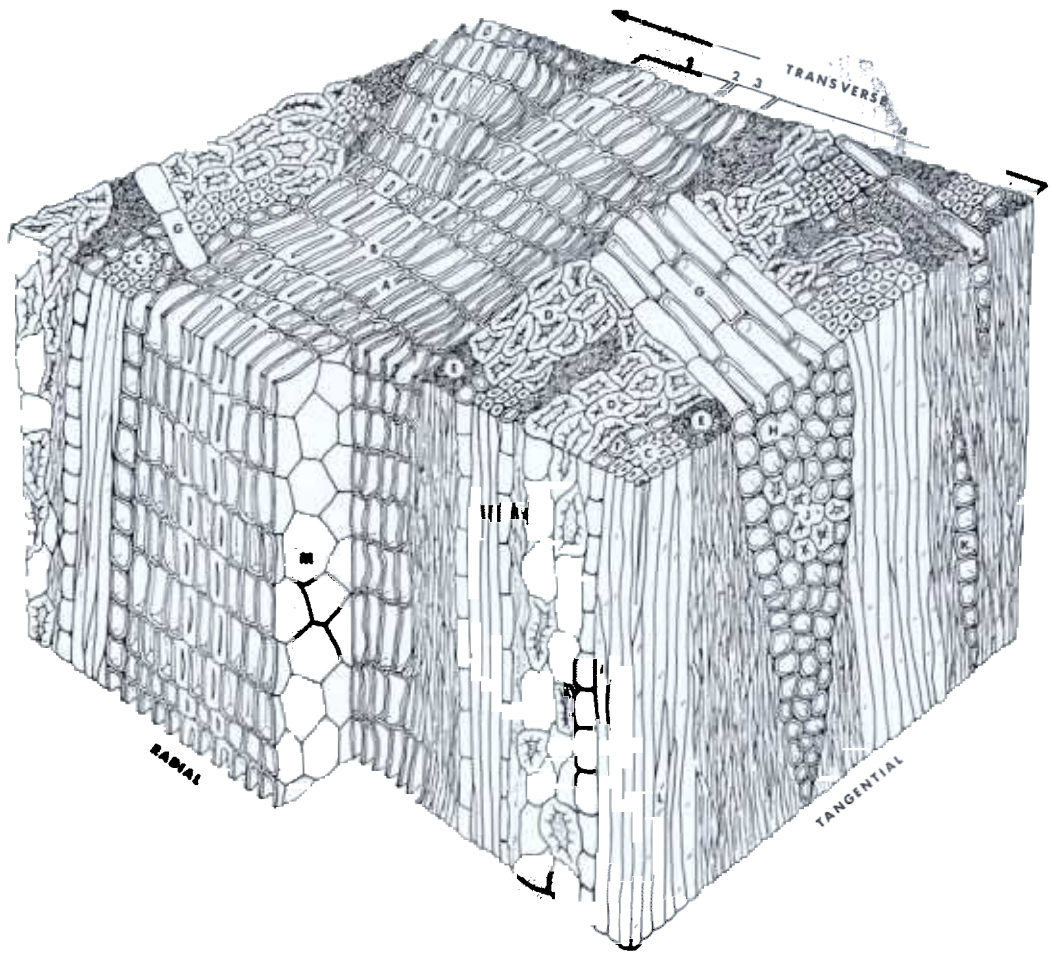

FIG. 3. Schematic drawing of outer bark from southern upland oaks. Periderm is comprised of 1, 2, and 3. Arrow points toward tree exterior. *Transverse view.* 1.—Phellem: A, typical cork cells: B, thick-walled cork band. 2.—Phellogen (cork cambium). 3.—Phelloderm. 4.—Old phloem tissue: C, fibers; D, sclereids; E, collapsed thin-walled elements (sieve tubes, companion cells, parenchyma); F, crystal-bearing parenchyma along margins of fiber groups; G, ray parenchyma. *Tangential view.* H, broad ray; J, sclerified ray cells; K, narrow ray; L, fiber pits; M, polygonal phellem arrangement.

cellulosic walls. They communicate with other cells by means of specialized portions of the wall called sieve areas. Sieve areas have clusters of perforations or pores through which connecting strands join adjacent sieve elements. Plasmodesmata connect the sieve areas with parenchyma cells (Esau 1965, 1969). During the functioning life of the sieve element, a deposit called callose builds up around each connecting strand and eventually over the whole sieve area. Callose usually disappears after conduction ceases; sieve areas then appear as thin areas with numerous tiny perforations. On the end walls, sieve areas are grouped into compound sieve plates, structures comparable to perforations of vessels in wood. The number of sieve areas in each plate varies. Chang (1954) describes white and northern red oaks as usually having three to eight sieve areas per plate, rarely over twelve. Sieve areas on side walls usually are less highly specialized and do not form sieve plates. Pores of these sieve areas

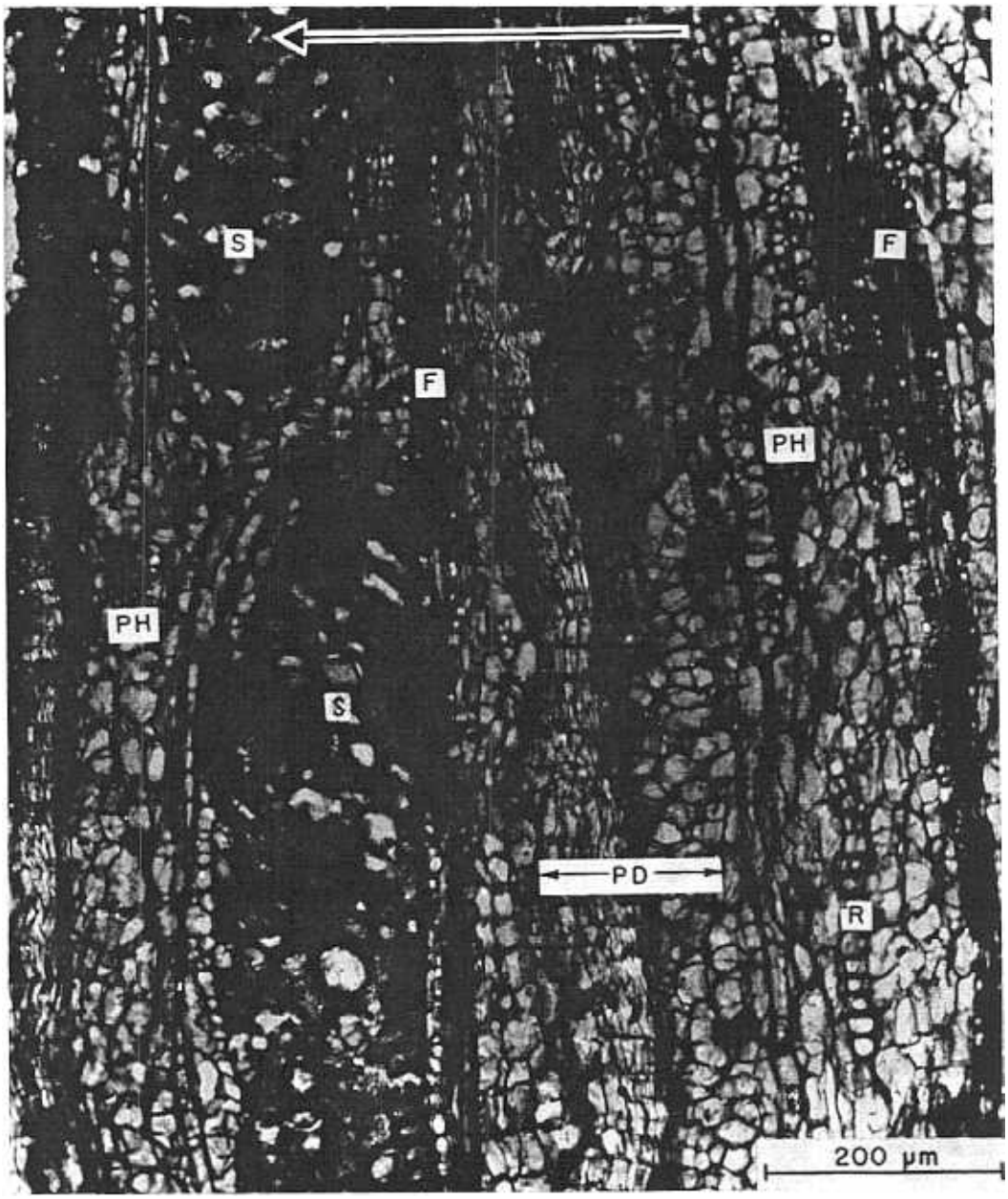

FIG. 4. Radial section of post oak bark. Arrow indicates exterior of tree. Fibers (F) accompanied by crystal-containing parenchyma, periderm (PD), old phloem tissue (PH), narrow ray (R) seen in end view after tissue collapse and distortion, sclereid groups (S).

generally are smaller than those of the ends (Evert et al. 1971).

Oak sieve tube members sometimes can be difficult to study in detail because they are usually crushed outside the narrow conducting zone; the delicate and extremely thin walls appear almost transparent in macerations (Fig. 2), and in cross section

they can be distinguished from parenchyma only if the sieve areas at the end are in view.

Fibers.—The mechanical strength of oak bark is provided by two cell types—fibers and sclereids. Oaks have typical phloem fibers. These are oriented vertically and are the only greatly elongated cells of the bark (Figs. 2 and 3). In *Quercus*, fibers develop secondary walls and differentiate as mechanical cells close to the cambium. They often mature in the current growth season (Esau et al. 1953). The phloem fibers are somewhat shorter than corresponding wood fibers but are otherwise similar in appearance. They are long and slender with tapered overlapping ends, thick walls, and narrow lumens. Fibers of all species examined had lignified walls. A tendency of the broad inner portion of the cell wall to separate from the outer portion during microtoming was noted.[3] A few narrow simple pits are found in the walls; occasional bordered pits may occur.

The fibers are in small groups arranged as widely spaced, discontinuous tangential bands, which are usually only about two to five cells wide. Strands of crystal-bearing parenchyma are found along the margins of the fiber band. In older, nonfunctioning phloem, groups of sclereids develop adjacent to the fibers, usually on the side away from the cambium (Fig. 4). Occasionally the fibers may be found completely enclosed within sclereid groups.

Sclereids.—Sclereids form a high proportion of oak bark and greatly influence its physical and mechanical characteristics. These dense cells lend rigidity, hardness, and brittleness to the bark and are responsible for some processing problems in products such as fine papers. These hard, irregular cells (frequently called "stone cells") are grouped into compact masses that are readily visible on cut surfaces of both inner and outer bark (Figs. 1 and 4).

[3] R. F. Evert (personal communication) notes that these layers tend to separate because phloem fibers in oak are gelatinous. Only the outer part, which consists of middle lamella, primary wall, and some secondary wall, is not gelatinous.

FIG. 5. Sclereids and crystals of southern red oak bark. Sclereid walls are birefringent and have numerous tiny pits that give a "granular" appearance in polarized light.

On cross sections they appear as shiny spots that often form short tangential bands.

Sclereids originate from ordinary parenchyma cells in the phloem (usually in older nonconducting phloem) and thus are formed later than fibers. Hardwood sclereids often undergo some changes in shape and size during their transformation from parenchymatous cells, but they usually do not become as twisted or branched as those in conifers. Sclereid walls are thick and heavily lignified and have distinct lamellate layers with numerous simple pits (Fig. 5).

Parenchyma.—Parenchyma of phloem is arranged in two systems: longitudinal (primarily in strands) and horizontal (rays). Longitudinal parenchyma is rather abundant in oaks; the amount varies within a species and with the environment (Zahur 1959). These cells are usually irregularly distributed among sieve tubes but sometimes are in tangential bands if the tissues have not yet become greatly distorted.

Phloem parenchyma cells are somewhat cylindrical in cross section and usually have only thin cellulosic walls with numerous primary pit fields by which they communicate with each other and ray cells. They contain stored products such as tannins and other phenolic compounds, starches, oils, fats, and various types of crystals. Parenchyma remain functional long after the sieve elements die, and some of the parenchyma cells acquire thick secondary walls and become modified as sclereids.

Rays.—Phloem rays provide horizontal conduction within the inner bark. They transport nutrients from the actively conducting zone to living parenchyma and the innermost phellogen. The outer portions of rays die when eventually sealed off by formation of a new and deeper periderm.

When oak bark is split from the wood at or near the cambium, rays are readily visible on the inner surface of the phloem and usually protrude from the bark (Fig. 1). They are the outward continuation of the wood rays, and like them, occur in two distinct sizes: narrow rays (uniseriate or partially biseriate) and broad, multiseriate rays. They are homocellular, i.e., comprised of only procumbent ray cells that are usually fairly short and thin-walled.

Many ray cells undergo modification to become sclereids. They develop thick, lignified secondary walls with numerous simple pits and sometimes change in shape. The sclerification process begins near the cambium and increases as the cells are pushed outward.

Because of the functional and structural changes occurring in the bark and the resulting physical stresses, the rays may become distorted in nonfunctioning phloem and the outer bark. Some rays dilate by multiplication of cells within the ray, producing an archlike pattern in the outer portion of the inner bark.

Companion cells.—Companion cells are narrow, highly specialized parenchymatous cells that appear to be intimately associated with sieve elements. They are produced by the same cambial cell that produced the accompanying sieve tube member. The two types of cells die and collapse simultaneously; they often remain attached in macerated material. In the oaks studied, companion cells were often difficult to distinguish from ordinary parenchyma by light microscopy.

Crystals.—Crystals of various types are abundant throughout the bark of all oaks examined. As in phloem of many other plants, they are probably composed of calcium oxalate deposited as a byproduct of metabolism (Esau 1965). Crystals occur clustered within a cell or are solitary. Parenchyma strands with one crystal filling each cell are quite common in oaks and are usually associated with fibers and sclereids. A variety of shapes are found among oak crystals. Spiculate clusters (druses) are especially frequent, and various polygonal crystals also abound (Fig. 5). Most are fairly isodiametric (about 12–35 μm), and no greatly elongated forms were found.

Rhytidome

The rhytidome, or outer bark, is the dark-colored, dead tissue outside the newest periderm. It insulates the tree and protects it from mechanical injury and desiccation.

Several marked changes occur in the transformation of phloem tissue into rhytidome: appearance of the cork cambium (phellogen) and production of the periderm, accumulation of considerable deposits of dark-colored substances within the cells, and subsequent death of all tissues outside the new periderm.

Periderms.—The periderms protect the inner bark from moisture loss. They are readily visible on cut surfaces as discontinuous lines of variable pattern more or less parallel to the circumference. Only the innermost periderm is alive. Its formation seals off vital food and water supplies from inner bark to the previous periderm.

A periderm is composed of three tissues—phellogen, phellem, and phelloderm. The phellogen, or cork cambium, is the layer of cells that forms cork (phellem) toward

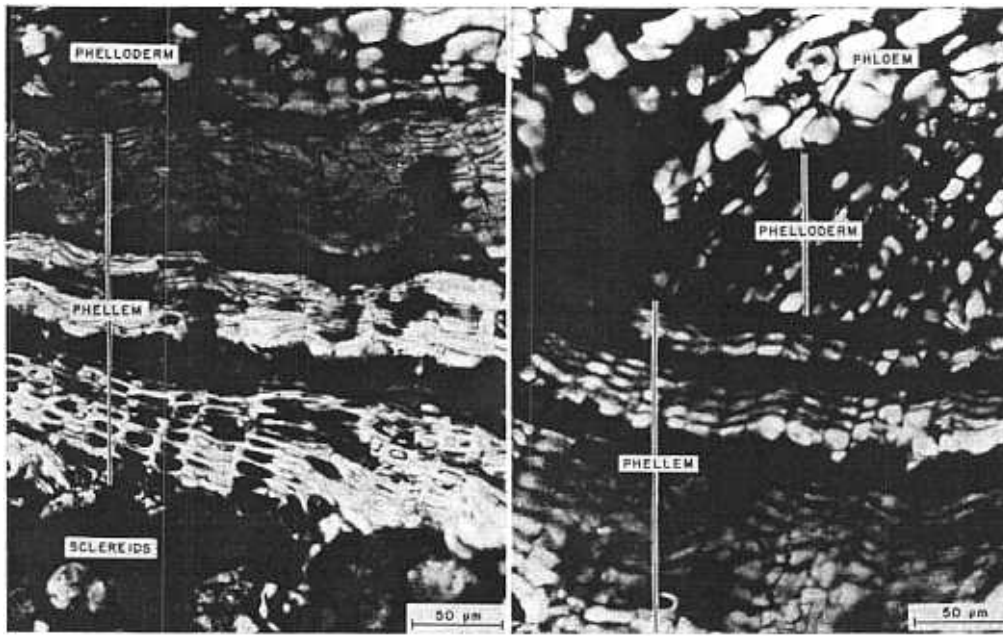

FIG. 6. Walls of phellem cells are considerably thicker in red oaks (left) than in white oaks (right). In both, narrow bands of lignified cells (dark lines) alternate with ordinary cork tissue.

the outside and parenchyma (phelloderm) on the inside. Early phellogens originate from cortical cells, but in older bark they arise from parenchyma of the nonfunctional phloem. The derivative cells retain the polygonal shape of the mother phellogen cell for the most part but differ in wall structure. They are in distinct radial alignment but are not aligned tangentially (Fig. 3). Periderm width depends on length of life of its phellogen; if it is replaced by a new phellogen deeper in the bark after it has been active for a short duration, only a few layers of cells would have been produced and the periderm would be narrow.

The phellem, or cork tissue, is primarily responsible for preventing moisture loss from the stem. Oaks of the species studied do not produce extensive cork layers as does cork oak (*Quercus suber* L.). Phellem is a compact tissue of small cells that appear as flat rectangles in radial and cross sections, and are polygonal in tangential view (Fig. 3). Typical hardwood cork cells possess unpitted cellulose walls with a secondary wall of suberin, composed of alternating phenolic and wax lamellae, that renders them practically impervious to moisture and gases (Sitte 1957; Esau 1965). In the oaks studied, typical cork cells comprise most of the phellem. Narrow bands of lignified cells, often only one cell wide, frequently alternate with wider bands of the typical cells (Fig. 6). The lignified cells appear to have become somewhat sclerotic; the walls are thickened and pitted, but the cells retain their original shape. As Chang (1954) observed, walls of phellem cells are usually noticeably thicker in red oaks than in white oaks, often twice as thick (Fig. 6). In this study, this distinction was found to be generally true; but in red oaks some areas of phellem had quite thin walls, and a gradual increase in wall thickness across the periderm was frequently observed.

Phelloderm, to the inside of the phellogen, is inconspicuous and resembles adjacent parenchyma. Only a few layers are present, generally six to eight cells or less, and these often cannot be distinguished

FIG. 7. Great differences in surface texture are evident among these three northern red oak slabs, all from 2 to 6 feet above ground.

from neighboring parenchyma unless their radial alignment is evident (Fig. 4; Fig. 6, right); consequently, this inner portion of the periderm is often overlooked by many observers. The function of this tissue is uncertain.

Deposited Materials.—Rhytidome contains an abundance of deposited materials that provide its dark coloraton. These dark reddish-brown deposits—mainly phenolic substances such as tannins and phlobaphenes—are found primarily in parenchyma and crushed sieve tubes. It is thought that these materials act as antioxidants and inhibitors of fungal attack (Srivastava 1964; Somers and Harrison 1967). Their value in tanning leather has long been recognized, and they are considered a possible source of phenolics for adhesives.

SPECIES COMPARISON

In oaks, as in other trees, bark surface characteristics can be of supplementary value in the identification of species. The exterior surface of white oak bark is usually lighter in color than that of other species. Most oaks have rough bark with longitudinal furrows and ridges; but laurel, water, and white oaks usually have relatively smooth bark. Smooth bark is also found on young growth, on upper stems and branches, and on some individual trees of high growth rate. Of the small-diameter trees examined, blackjack, post, and southern red oaks had thick bark; the laurel, cherrybark, water, and white oak samples were usually thin-barked. Other species were either intermediate in thickness or showed considerable variation. Southern upland oaks of small diameter generally have fibrous, stringy bark. Bark from most red oaks is hard and friable when cut across the grain, but the outer bark of white and post oaks tends to be soft and flaky. This difference in hardness may be due mostly to the amounts of sclereids present, but such a conclusion awaits quantitative comparisons of cell types for the various species.

Bark surface characteristics, however, are not a totally reliable indicator for species identification since they can be greatly modified by environmental influences. Thus, a high degree of variability is found within species (Fig. 7). Gross features such as bark thickness, proportion of inner and outer bark, scaliness, and depth of fissures depend to a great degree on tree vigor and growth rate, age, and height on the tree. Guttenberg's (1951) photographs demonstrate the marked increase in oak bark roughness with decline in tree vigor.

Anatomical differences in oak bark offer some additional help in identifying species. As noted by Chang (1954), cork cells of white oaks generally have thinner walls than those of red oaks. White oaks retain their original phloem structure to a greater degree than red oaks. White oak rays are generally evident in a straight course past periderms (Fig. 8). Chang (1954) reported that an archlike pattern in older phloem was a characteristic distinguishing red oaks from white oaks, but in the present study such patterns were frequently found in the white oaks as well.

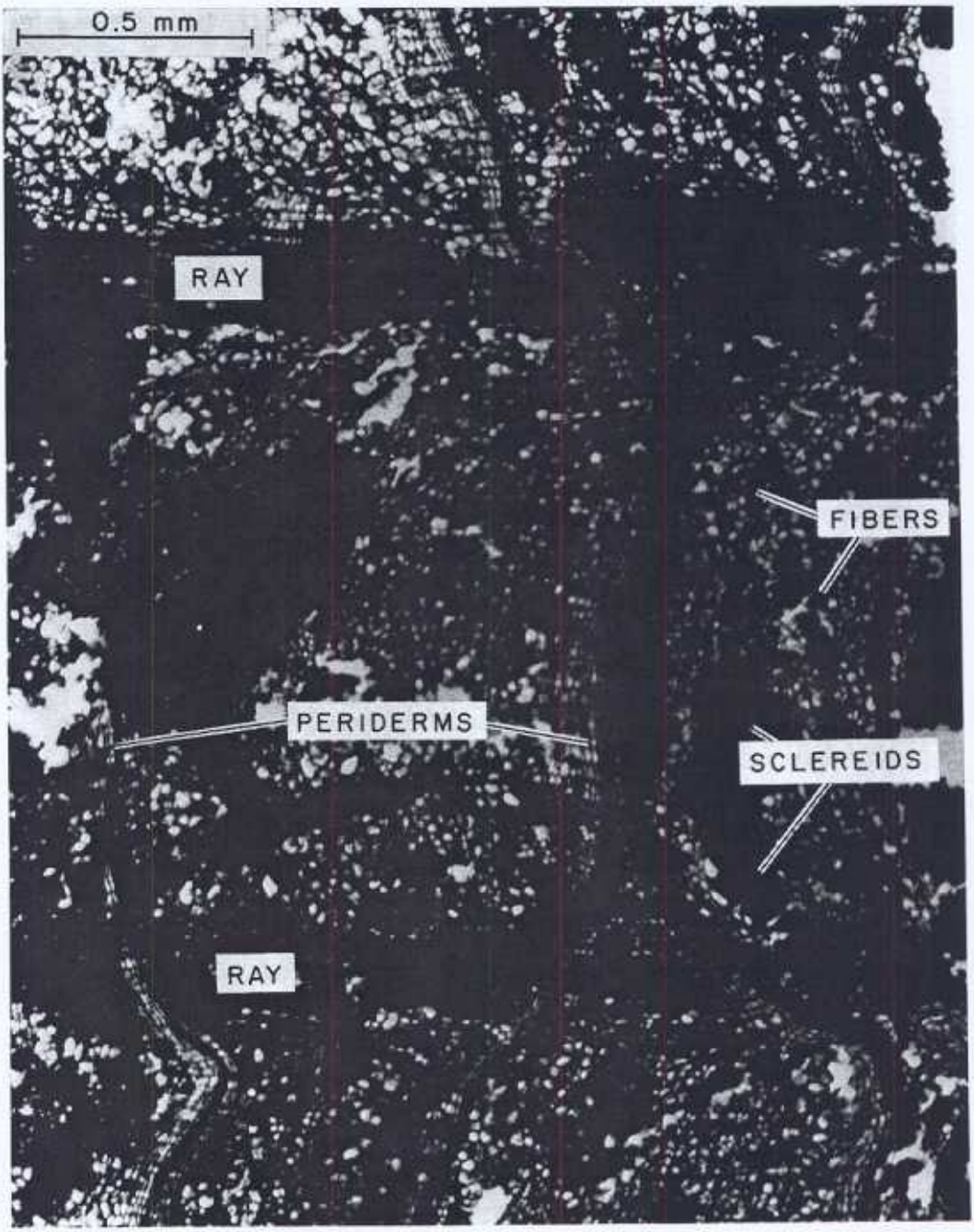

FIG. 8. Rays of the white oaks are readily evident in the rhytidome, aligned straight with their phloem position. (*Q. stellata* Wangenh.)

Other characteristics given by Chang (1954) as general differences between the two groups were not confirmed by the present study. These included his comparison of inner to outer bark thickness, and the description of periderms and sclerenchyma as being in distinct tangential alignment in white oaks (in contrast to a loose irregular arrangement in red oaks). Both types of arrangements were observed in both groups of oaks; bark thickness was far too variable in these samples to serve as a distinguishing characteristic between the two groups.

Inner bark of black oak is bright gold when freshly cut, but the color may not be found in dry samples. No other characteristic was found that would, with certainty, identify an individual tree as a member of a particular species.

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