AN ANATOMICAL STUDY OF THE SECONDARY TISSUES IN ROOTS AND STEMS OF UMBELLULARIA CALIFORNICA NUTT. AND LAURUS NOBILIS L.

BAKI KASAPLIGIL

This paper, dealing with the secondary tissues of roots and stems of *Umbellularia* and *Laurus* is a continuation of the author's comparative studies (1951, 1954) of these laureceous genera seeking evidence regarding their phylogenetic relationships.

Normal secondary growth is essentially the same in the roots and stems of both gymnosperms and woody dicotyledons, but because routine collections of woody plants do not usually include roots, details of root structure are less well known than are those of stems. Roots are considered "conservative" organs, but Beakbane (1941) found the anatomy of apple roots to be affected by the environment. Fegel's work (1941) demonstrated the relatively primitive structural features of roots, and Noelle (1910) applied the anatomical characters of roots to the classification of the Coniferae.

MATERIALS AND METHODS

Native material of *Laurus nobilis* L. was collected at Antalya, Turkey, while native material of *Umbellularia californica* Nutt. was collected in California. Cultivated material of both species was collected in the Botanical Garden of the University of California at Berkeley.

The material was studied partly in freehand sections and partly after maceration. Useful microtechnical methods were found in the publications of Gassner (1931), Ball (1941), and Foster (1949, Appendix).

HISTOLOGY OF SECONDARY XYLEM ELEMENTS

Roots

PERIDERM. There are no essential differences in the periderm of *Umbellularia* and *Laurus*. The outermost cell layer of the pericycle functions as a phellogen and produces 8–10 regular rows of phellem toward the periphery. The primary cortex breaks up and disappears. Phellem cells die as their cell walls gradually acquire suberized thickenings. Meanwhile, the phellogen also forms a phelloderm tissue toward the inside, which is composed of parenchymatous cells containing starch grains and oil globules. Phelloderm cells closely resemble cortical parenchyma cells and they join the phloem parenchyma farther toward the inside. It is almost impossible to make a sharp distinction between phelloderm and phloem. Idioblastic secretory cells are abundant and diffusely distributed in phelloderm, while lenticels appear in the periderm during later stages of secondary growth.

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SECONDARY PHLOEM. The primary phloem is obliterated during the secondary growth of *Umbellularia* roots, but sometimes remains distinguishable as a faint line in transverse section. The secondary phloem is composed of cells which are more or less uniform in cross section. A large portion of this tissue consists of parenchyma cells containing starch grains. Sieve tubes and companion cells form small groups which can be identified by the absence of starch grains. Phloem rays are indistinguishable and no fibers were observed. Parenchyma cells containing tannic substances are abundant; they are distributed at random in the secondary phloem and phelloderm.

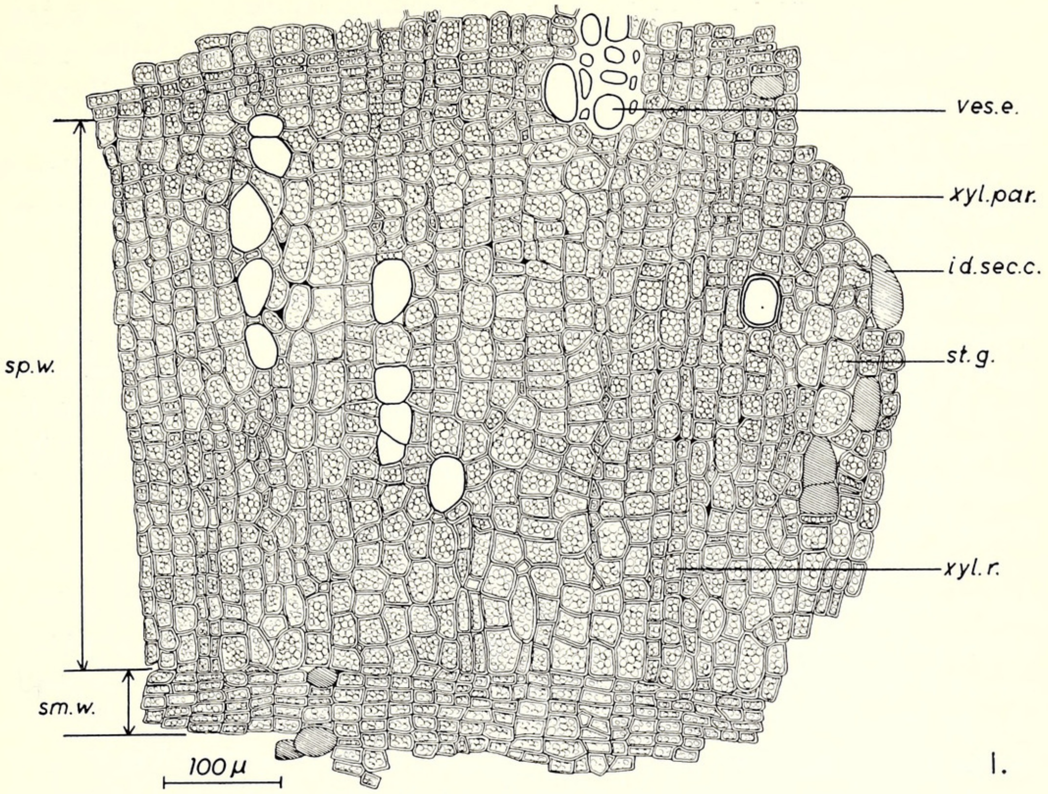
The secondary phloem of *Laurus* exhibits certain differences. It contains fibers, of reduced cross sectional area and angular form, with thick walls and reduced lumina. Phloem rays expand in conical shape and can be distinguished easily. The tannin-containing cells in the secondary phloem and phelloderm are arranged in regular tangential rows.

SECONDARY XYLEM. **a. Transverse sections.** The root wood of both genera is diffuse porous (figs. 1 and 2). Huber (1935) and Gilbert (1940) consider diffuse porosity more primitive than ring porosity. Vessel elements in *Umbellularia* have large diameters in spring wood and small diameters in summer wood. Occasionally 10–12 vessel elements of varying diameters are grouped together in summer wood. Vessel elements with large or small diameters are distributed in spring and summer woods of *Laurus* more or less in the same ratio. As an average there are about 64 vessel elements per square millimeter of *Umbellularia* root compared to about 100 for *Laurus*. No tyloses are produced; apparently the vessels in the roots of both genera are entirely functional. Alten (1908) pointed out the abundance of tylosis formation in root woods of many trees. However, the studies of Klein (1923) Liese (1925) and Fegel (1941) show the absence of tyloses in the root woods of forest trees.

The outer and inner boundaries of the growth layers of summer wood are distinct in both genera. The width of growth layers is variable, but the proportion of spring and summer woods within the growth layers seems to be constant. Summer wood occupies approximately one tenth of the growth layer in *Umbellularia* and about one third of the growth layer in *Laurus*.

Xylem rays are heterocellular, uni-, or multiseriate in both genera. Ray parenchyma cells contain an abundance of starch grains and tannic substances. Idioblastic secretory cells occur commonly within the xylem rays. Xylem rays are less abundant in *Umbellularia* than in *Laurus*. In *Umbellularia,* the cells of ray parenchyma are larger in spring wood than in summer wood; in *Laurus* they are of nearly uniform size.

Xylem parenchyma is apotracheal-diffuse in both genera, i.e., the parenchyma cells are distributed throughout the root wood independent of vessel elements. This is a very different situation from the paratracheal and metatracheal distribution patterns of the xylem parenchyma in stem



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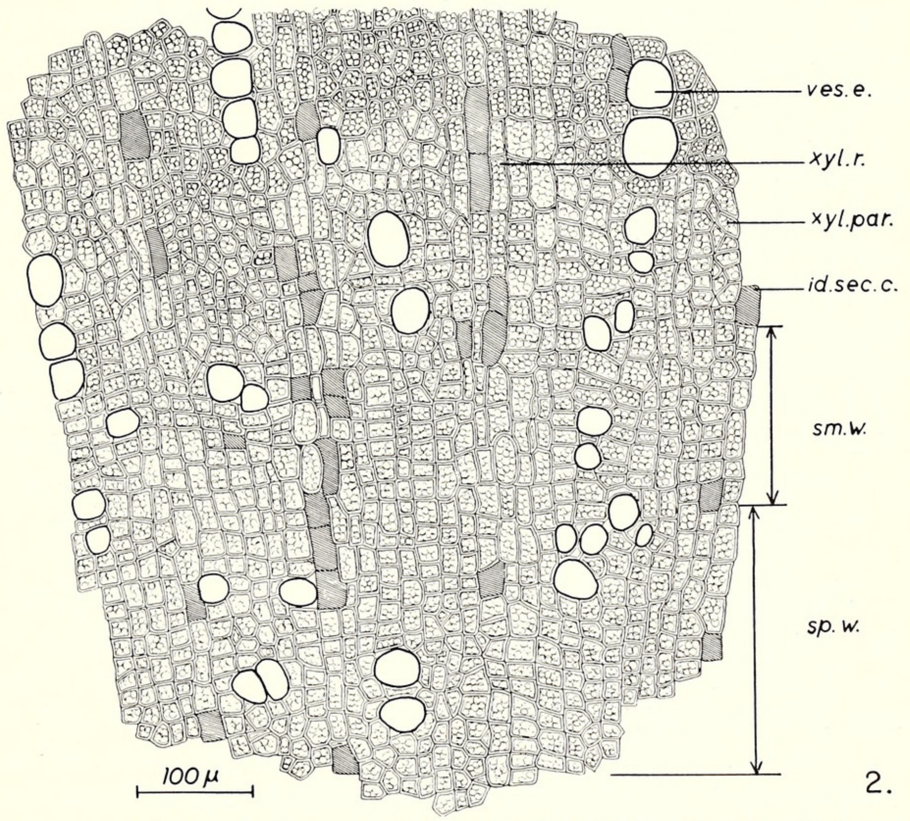

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FIGS. 1–2. Transverse sections of root wood: 1, *Umbellularia californica;* 2, *Laurus nobilis*. Legends: ves. e.=vessel element, sm.w.=summer wood, sp.w.=spring wood, xyl.par.=xylem parenchyma, xyl.r.=xylem ray, id. sec.c.=idioblastic secretory cell, st.g.=starch grains.

woods which will be described later. Apotracheal-diffuse type is considered as an unspecialized feature by Metcalfe and Chalk (1950). The xylem parenchyma cells form radially extending rows mixed with wood fibers.

In *Umbellularia* the pith consists of thin-walled parenchyma cells; in *Laurus* it consists of sclerenchymatous cells. In both cases the cells contain much starch.

b. Radial sections. In both genera, superimposed series of vessel members are very distinct if they fall on the plane of the sections (fig. 4). Xylem rays are composed of rectangular parenchyma cells containing starch grains. Libriform wood fibers are empty and dead, while the wood parenchyma cells are filled with starch grains. Idioblastic secretory cells appear rectangular or isodiametric in form, and they occur frequently in xylem rays as well as outside of the rays.

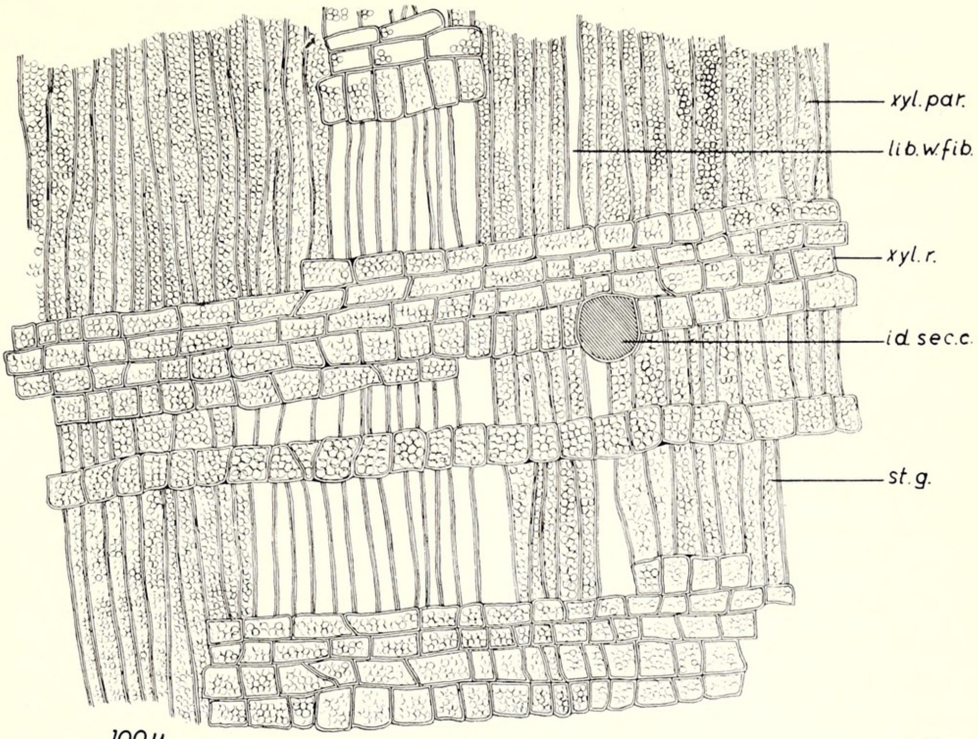
c. Tangential sections. In *Umbellularia* roots the xylem rays are 1–4 cells wide and 5–17 cells high (fig. 5), with a single cell at their pointed upper and lower margins. Xylem parenchyma occupies the spaces between the rays with a few libriform wood fibers. Generally, the xylem parenchyma appears as long, narrow cells with tapering ends, but often the parenchyma cells also form superimposed vertical series. These series overlap one another so that there is no storied condition. Idioblastic secretory cells within the xylem rays are either scattered individually or form small roundish groups of 2–3 cells or even vertical series of 3–5 cells (fig. 5).

The xylem rays of *Laurus* roots are 1–3 cells wide and 1–13 cells high in transectional outlines. Idioblastic secretory cells may be scattered individually or may form small groups within the rays, but they generally occupy upper and lower margins of the rays. The rays taper gradually toward the upper and lower margins, which are generally straight instead of pointed (fig. 6). Usually these margins are in contact with xylem parenchyma. The "vertical xylem parenchyma" forms superimposed series of 3–8 cells, and these series run parallel to xylem rays. Libriform wood fibers occur in spaces between xylem rays and vertical series of wood parenchyma and are more abundant than in *Umbellularia*.

Stems

The secondary xylem of *Umbellularia* and *Laurus* is described and illustrated in various atlases and books for timber identification (Brown and Panshin, 1940, and Record, 1934, for *Umbellularia;* Greguss, 1945, and Huber, 1954, for *Laurus;* Stern, 1954, for these and many other Lauraceae). However, the secondary structure of stems will be described here briefly to provide a basis for the comparison with the root structure of *Umbellularia* and *Laurus*.

UMBELLULARIA CALIFORNICA. A phellogen tissue is formed by the outermost cell layer of cortex parenchyma. The epidermal tissue is broken in



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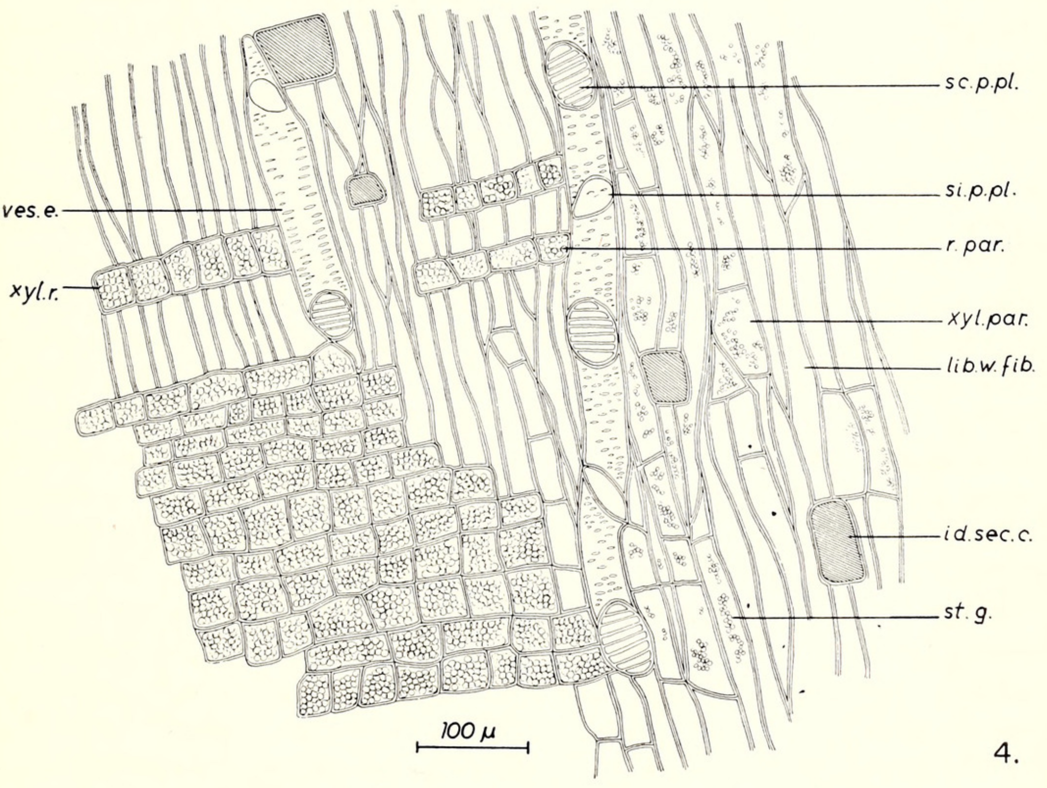

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FIGS. 3–4. Radial sections of root wood: 3, *Umbellularia californica;* 4, *Laurus nobilis.* Legends: sc.p.pl.=scalariform perforation plate, si.p.pl.=simple perforation plate, r.par.=ray parenchyma, xyl. par.=xylem parenchyma, lib.w.fib.=libriform wood fiber, id.sec.c.=idioblastic secretory cell, st.g.=starch grain, ves.e.=vessel element, xyl.r.=xylem ray.

places as the result of secondary thickening of the stem. Phellem and phelloderm layers produced as the result of the activity of this secondary meristematic tissue are shown in fig. 7. The cortex parenchyma below the periderm consists of 8–10 cell layers in which idioblastic secretory cells are distributed without a regular pattern. The innermost cell layers of the cortex—adjacent to the primary phloem—form one to several layers of hippocrepiform sclereids (cf. Bailey and Swamy 1948). The sheath of hippocrepiform sclereids in stems is composed of one or more cell layers which form a regular cylinder interrupted by phloem fibers. The inner tangential walls and the radial walls of these sclereids are thick and lignified heavily, while their outer tangential walls are unthickened. Thus the hippocrepiform sclereids appear U-shaped in transectional view resembling endodermal cells at the tertiary stage of thickening. The thick walls of these sclereids are provided with simple pits. These pits are generally opposite the pits of the adjacent cells, forming simple pit pairs. However, blind pits are also observed along the radial walls. Hippocrepiform sclereids of secondary stems 6–7 years old are living cells with large lumina. The cytoplasm is peripheral, while the central part of the cell is occupied by a vacuole. Some of these sclereids contain granular tannic substances and appear dark.

The derivative cells of the vascular cambium form the secondary phloem externally and in this way the primary phloem is pushed outward. The primary phloem in older portions of the stem is crushed by the internal pressure and in the later stages of development the primary phloem may be entirely obliterated. However, the phloem fibers with thick and resistant cell walls remain in groups along the outer boundary of the primary phloem (fig. 7).

Stem wood is hard and exhibits distinct growth layers. Heart and sap woods are distinguishable in old and thick stem portions. Heart wood is grayish or dark brown while the sapwood is whitish or light brown. Porosity is of the diffuse type as in the root wood. Xylem rays are very fine in transverse section and hardly distinguishable to the naked eye. Typically the rays are heterocellular and the xylem rays together with phloem rays form continuous vascular rays. The rays are not as dense as in the stem wood of *Laurus* and there are about ten rays per millimeter in transverse section.

Wood fibers form regular rows extending radially. The xylem parenchyma exhibits paratracheal-vasicentric arrangement. One to three cell layers of xylem parenchyma encircle the vessel elements as seen in the lower left corner of figure 7. The distribution of xylem parenchyma in the stem wood of *Umbellularia* exhibits a more advanced and specialized condition when compared to the apotracheal-diffuse type of arrangement in the root wood of the same species. The xylem parenchyma cells in the stem have thick lignified walls and contain starch grains. The primary xylem elements are readily identified in small groups adjacent to the pith.

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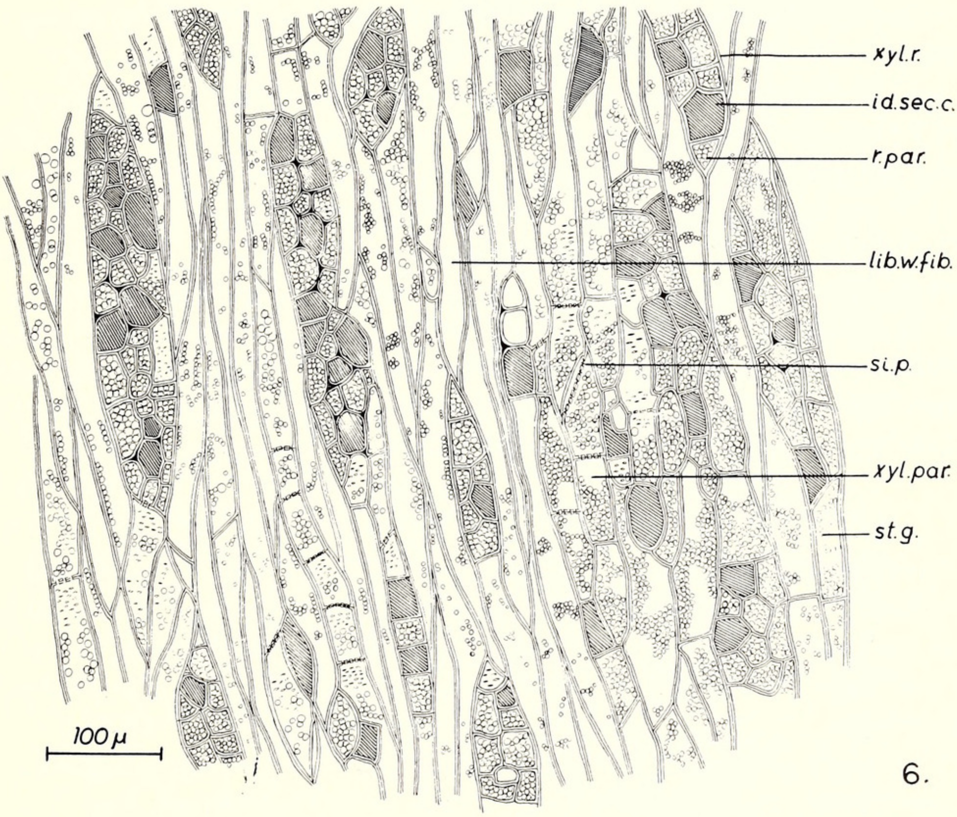


6.

FIGS. 5–6. Tangential sections of the root wood: 5, *Umbellularia californica;* 6, *Laurus nobilis.* Legends: xyl.r.=xylem ray, id.sec.c.=idioblastic secretory cell, r.par.= ray parenchyma, lib.w.fib.=libriform wood fiber, si.p.=simple pits, xyl.par.=xylem parenchyma, co.st.g.=compound starch grain, si.st.g.=simple starch grains.

They possess thicker cell walls and small diameters and lumina as compared to the secondary xylem elements. The pith is composed of large isodiametric parenchyma cells. The outer 4–5 cell layers of the pith cylinder in the old portions of stems remain alive and contain starch grains while the inner cells of the pith die. The simple pits of the pith parenchyma are distinct, but the intercellular spaces are obscure.

LAURUS NOBILIS. Epidermis, periderm and cortex tissues of the *Laurus* stem are essentially similar to those in the *Umbellularia* stem.

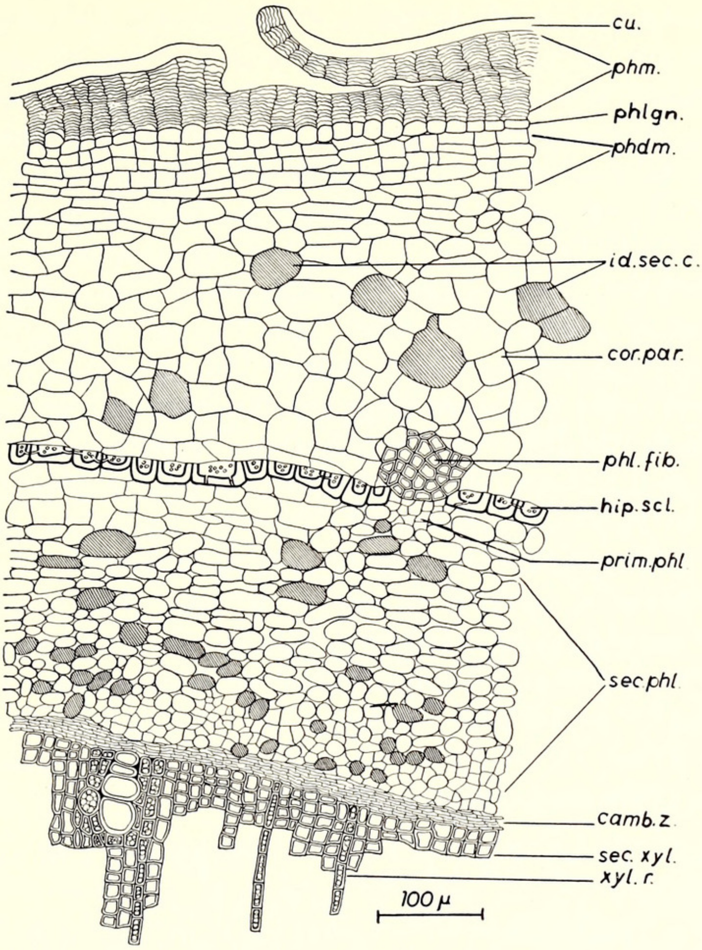
The primary and secondary phloem groups are intersected by phloem rays. Figure 8 represents a transverse section of a young stem in which the primary phloem tissues are not obliterated. It was not possible to draw a clear demarcation line between primary and secondary phloem. However, the fiber groups shown in figure 8 help determine the approximate position of the primary phloem groups. The phloem fibers appear as polyhedral, thick walled cells grouped compactly in transectional view. The position of the secondary phloem is determined approximately in figure 8 according to its position relative to the vascular cambium. The vascular cambium appears as if it contains 30 cell layers since the stem material was collected during cambial activity in July. Theoretically only one cell layer forms the cambial initials while the rest of the cells represent undifferentiated derivatives of the cambium in both inner and outer directions. However, the vascular tissues produced by the earlier activity of the cambium are already differentiated into secondary structure.

The secondary xylem is diffuse porous. The vessel elements are scattered individually or in twos in the spring wood, while three or four of them are arranged in small radial rows in the summer wood. The growth layers are distinct due to the fact that the wood fibers along the border lines of the growth layers are flattened and have very small diameters. Xylem rays are heterocellular, uni-, or biseriate. There are 12 xylem rays per millimeter in transverse section. The xylem parenchyma of the stem exhibits metatracheal arrangement which represents a more specialized condition compared to the apotracheal diffuse arrangement of the xylem parenchyma of the secondary roots of the same species.

MORPHOLOGY OF THE SECONDARY XYLEM ELEMENTS

Anatomical features exhibited by various sections of root and stem woods of *Umbellularia* and *Laurus* have been described above. In addition, macerated material of root and stem woods was studied in the hope of finding other characters that might be considered of phylogenetic importance.

The phylogenetic value of wood anatomy in systematic studies was shown clearly by Record (1934), Chalk (1937), Heimsch and Wetmore (1939), Tippo (1946) and others. Metcalf and Chalk (1950) emphasize the fact that wood structures exhibit more conservative characters than do external features of plants.



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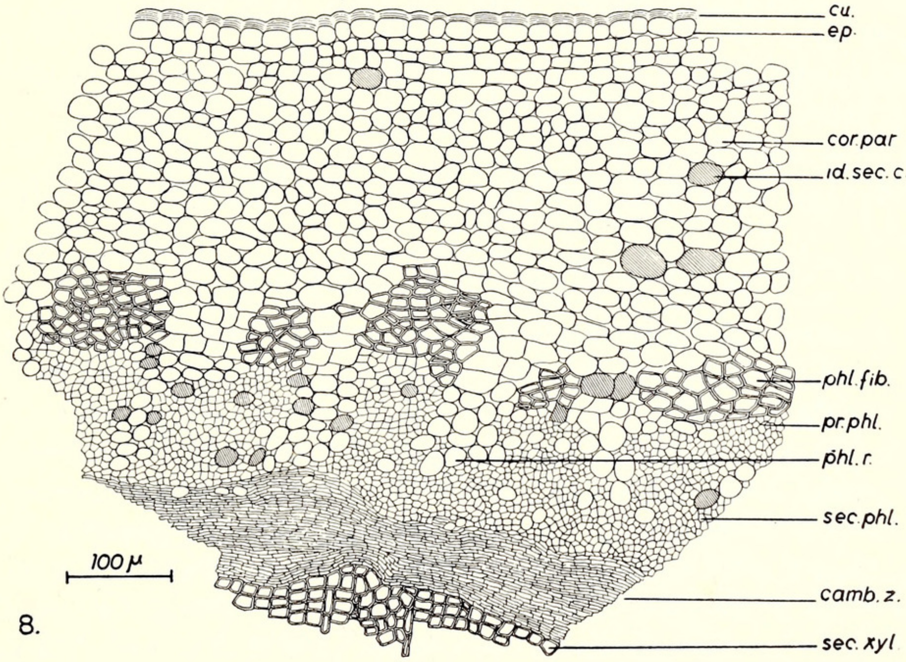


8.

FIGS. 7–8. Portions of transverse stem sections showing secondary growth: 7, *Umbellularia californica;* 8, *Laurus nobilis.* Legends: cu.=cuticle, phm.=phellem, phlgn.=phellogen, phdm.=phelloderm, id.sec.c.=idioblastic secretory cell, cor.par.= cortical parenchyma, phl. fib.=phoem fibers, hip.scl.=hippocrepiform sclereids, prim.phl.=primary phloem, sec.phl.=secondary phloem, camb.z.=cambial zone, sec.xyl.=secondary xylem, xyl.r.=xylem ray, ep.=epidermis.

The dimensions of wood elements are significant for both diagnostic and phylogenetic interpretations. In general, long and narrow wood elements are considered more primitive than short and wide ones. However, the dimensions of wood elements exhibit considerable variation in various organs of the same plant or even in different regions of the same organ, and Sanio (1872) demonstrated the length increase of the wood elements from central toward the peripheral regions of *Pinus sylvestris* roots. Gerry (1915) showed that the root tracheids are longer than stem tracheids in *P. palustris* and *P. strobus*. Anderson (1951) found that the length of the tracheids in conifers tends to increase with the increase of distance from the pith and that the tracheids of spring wood are shorter than those of summer wood within the same "annual ring." Dimensional variations of the xylem elements in the root and stem woods of *Umbellularia* are obvious in tables given below. An interesting subject for further investigation would be the relationship of these variations to different stages of growth.

The morphological features of wood elements may also be used to interpret the degree of specialization. The conclusions regarding the primitive and advanced characters of the secondary xylem elements reached by wood anatomists (Bailey and Tupper, 1918; Bailey and Howard, 1941; Fegel, 1941; Frost, 1930a, b, 1931; Gilbert, 1940; Metcalfe and Chalk, 1950; Tippo, 1946) are summarized below.

Primitive Characters	Advanced Characters
1. Diffuse porous.	1. Ring porous.
2. Scattered vessel elements.	2. Grouped vessel elements.
3. Small perforation plates with many bars.	3. Wide perforation plates with a few bars.
4. Scalariform perforation plates.	4. Simple perforation plates.
5. Polyhedral vessel elements.	5. Round vessel elements.
6. Inclined end-walls.	6. Transverse end-walls.
7. Fiber tracheids with bordered pits.	7. Libriform wood fibers with small simple pits.
8. Scalariform and bordered pits.	8. Simple pits.

The anatomical features set forth above have been used as a basis to judge and compare the primitive and advanced characteristics of the xylem elements in the secondary structures of roots and stems in *Umbellularia* and *Laurus* in the present paper. According to the suggestion of Chalk and Chattaway (1934), the vessel elements were measured from tip to tip to obtain the length dimension. To calculate average dimensions, at least fifty measurements have been made for each element. The terminology proposed by the Committee on Nomenclature of the International Association of Wood Anatomists (1957) has been followed in describing the wood elements.

Secondary Xylem Elements of Umbellularia Roots. Wood parenchyma, fiber tracheids, and septate fiber tracheids are abundant.

The average length of vessel elements is 250 microns and their average width is 40 microns. Therefore the vessel elements in question fall into the group "small and short" in Metcalfe and Chalk's (1950) classification. In general they are shorter and narrower than the vessel elements found in the stem wood of the same species.

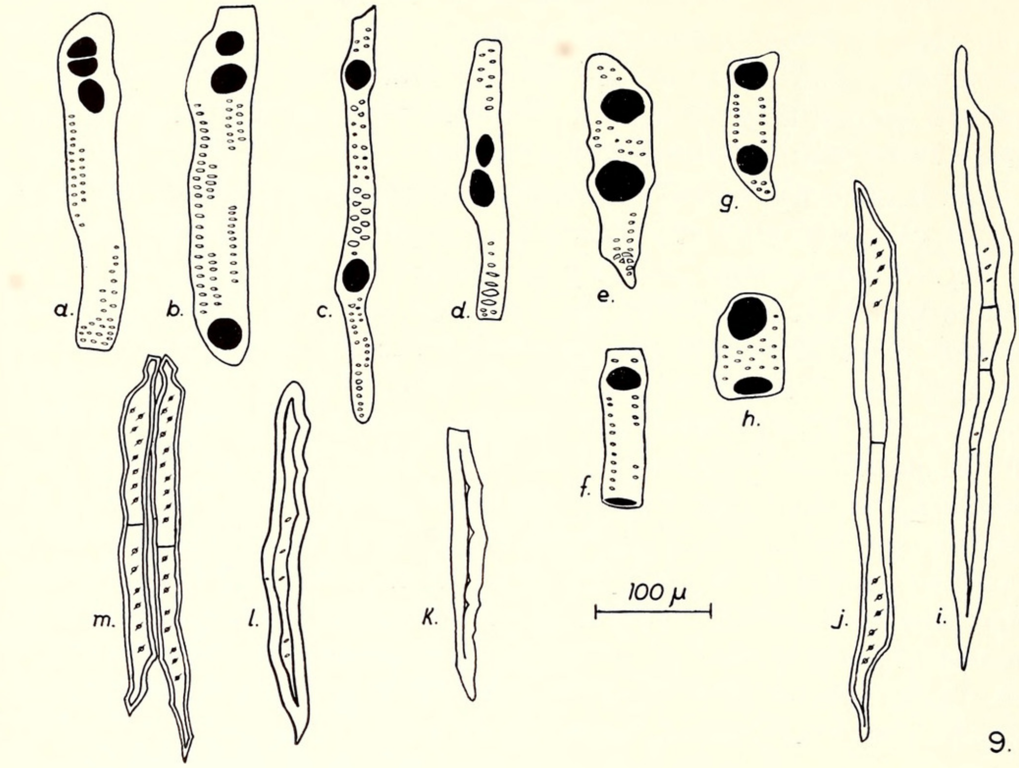
The ligulate tips of the vessel elements are generally long and broad (fig. 9, c). Vessel elements approaching a cylindrical shape are rare (fig. 9, f-h). In transectional view they are polyhedral in form (fig. 1).

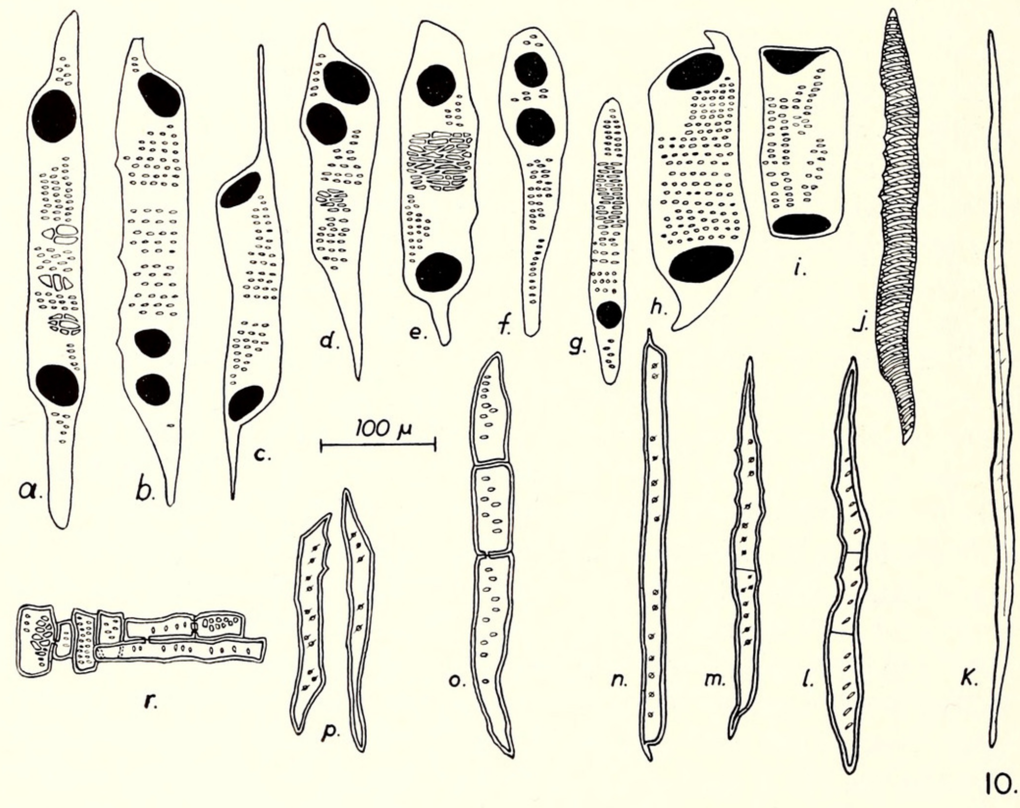
The perforation plates of the vessel elements are generally simple, oblique, and distant from the ligulate tips. Scalariform perforation plates are very rare. A scalariform perforation plate with a single bar is shown in fig. 9, a. Although the vessel elements are usually provided with two simple perforation plates (fig. 9, c, e-h), vessel elements with three simple perforation plates have also been observed (fig. 9, b). In the latter instance, there are two simple perforation plates in one end of the vessel element and one perforation plate in the other end of the element. Some vessel elements have two perforation plates side by side in the middle of a vessel element without perforations at the cell ends (fig. 9, d). These latter two cases are characterized by profuse pitting at the ligulate tips of the vessel elements (fig. 9, a, d).

The simple pits on the lateral walls of the vessel elements are small and generally at equal dimensions. Opposite and alternate pitting may be found on the walls of the same vessel element. The ligulate tips of the vessel elements are usually pitted, but no pitting is found in cases where the tips are short.

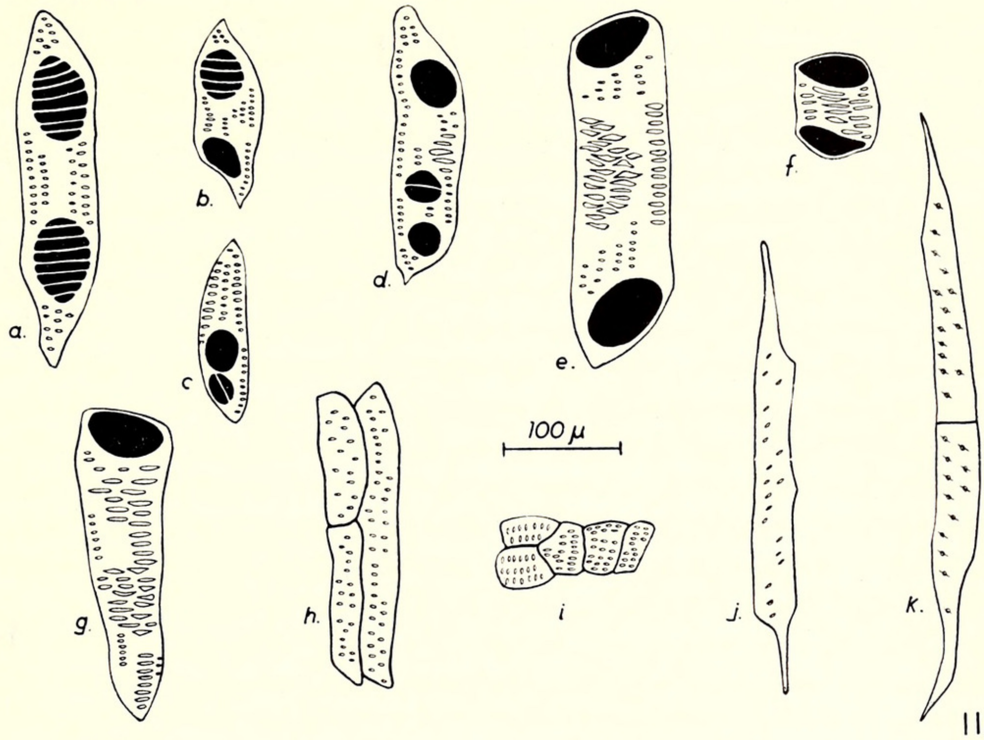
The fiber tracheids and the septate fiber tracheids possess pits. The septations of these elements are primary walls and do not exhibit secondary thickenings (fig. 9, m). An interesting type of septate fiber tracheid is shown in figure 9, j, in which the lateral walls are about three times thicker than the terminal portions of the lateral walls. These tracheids recall "gelatinous fibers" (cf. Esau, 1953, p. 205), but their thick walls did not shrink during the process of dehydration.

The wood fibers have very thick secondary walls with vestigial simple pits. Some of the wood fibers have wide lumina (fig. 9, l), but some of them have an extremely reduced lumen (fig. 9, k) appearing like a line along the longitudinal axis of the cell. Septate wood fibers (fig. 9, i) are very similar to septate tracheids, but are distinguished from the latter by the presence of vestigial simple pits. Septate wood fibers may possess one or two partition walls of a primary nature. According to Metcalf and Chalk (1950), septate tracheids and septate fibers commonly occur in tropical woods and serve as a useful feature for determining phylogenetic relationships. As a matter of fact, most Lauraceae are distributed in tropical regions and contain either one of the septate elements or both types in their woods. The wood fibers of *Umbellularia* roots are shorter but wider than the fibers of the stem wood.





FIGS. 9–10. Tracheary elements of *Umbellularia californica*: 9, root wood; 10, stem wood. (Explanation in text).



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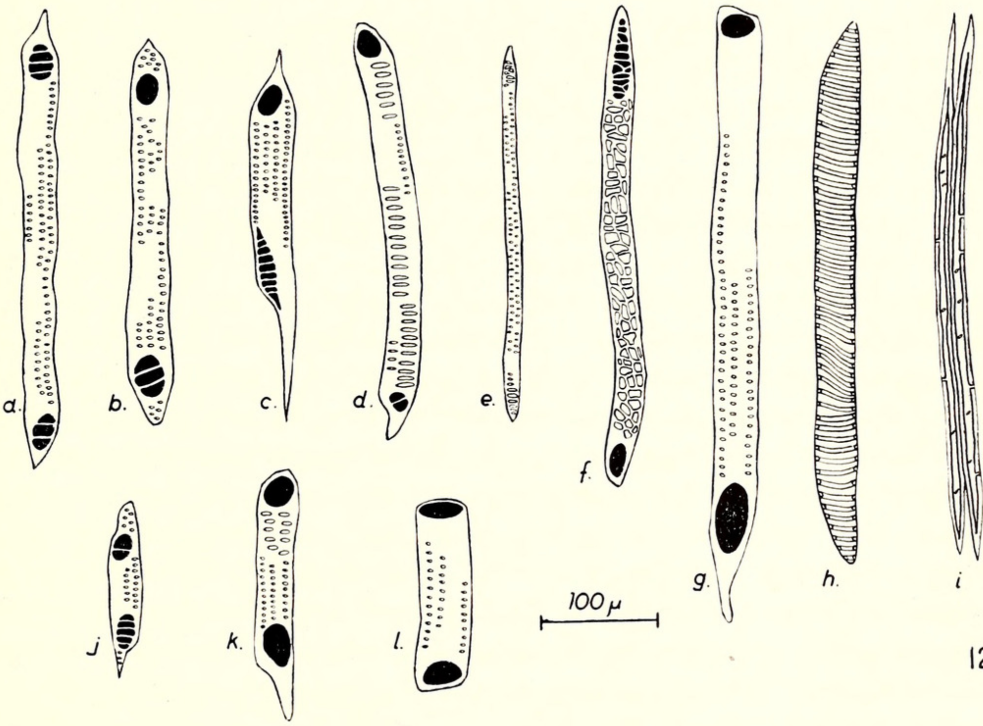

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FIGS. 11–12. Tracheary elements of *Laurus nobilis*: 11, root wood; 12, stem wood. (Explanation in text).

The parenchyma cells of the root wood possess lignified cell walls, but their cell walls are thinner than the cell walls of other xylem elements. Xylem parenchyma cells are elongated cells, while the ray parenchyma cells are smaller and tabular in shape.

SECONDARY XYLEM ELEMENTS OF UMBELLULARIA STEMS. Vessel elements of stem wood average 336 microns in length and 53 microns in width. This dimensional variation is not as pronounced as the size variation of the vessel elements in the root wood. The transverse outlines of the vessel elements do not exhibit sharp corners. Generally, they approach drum shape in spite of much variation in their form (fig. 10, i). They are provided with simple perforation plates, and scalariform perforations have never been observed. The ligulate tips of the vessel elements are generally small, those with transverse perforation plates having no ligulate tip (fig. 10, i). These characters indicate that the vessel elements of the stem wood exhibit a higher degree of specialization than the vessel elements in the root wood of *Umbellularia.*

The ligulate tips of the vessel elements may be long and wide at both ends of the cells, tapering gradually (fig. 10, a, b), or they may extend in slender needle-like form at both ends (fig. 10, c). These two are primitive types resembling tracheids. Some vessel elements have a single ligulate tip in one end of the cell that is mucronate, i.e., the end wall of the vessel element abruptly becomes a short tail (fig. 10, e). Some ligulate tips are curved inwardly. This is generally observed in short and wide vessel elements (fig. 10, h).

Although the vessel elements usually have two simple perforation plates, some of them are provided with three perforation plates (fig. 10, b) and still others have only one (fig. 10, g). Two perforation plates may be located side by side in one end of a vessel element and the other end of the cell in such vessel elements tapers gradually (fig. 10, d, f).

Intervascular pits on the lateral walls of the vessel elements are small and simple. Reticulate and broad simple pits are restricted to the surfaces of the lateral walls in contact with the xylem parenchyma cells (figs. 10, a, d, e, g). Scalariform pitting has not been observed.

Fiber tracheids have approximately the same diameter as those in root wood. The fiber tracheids are either uniform in width, and terminating in small ligulate tips at both ends (fig. 10, n), or they may be constricted, terminating in sloping end walls (fig. 10, p).

Septate fiber tracheids (fig. 10, m) are fusiform cells with gradually tapering ends. Their lateral walls are thickened equally in all directions. Fiber tracheids with unequal secondary wall thickening have not been found in the stem wood.

Libriform wood fibers have very thick secondary walls and highly reduced lumina which can be distinguished sometimes as a fine line extending lengthwise (fig. 10, k). Vestigial simple pits of the wood fibers are also extremely reduced, and they appear as small oblique lines along both sides of the lumen trace. Wood fibers with wider lumina are not rare, and their diameters are smaller than the wood fibers of the root wood.

Septate wood fibers are very similar to septate fiber tracheids in regard to their shapes and sizes, but they can be distinguished from the latter by the presence of simple pitting (fig. 10, l). They possess one or two partition walls; their lateral walls with secondary thickenings are thinner than the lateral walls of the septate fibers found in the root wood of *Umbellularia*.

Xylem parenchyma cells have thick secondary walls with simple pitting, forming superimposed vertical series (fig. 10, o). They resemble closely septate wood fibers even in macerated state, but are distinguished from the latter by the presence of secondary thickenings in their transverse walls (cf. fig. 10, a, l).

Ray parenchyma cells are rectangular cells with straight or slightly pointed end walls. Generally they possess simple pitting, but they also exhibit reticulate pitting on the areas in contact with vessel elements (fig. 10, r).

TABLE 1. COMPARISON OF THE DIMENSIONS OF SECONDARY XYLEM ELEMENTS IN THE ROOTS AND STEMS OF UMBELLULARIA CALIFORNICA AND LAURUS NOBILIS.

WOOD ELEMENTS	AVERAGE LENGTH (microns)				AVERAGE WIDTH (microns)			
	ROOT WOOD		STEM WOOD		ROOT WOOD		STEM WOOD	
	*U.c.**	*L.n.**	*U.c.*	*L.n.*	*U.c.*	*L.n.*	*U.c.*	*L.n.*
Vessel elements	250	263	336	353	40	84	53	29
Fiber tracheids	412	451	417	348	27	34	24	25
Septate fiber tracheids	512	555	504	459	26	30	27	23
Libriform wood fibers	443	521	511	456	19	18	13	12
Septate wood fibers	542	......	487	......	19	....	16	....
Xylem parenchyma	167	160	170	93	31	31	23	19
Ray parenchyma	63	60	74	44	36	29	21	28

* *U.C.* = *Umbellularia californica* Nutt.
* *L.n.* = *Laurus nobilis* L.

SECONDARY XYLEM ELEMENTS OF LAURUS ROOTS. The average length of the vessel elements in the root wood is 263 microns and the average width is 84 microns (table 1). Obviously they are shorter and wider compared to the vessel elements of the stem wood. They fall into the group of "small and short vessel elements" in the classification of Metcalfe and Chalk (1950) since their average width is smaller than 100 microns and their average length shorter than 350 microns. The ligulate tips of vessel elements are short and pointed (fig. 11, a, b, d). The transectional outline of the vessel elements is polyhedral.

The perforation plates of the vessel elements are either scalariform or simple and exhibit three types of combinations in individual vessel elements: a) both perforation plates may be scalariform (fig. 11, a); b) one of the perforation plates may be scalariform and the other one simple (fig. 11, b); c) both perforation plates may be simple (fig. 11, e, f). The number of bars in the perforation plates is generally 7–8, but rarely there may be only a single bar. Although in general there is one perforation plate at each end of the vessel elements, there are exceptions to this rule. Some vessel elements may have three perforation plates. For example, figure 11, d, illustrates a vessel element with two simple and one scalariform perforation plates. Still some vessel elements may have but one simple perforation plate (fig. 11, g). A solitary scalariform perforation plate has never been observed. The vessel elements with a single perforation plate exhibit abundant pitting on their lateral walls, and the imperforate end of the vessel element tapers gradually so that such vessel elements acquire a funnel shape. Both of the perforation plates may be located side by side in one end of some vessel elements, (fig. 11, c); the imperforate end of such a vessel element tapers gradually and possesses many simple pits. In general the simple perforation plates are either straight or slightly sloping (fig. 11, e-g). These three illustrations also show that the vessel elements terminating with simple perforation plates have either very short ligulate tips or none. The cylindrical vessel elements with simple perforation plates shown in figures 11, e and f, undoubtedly represent the most advanced types, but they occur together with the primitive types possessing scalariform perforation plates.

The vessel elements exhibit three types of pitting: a) scalariform pitting (fig. 11, d-g); b) reticulate pitting (fig. 11, e, g); c) simple pitting (fig. 11, a-c). According to Bailey (1954) scalariform pits represent a primitive type, but interestingly enough the scalariform pits are associated quite often with simple perforation plates in the same vessel elements, forming vertically arranged regular rows on the lateral cell walls. The scalariform pitting does not occur in the vessel elements of *Umbellularia,* hence they are more specialized than the vessel elements of *Laurus.* Reticulate simple pits are restricted to the wall areas of the vessel elements in contact with the ray parenchyma cells in the root wood of *Laurus.* Simple pits, however, are located on the lateral walls as well as in the ligulate tips of the vessel elements. Although some vessel elements possess exclusively simple pits, still others exhibit all three types of pitting at the same time (fig. 11, e).

The fiber tracheids are abundant in the root wood, and they are longer and wider than those in the stem wood (cf. table 1). The size variation of the fiber tracheids in the root wood is not as pronounced as the wide range of variation shown by the fiber tracheids of the stem wood.

The septate fiber tracheids are also longer and wider than those of the stem wood. They may be provided with one or several septa. Lumina are wide and they taper gradually toward the ends (fig. 11, k).

Libriform wood fibers possess secondary walls with varying degree of thickening. Consequently they exhibit wide as well as narrow lumina. Those with wide lumina resemble fiber tracheids, but they are distinguished by the presence of vestigial simple pits (fig. 11, j). The proportion of libriform wood fibers in the secondary xylem of *Laurus* roots is relatively smaller than the proportion of wood fibers in the secondary xylem of stems. Septate wood fibers have not been observed, and the septate elements resembling fibers are actually tracheids.

Xylem parenchyma cells exhibit a greater size variation than those in the stem wood. They are provided with oval simple pits. Cell shape is elongated and terminates in straight or abruptly tapering end walls (fig. 11, h).

Ray parenchyma cells are isodiametric and show slight variation in size (fig. 11, i). They are provided with simple as well as with reticulate pitting.

SECONDARY XYLEM ELEMENTS OF LAURUS STEMS. The vessel elements exhibit considerable size variation (cf. fig. 12, g, j). As an average they are longer and narrower than the vessel elements of the roots (cf. table 1). The ligulate tips of the vessel elements are more conspicuous, more slender and longer than those of the root wood (fig. 12, c, d, g, j, k). This situation is similar to that described for *Umbellularia*. The vessel elements which approach the cylindrical form are rare (fig. 12, l). The transectional view of the vessel elements is angular in form.

Tertiary thickenings in the form of spiral bands on the secondary walls have not been observed although they were reported by Greguss (1945). The vessel elements are generally plugged by tyloses which do not occur in the vessel elements of the root wood of *Laurus*. The formation of tyloses in the vessel elements of *Laurus* stem distinguishes these elements from the vessel elements of the root and stem of *Umbellularia*. The presence of tyloses in other members of Lauraceae is reported in the literature. For example, Carpenter and Leney (1952) demonstrated the formation of tyloses in vessel elements of *Sassafras albidum* (Nutt.) Nees.

The vessel elements are provided with scalariform or simple perforation plates like those in the secondary xylem of the roots. However, a notable difference is the occurrence of reticulate perforation plates (fig. 12, e, f). The number of bars in scalariform perforation plates is reduced, and perforations with one or two bars are fairly common. The vessel elements always possess two perforations which are terminal in position. The occurrence of one or three perforations has not been observed although this situation is common in the vessel elements of the secondary xylem of the root. Either both of the perforation plates may be scalariform (fig. 12, a, j) or one of them scalariform and the other one simple (fig. 12, b-d) or both of them may be simple (fig. 12, g, k, l). The vessel elements with reticulate perforation plates also exhibit similar variation (fig. 12, e, f). In general, the perforation plates are inclined; occasionally they become horizontal in cylindrical vessel elements.

Scalariform, reticulate, and oval simple pits occur in varying combinations. Scalariform and simple pits may occur together on the longitudinal walls of vessel elements (fig. 12, d, k). Reticulate pits are commonly associated with reticulate perforation plates (fig. 12, f). Simple pits are arranged oppositely as well as alternately in vertical rows.

The fiber tracheids and septate fiber tracheids are rare in the secondary xylem but common in the primary xylem. The latter may be provided with one or two septa. The fiber tracheids in the stem are smaller than those in the roots.

Libriform wood fibers are the dominant wood elements of the stem structure. They are characterized by their gradually tapering forms, thick secondary walls, narrow lumina, and very small diameters (fig. 12, i).

Septate libriform wood fibers do not occur in stem wood.

Xylem and ray parenchyma cells of the stem wood are similar to those in the root wood. However, there are fewer parenchyma cells in the stem wood than in the root wood.

Conclusion and Summary

1. The secondary root and stem structures of *Umbellularia californica* and *Laurus nobilis* are compared anatomically. The pith of *Umbellularia* roots is composed of parenchyma cells, while the pith of *Laurus* roots consists of sclerenchyma cells. Idioblastic secretory cells and cells containing tannic substances are abundant throughout the secondary root and stem tissues of both genera.

2. Diffuse porosity is a common feature of the secondary xylem in the roots and stems of both species.

3. The wood parenchyma of *Umbellularia* roots exhibits an "apotracheal-diffuse" arrangement, while the wood parenchyma of *Umbellularia* stems exhibits a more advanced "paratracheal-vasicentric" arrangement. Wood parenchyma of *Laurus* roots is "apotracheal-diffuse," while the stem wood is "metatracheal," a more specialized condition.

4. The vessel elements in the secondary xylem of *Umbellularia* roots are provided with elongated ligulate tips, inclined perforation plates, and in transectional view, they are angular in form. These are considered primitive as compared to the vessel elements in the stem wood of the same species, the latter having short ligulate tips, transverse simple perforations, and a circular form in transectional view.

5. The arrangement of wood parenchyma and the comparative morphology of the tracheary elements reveal the fact that primitive characters are retained in roots, thus providing a useful anatomical tool for phylogenetic studies.

6. The vessel elements of the root and stem woods of *Umbellularia* are devoid of tyloses. Likewise, the tracheary elements in the root wood of *Laurus* lack tyloses, but the vessel elements of the stem woods of *Laurus* are often plugged by the development of tyloses.

7. The vessel elements in the root and stem woods of *Laurus* possess scalariform, reticulate, and simple perforation plates, and their longitudinal walls are provided with scalariform and simple pitting. In these

respects they resemble the tracheids. The vessel elements of *Umbellularia* are more specialized than those of *Laurus*.

8. Fiber tracheids, septate fiber tracheids, and libriform wood fibers occur throughout the secondary tissues of both species in varying sizes and proportions. On the other hand the septate libriform wood fibers and "gelatinous tracheids" are restricted to the secondary xylem of *Umbellularia*, but are entirely absent in the secondary xylem of *Laurus*.

9. These differences suggest that the phylogenetic affinity between these two genera is somewhat distant within the family, although both genera perfectly fit the natural group of Lauraceae in many respects.

Department of Biology,
Mills College, Oakland, California

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RUFUS DAVIS ALDERSON
(1858–1932)

REID MORAN

The name of R. D. Alderson has been known to botanists both from his large collections in San Diego County, California, and from the writings of E. L. Greene, who based several species on these collections and named for Alderson a phacelia, a helianthemum, and a rose. Yet to present-day botanists, Alderson is no more than a name.

Rufus Davis Alderson was born in Alderson, [now West] Virginia, November 2, 1858, the younger son of Rufus Davis Alderson and Hester Ann Ammen Alderson. After teaching for three years in West Virginia, he attended the National Normal School, in Lebanon, Ohio, receiving a bachelor of science degree in August 1882. His subjects included botany, zoology, natural philosophy, physiology, herbarium, and astronomy. After two more years of teaching, he was from 1884 to 1887 the proprietor and editor of the Alderson *Statesman*. The word "PRINTERY" on his door struck the fancy of a fellow editor, who, about 1885, wrote in the Pomeroy, Ohio, *Democrat:*