

ADAPTIVE WOOD ANATOMY OF CHAPARRAL SHRUBS

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ABSTRACT. The nature of conductive safety in woods of Californian chaparral shrubs is examined in terms of anatomical structure. Presence of true tracheids accompanied by simplification of the perforation plate is held to characterize phylads with primitive (tracheid-bearing) wood that have entered the seasonally dry chaparral habitats. Of those more specialized woods that possess fiber-tracheids or libriform fibers, a surprisingly large percentage have acquired vasicentric tracheids. Vasicentric tracheids potentially form sheaths around vessels, but have greater conductive safety (resistance to embolisms) than vessels; they maintain the three-dimensional pattern of conduction in the wood and therefore permit evergreen leaves to be supplied with water even, theoretically, should all vessels embolize. Woods without true tracheids or vasicentric tracheids have, in some cases, developed vascular tracheids (tracheids formed as a band in last-formed latewood); vascular tracheids theoretically safeguard the cambium but may be unable to supply foliage, and characterize drought-deciduous species. Various other wood features are considered adaptations of an additive nature that individually and in concert increase the conductive safety of a wood. These features include presence of growth rings (various degrees of ring porosity), narrowness of vessels, high number of vessels per unit transection, shortness of vessel elements, grouping of vessel elements (multiples, clusters) as seen in transection, and various forms of helical sculpture within vessels. Data pertinent to chaparral, derived from earlier papers, are repeated in tables and text.

INTRODUCTION

Until recently, wood anatomy of chaparral shrubs and shrubs of similar ecological associations remained little studied. With a few exceptions, the study of wood anatomy prior to about 1960 was the study of wood anatomy of tree species. Wood

collections were mostly related to forestry institutions, and many wood anatomists therefore tended to work at those institutions. Studies on wood structure therefore tended to emphasize tree species, and most trees large enough to be of economic interest grow in wet temperate or wet tropical areas. This bias by wood anatomists tended to delay our understanding of woods of other ecological associations, such as chaparral. Woods of wet temperate or tropical forest show few structural adaptations for drought resistance; consequently such adaptations in woods of drier areas remained undiscovered until recently.

In the late 1970's, a noted wood physiologist wrote to me that wood structure could be explained entirely as a rheological construct, that is, as a series of tubes designed for maximal conduction efficiency. The Hagen-Poiseuille equation was thought to explain wood conduction. The Hagen-Poiseuille equation is basically a formula relating radius of a tube—vessels in the case of wood—to conductive rates. Wood is not, however, an ideal series of tubes. Vessels end blindly and are interconnected in networks. More importantly, they have such features as redundancy—formation of excess numbers of conducting cells to permit conduction despite deactivation of a part of the tissue. Such features of wood can be considered forms of "safety," the ability for water columns to survive dry periods or other ecological extremes. The Hagen-Poiseuille equation, however, does not take safety into account, so figures obtained with that equation tend to give us the impression that some woods are superior at conducting volumes of water rapidly, other woods are inferior; in fact, the woods that look inferior at conduction are higher in conductive safety (resistance to formation and spread of air embolisms in the water columns). With study of woods

from dry areas, we can now understand that structure of wood is definitely related to ecology. Woods from dry areas tend to show modes of construction higher in safety than in conductive efficiency, but in fact, each species can be regarded as an intricate series of adaptations for both efficiency and safety. Wood anatomy of chaparral shrubs proves unexpectedly interesting because of the high degree to which features adaptive for potential safety are represented.

So interesting and persuasive are these features of wood anatomy that one could easily overemphasize them. The purpose of this paper is to introduce these features and show the extent to which they are represented in California chaparral. Such features as C_4 photosynthesis, midday stomatal closure, drought-deciduousness of foliage, and branch dieback must also be appreciated. Because work on adaptive nature of chaparral wood has been delayed, however, some may have tended to think that wood anatomy plays a minimal role in survivorship of these plants through the dry season. *A priori* reasoning alone would suggest that evolution does not omit any pertinent structure in adaptation, and the data presented below demonstrate that wood anatomy of chaparral shrubs reveals for each species a rich collection of features apparently adaptive for the promotion of safety.

To be sure, the basis of this study is comparative rather than experimental. There are pertinent experimental data that will be cited, and certainly I would welcome addition of any kinds of experimental studies. The comparative nature of this effort does not, I think, invalidate it. Indeed, I cannot imagine any other way in which hypotheses suitable for experimental testing could be engendered. More importantly, if particular wood features can arise polyphyletically, as they certainly do, the various phylads in an ecological association such as chaparral are like subdivisions of an experimental material, and have the validity of natural experiments.

THE NATURE OF SAFETY

The term "safety" has been cited above. With respect to wood anatomy, maintenance of the integrity of water columns through drought and the attendant high tensions of those water columns is what is connoted. If one views a chaparral shrub as typically evergreen, at least some of the water columns must survive the dry season in order to supply that foliage, so the concept of safety inevitably involves the proportion of conducting cells that bear intact water columns despite water stress. Less obvious in the concept of safety than temporal and numerical persistence of water columns are the spatial distribution of these columns in the wood and the cell types bearing them. The findings reported here are of especial interest in these latter respects.

In order to present a picture of evolution of safety in woods, I must review some basic wood anat-

omy. Although bordered pits are universal in vascular plants, the significance of bordered pits is never explained. Conductive safety is achieved because of particular features of the bordered pit. Therefore, the nature and function of the bordered pit, a topic inadequately covered in textbooks, must be explained here.

The bordered pit (Fig. 1) is a compromise between wall strength, conductive efficiency, and conductive safety. The broad pit membrane (much larger than the pit aperture) facilitates conduction by presenting relatively large areas (considered as total pit membrane areas per cell) that can be traversed by water because they contain numerous ultramicroscopic pores. However, if the pit membrane area is large, the strength of the cell wall is correspondingly reduced (the secondary wall provides by far the majority of wall strength in a xylem cell). This weakening of the wall is lessened by the overarching of the pit border. The loss of strength can be said to be only as great as the area not covered by the border, that is to say, the pit aperture. The narrower the pit aperture, the stronger the wall; how narrow can the pit aperture be without impeding flow through the pit? The answer lies in the size and number of the ultramicroscopic pores. Air bubbles have a minimal size based on physical factors, and the ultramicroscopic pores are smaller than that minimal size. Thus, if air bubbles (which would deactivate the water column of a conducting cell) form in Cell A, the bubbles cannot traverse the pit membrane and deactivate Cell B. In this fashion, damage to the conductive system is localized. If this form of air-bubble localization were not desirable, a better conduction could be achieved by loss of the pit membrane, and that is exactly what does happen in vessel elements, in which the end walls do lose pit membranes and are thus true perforations. If, however, a conductive cell has no perforations, only bordered pits with their micropores, it is a tracheid and has optimal safety, isolation from entry of air bubbles. The pit membrane with its ultramicroscopic pores is, however, less than ideal at water conduction because the small size of these pores increases their surface tension or friction. The total combined flow capacity of the pores of a pit membrane can be said to equal the flow capacity of the pit aperture. Now we have the answer to the question of how narrow the pit aperture can be without impeding water flow. In the context of the present paper, I will stress that a cell with only bordered pits, a tracheid (according to the IAWA Committee on Nomenclature 1964), has maximal safety.

LOSS OF SAFETY DURING WOOD EVOLUTION

In Figure 2, we see a schematization for wood evolution in dicotyledons as a whole. This scheme is similar to that shown in some textbooks in that it attempts to show the simplification of the end wall

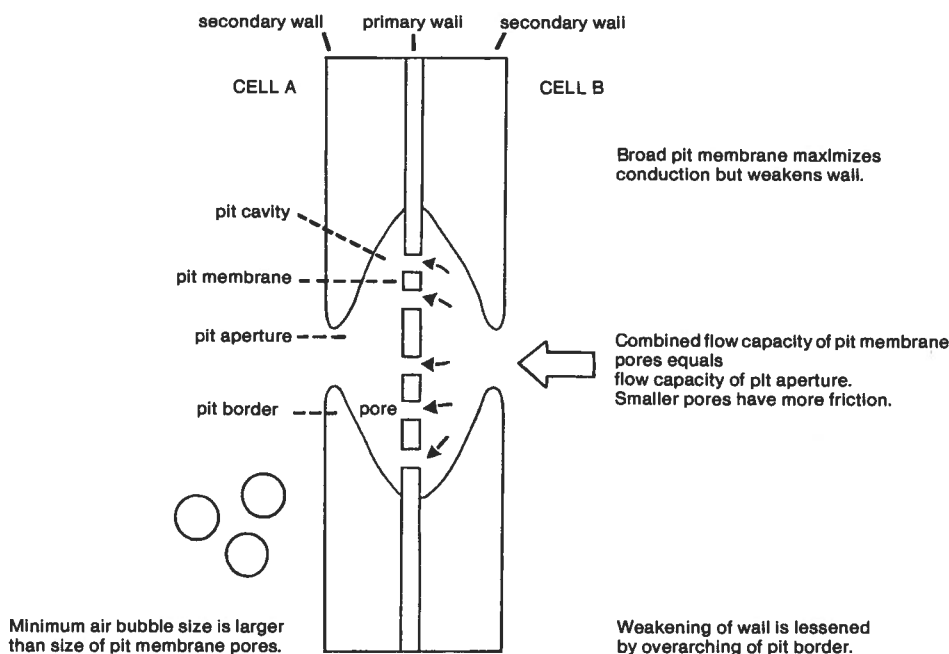


Figure 1. Bordered pit in sectional view, showing how morphological features are related to factors involved in water conduction in xylem.

of the vessel element, the perforation plate. However, it is not similar to textbook figures in that cells that accompany vessels in a wood are shown also. Thus the evolution of vessel elements is accompanied by evolution of imperforate tracheary elements. In general, we might expect primitive vessel elements with scalariform perforation plates to be accompanied by tracheids, with numerous large bordered pits, each of which has a wide border (or a large pit membrane area), as shown at the left in Figure 2. An intermediate stage, shown in the center of Figure 2, shows that the several perforations on the end walls of vessel elements have been replaced by fewer perforations; simultaneously, the pit membranes on the fiber-tracheids (as we may now call them) are reduced in size. In fact, this reduction of pit membranes on fiber-tracheids renders fiber-tracheids poor at conduction, and circumstantial evidence shows that their role in conduction is negligible. In the most specialized condition (Fig. 2, right), vessel elements have single (simple) perforation plates; on the imperforate tracheary elements, pit borders are lacking, and only slitlike pits containing minute pit membranes are present and we now term these cells libriform fibers.

The evolutionary series shown in Figure 2 can be called division of labor between increasingly efficient conductive cells and increasingly efficient mechanical support cells accompanying them in any given wood. The end product (characteristic of perhaps 90% of dicotyledons) is a vessel element with an end wall that minimally obstructs water flow; the bars on scalariform perforation plates do impede

flow. The most specialized imperforate tracheary element, the libriform fiber, is optimally strong because the pits are simple, not bordered; the pit membrane areas are thus minimal, and the slitlike pit apertures run parallel to the cellulose microfibrils and thus diminish wall strength minimally.

The trends shown in Figure 2 represent gains in conductive efficiency of the vessel elements and mechanical strength of the imperforate tracheary elements. If no other features of the wood were changed, however, these gains would be at the cost of loss of safety. The wood type at the right in Figure 2 has only vessel elements as the conductive cells, and should air bubbles form in one vessel element, they could spread unchecked into vessel elements above and below, disabling a whole vertical file of vessel elements. The conductive cell vital for safety, the tracheid, has been lost.

We know that woods corresponding to the drawing in Figure 2, left, occur only in very mesic situations; they are abundant only in cloud forests and rain forests (Carlquist 1975). In the southern California flora, *Alnus rhombifolia* Nutt. and *Cornus nuttallii* Aud. are virtually the only species with such primitive wood. Perhaps because of the conductive inefficiency of the scalariform perforation plates, these primitive woods tend not to occur in areas where transpiration and conductive rates fluctuate markedly, as they do in most seasonally dry areas.

Species with wood of intermediate types of specialization (e.g., *Ribes*) also tend to be restricted to areas where underground water is available for pro-

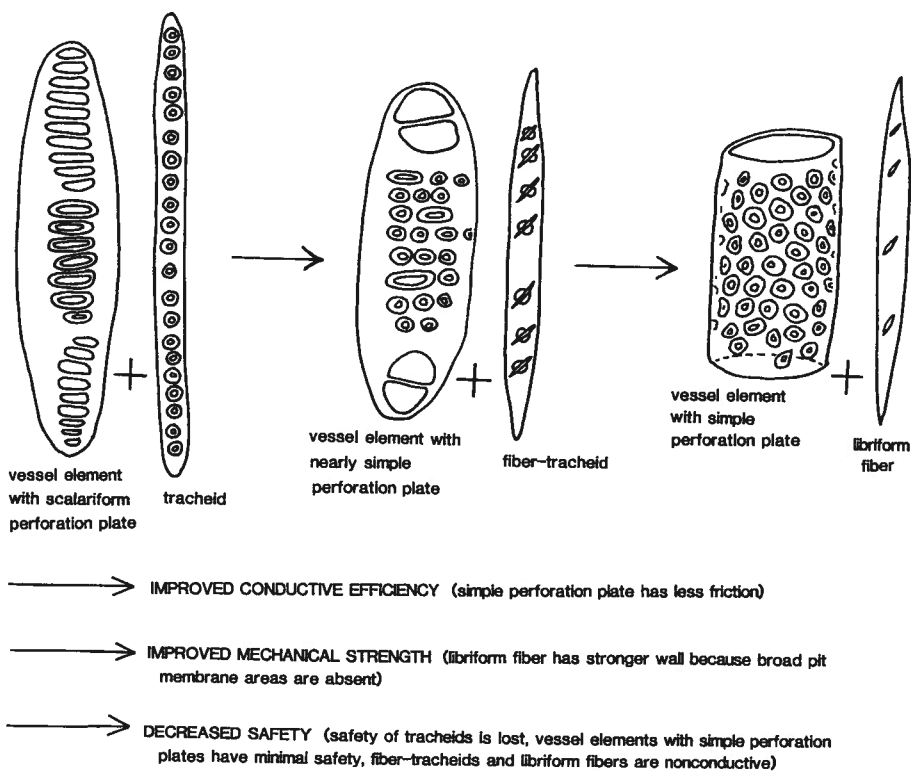


Figure 2. Schematic representation of wood evolution beginning with a type with scalariform perforation plates in vessels and ending with a type that has simple perforation plates in vessels. An imperforate tracheary element is shown alongside the vessel element in each case; although synchronization may vary widely from the pairings shown, one might most frequently find a tracheid associated with a primitive vessel element and a libriform fiber associated with a specialized vessel element. At the bottom of the figure, the physiological and mechanical consequences of the evolutionary series shown are summarized.

longed periods. The woods corresponding to the right part of Figure 2 are also restricted to wet areas unless they evolve some alterations that can increase safety. The hypothesis of this paper, then, is that woods of chaparral shrubs do not represent any of the types shown in Figure 2, but that some kind of modification must be achieved to increase safety, and that does appear to be what has happened according to recent data from California and from other regions as well (Carlquist 1985, Carlquist and Hoekman 1985).

MODIFICATION OF PRIMITIVE WOODS

On the left side of Figure 3, we see a phyletic that has not been stressed in earlier studies on wood evolution, although wood anatomists were certainly aware of it. We see, essentially, that change has occurred only in the vessel elements, which have attained simple perforation plates. The tracheids have remained unchanged during this phyletic. The tracheids at the left in Figure 3 are termed "true tracheids" because they are interpreted as relictual and are contrasted with other kinds of tracheids, mentioned later, which occur in other dicotyle-

dons. However, the change at the left side of Figure 3 is a significant one in that by simplifying the perforation plate, adaptation to fluctuations in conductive rate has occurred. Even if a vessel is fairly narrow, no bars across the end wall obstruct flow. What has not changed is equally significant: the tracheid has been retained, and thus safety has not been sacrificed. If, under high water stress, *every* vessel in the stem of a plant with such wood were disabled by air bubbles, conduction could still occur because the ground mass of the wood, composed of tracheids, would potentially be intact. Moreover, the three-dimensional pattern of conduction would not be altered, because the tracheids are not localized in particular parts of the wood; they are the background cell type of the wood. If the three-dimensional pattern of conduction remains unchanged when vessels are disabled, each stem and each leaf ought to survive, so that the evergreen habit is permitted. To be sure, the conductive rate of tracheids is slower than that of vessels, but transpiration is low during periods of water stress, so high conductive rates are not a requisite for the wood at such times.

Although one might not expect that woods prim-

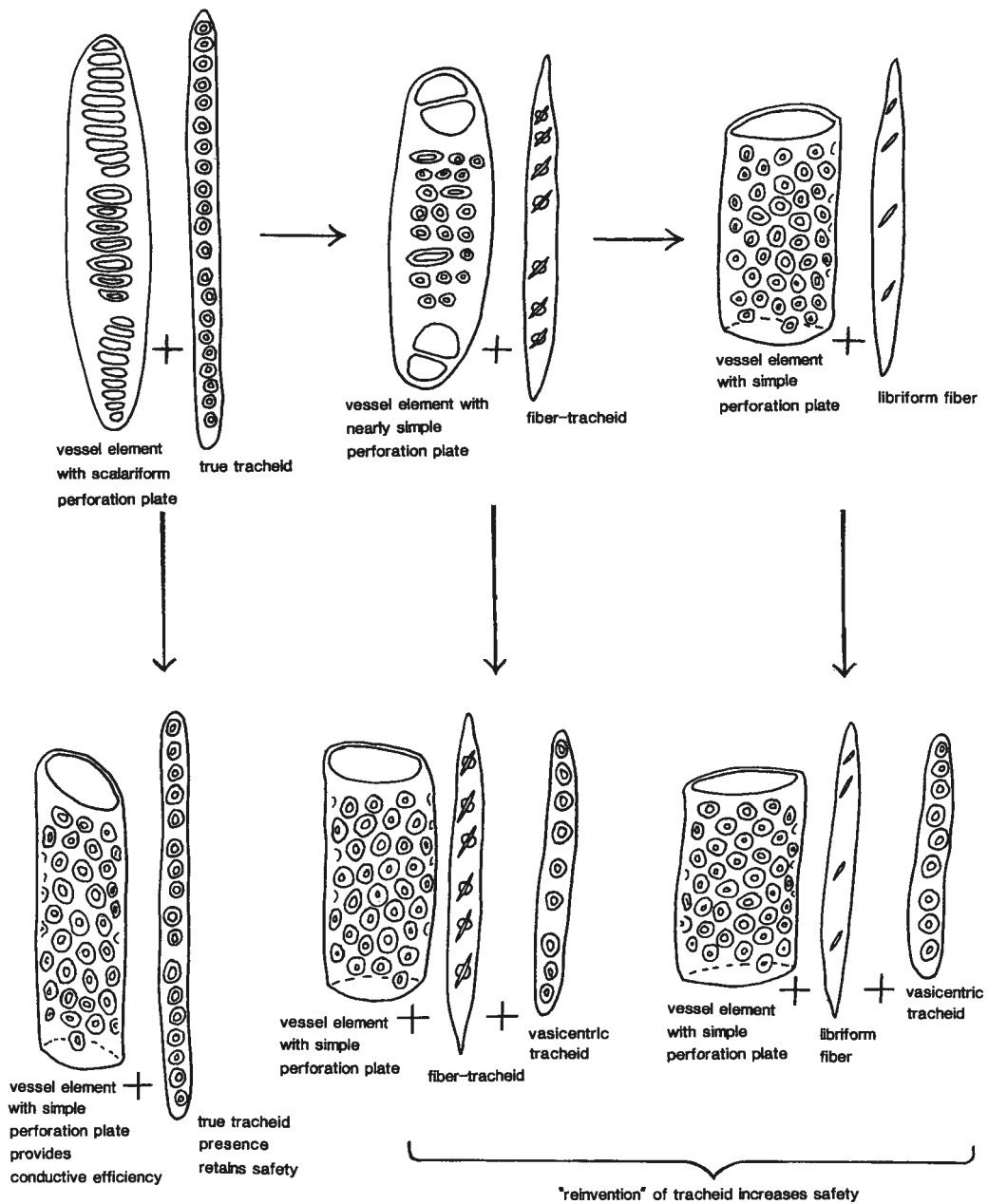


Figure 3. The evolution of vessel elements (and associated imperforate tracheary elements) as shown in Figure 2 (above), to which have been added (below) other trends prominent in the southern California flora. At lower left, retention of tracheids concomitant with simplification of perforation plates in vessel elements. Below, center and right, "re-invention" of the tracheid in phylads in which fiber-tracheids and libriform fibers are present; although not shown, the vasicentric tracheids are only adjacent to vessels in these woods, and the fiber-tracheids or libriform fibers form the ground mass of the woods.

itive by virtue of relictual presence of tracheids would be present in the chaparral of southern California, 24.4% of the species surveyed mostly with 1-2 species per genus, so the results should be interpreted more in terms of genera) had true tracheids plus vessels with simple perforation plates.

The genera in this category are some important and conspicuous ones, and include *Adenostoma*, *Cercocarpus*, *Eriodictyon*, *Garrya*, *Heteromeles*, and *Leptodactylon*. A survey of woods in shrubs of associations comparable to chaparral in the four areas of the world other than southern California

Table 1. Occurrence of vasicentric tracheids among plant communities of southern California (for further explanation, see Carlquist and Hoekman, 1985).

Habitat	% without true or vascular tracheids	% with vasicentric tracheids	Vasicentric tracheid % as % of left column
Riparian	26.5	00.0	00.0
Chaparral	58.5	43.9	75.0
Coastal sage	69.7	33.3	47.7
Alpine	41.7	41.7	100.0
Desert scrub	52.0	40.0	77.0
Flora (—207 spp.)	63.7	33.3	52.3
Prorated flora (512 spp.)	73.0	37.8	51.8

with mediterranean-type climates reveals that woods of this type also bulk about as large as they do in the southern California flora (Carlquist 1985).

REINVENTION OF THE TRACHEID

If a phylad has evolved more specialized woods in which tracheids have been supplanted by fiber-tracheids or libriform fibers, an evolutionary change in which tracheids have been reinvented can occur. This change is indicated in the bottom center and bottom right of figure 3. The fiber-tracheids and libriform fibers do not disappear if tracheids are reinvented by a phylad, they remain, but the newly acquired tracheids are distributed only in sheaths around the vessels, a fact not shown in Figure 3. This habit is connoted in the term "vasicentric tracheid." Functionally, the occurrence of the vasicentric tracheids only as sheaths around vessels is significant. If a vessel is disabled by an embolism, the vasicentric tracheids around it can maintain the same three-dimensional pattern of conduction. Obviously the conductive rate will be lessened, but as noted above, low transpiration and conductive rates may be expected during periods of water stress anyway. By virtue of maintaining the same spatial water-conducting pathways in wood, all the stems and leaves of a branch can continue to be supplied, so that the evergreen habit so characteristic of chaparral shrubs is not endangered.

Vasicentric tracheids have been known to wood anatomists for a long period of time—they are characteristic of *Quercus*, for example. However, in the world flora at large, they were thought to be infrequent, and Metcalfe and Chalk (1950) reported them in 30 families. Therefore, I was astonished to find vasicentric tracheids appearing prominently in chaparral shrubs (Carlquist 1985) when I surveyed the southern California flora. The chaparral genera in which vasicentric tracheids are characteristically present reads like a roster of the chaparral itself: *Arctostaphylos*, *Berberis*, *Ceanothus*, *Cneoridium*, *Comarostaphylis*, *Dendromecon*, *Haplopappus*,

Lepechinia, *Malacothamnus*, *Monardella*, *Prunus*, *Quercus*, *Rhamnus*, *Rhus*, *Romneya*, *Salvia*, and *Trichostema* are the most important genera. In the southern California chaparral flora, the percentage of species studied (essentially a generic sampling, with two or three species only in a few large genera) that have vasicentric tracheids is 43.9%. This listing contains many families or familial groupings for the first time, e.g., Anacardiaceae, Ericaceae, Malvaceae, and Papaveraceae. Apparently all Arbutioideae of Ericaceae have vasicentric tracheids, as do most dryland Rhamnaceae and all evergreen species of *Prunus*. These discoveries are mentioned by way of emphasizing the overrepresentation of this feature in chaparral in comparison to the world flora at large. As one might expect, in the evergreen shrubs of the other mediterranean-type floras of the world, vasicentric tracheids also bulk large. For example, in southwestern Australia vasicentric tracheids characterize most Myrtaceae and all Proteaceae.

Another mode of tracheid reinvention is represented by the vascular tracheid (Fig. 4). As I have defined this cell type, a vascular tracheid is a tracheid formed only at the end of a growth ring. In the earlier portion of a growth ring, vessels plus fiber-tracheids or vessels plus libriform fibers occur. In latewood, narrow vessels yield to vascular tracheids, which terminate the growth ring. Vascular tracheids may be considered vessel elements so narrow that no space is available at their tips for formation of perforation plates. Vascular tracheids tend not to be intermixed with vessels, as vasicentric tracheids are. Rather, they supplant vessels in the last few cell layers added to the xylem at the end of a growing season. Vascular tracheids thus would provide the safest possible conductive tissue at the time water is least available to the plant. However, the three-dimensional pattern of conduction within the stem is not maintained, and thus not all of the stems and leaves of a branch are supplied by vascular tracheids. Vascular tracheids, by retaining water columns at the end of a growing season, can be said to protect the cambium. In some species with vascular tracheids, the cambium might be the only living cell layer in a stem in times of extreme drought. Because the pattern of vascular tracheids does not maintain three-dimensional pathways, species with vascular tracheids tend to be those with drought-deciduous leaves. Species with drought-deciduous leaves are less common in chaparral than in coastal sage. Thus, vascular tracheids typify *Artemisia californica* Less., *Eriophyllum confertiflorum* (DC.) Gray, *Mimulus* sect. *Diplacus*, *Samolus* spp., and *Toxicodendron*. In chaparral, 17.1% of species studied have vascular tracheids (Table 2).

True tracheids, vascular tracheids, and vasicentric tracheids are defined here as mutually exclusive. Of the three categories, vasicentric tracheids are the most important in chaparral and other dryland plants (Tables 1, 2). In Table 1, one can see that 75% of the chaparral species studied that could possibly have vasicentric tracheids do have them. Desert

Table 2. Wood features in the southern California flora (for full explanation of conventions, see Carlquist and Hoekman 1985).

Habitat	VMM*	TT	VasiT	VascT	GRing	Meso
Riparian	163	37.5	00.0	00.0	56.3	253
Moist	198	30.0	20.0	10.0	75.0	106
Chaparral	299	24.4	43.9	17.1	62.2	67
Coastal sage	212	6.1	33.3	24.2	65.2	81
Alpine	442	58.3	41.7	00.0	75.0	27
Desert scrub	361	40.0	40.0	8.0	80.0	21
Succulent	45	00.0	33.3	00.0	66.7	368
Halophyte	158	00.0	50.0	00.0	50.0	26
Flora (—207 spp.)	251	23.7	33.3	13.0	66.9	123
Prorated flora (512 spp.)	257	15.3	37.8	11.7	69.1	120

* Explanation of columns: VMM, mean number of vessels per mm²; TT, percentage of species with true tracheids; VasiT, percentage of species with vasicentric tracheids; VascT, percentage of species with vascular tracheids; GRing, percentage of species with either marked or inconspicuous growth rings; Meso, mesomorphy ratio (vessel diameter times vessel element length divided by number of vessels per mm²).

shrubs have evolved vasicentric tracheids to nearly the same extent.

OTHER SAFETY MECHANISMS

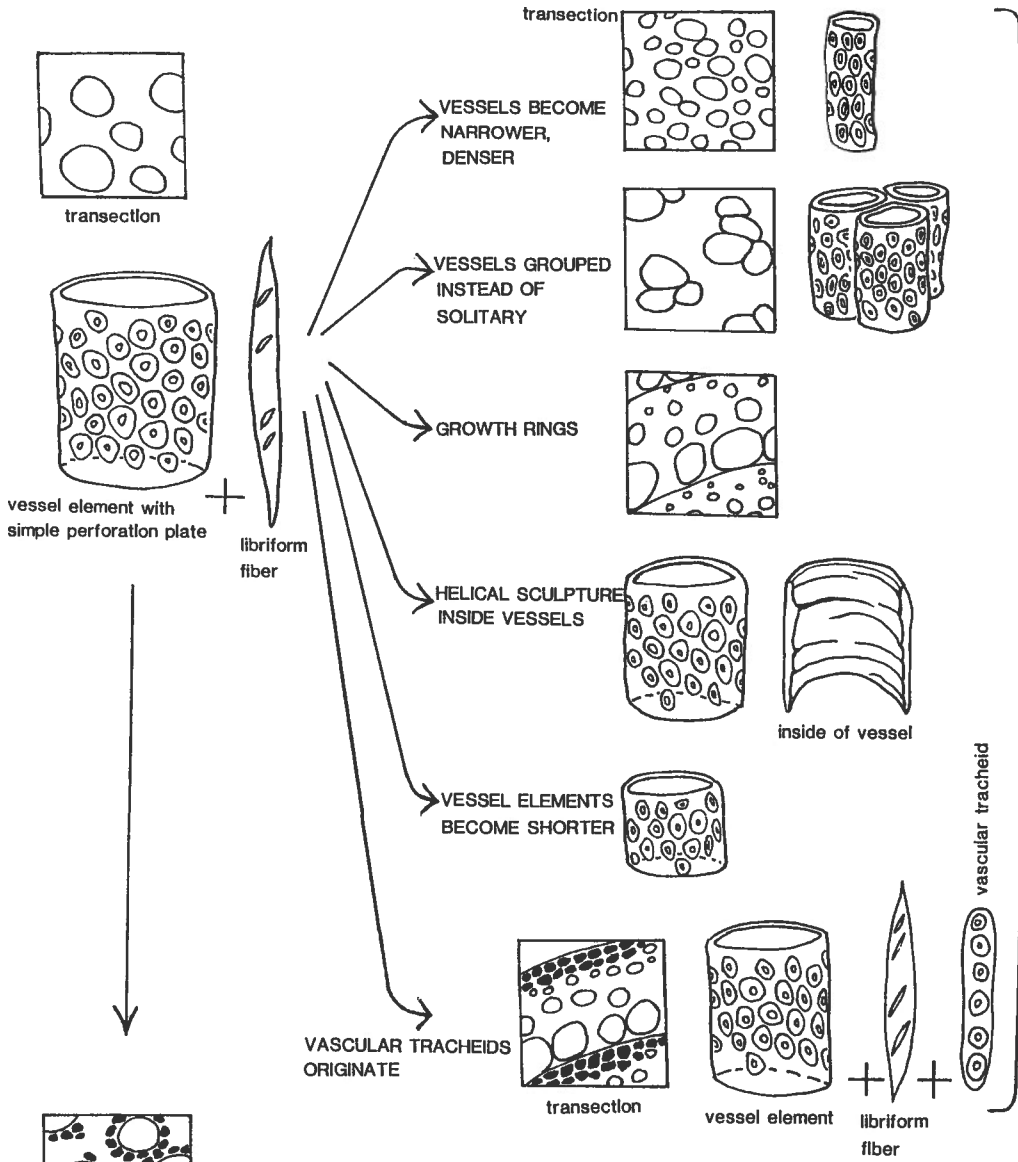
As shown in Figure 4, one of the simplest safety mechanisms characteristic of chaparral wood adaptations is narrowing of vessels. The mean diameter of vessels in southern California chaparral is 20.2 μm , the narrowest of any plant association in this floristic region, including desert shrubs (Table 3). To put that figure into perspective, one should know that the mean vessel diameter for dicotyledons as a whole is 94 μm (Metcalf and Chalk 1950, appendix). Indeed, upon reading my manuscript surveying southern California woods as a whole (Carlquist and Hoekman 1985), R. Miller of the U.S. Forest Products Laboratory was surprised that in no species did mean vessel diameter exceed 100 μm —the wet temperate and tropical species with which he deals routinely have vessels wider than 100 μm . The adaptive value of narrow vessels lies in increased safety of water columns in narrow capillaries. There is experimental evidence to show that within a given wood under water stress, wider vessels fill with air embolisms before narrower ones do (Huber 1935, Zimmermann and Brown 1971, Ellmore and Ewers 1985). Theoretically, narrower vessels ought to maintain water columns better than wider ones because they have a greater surface to volume ratio, and a higher proportion of water molecules is therefore bonded to the vessel wall.

Related to vessel diameter but somewhat independent of it is vessel density, which may be expressed as number of vessels per mm² of wood transection. The relationship is an inverse one—the wider the vessels, the fewer per unit area. However, the density of vessels always falls well short of theoretical packing limits, and different species fall short to different degrees. The latter justifies

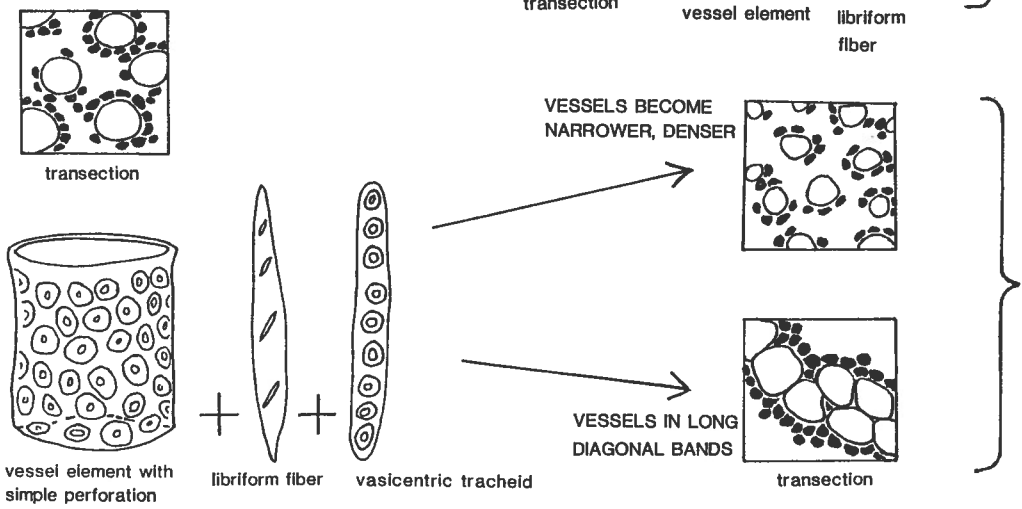
analysis of vessel density separately from vessel diameter. One can assert that numerous vessels per mm² confers safety by virtue of redundancy (Zimmermann 1982). In chaparral, the mean number of vessels per mm² is 299 (Table 2). This figure is exceeded in Californian alpine shrubs (442) and desert shrubs (361), but again, all of these figures are well above the figure for dicotyledons at large. Metcalfe and Chalk (1950, appendix) report an average of only 31 vessels per mm² in dicotyledons as a whole (one must remember, of course, that their sample is biased in favor of mesic species).

Vessel diameter and vessel density are both involved in yet another phenomenon, that of growth rings. In this familiar phenomenon, the safety of narrow vessels, numerous per mm², is conferred by the latewood vessels. Earlywood vessels are wider, and thus represent an accommodation to peak conductive rates earlier in the season. There is experimental evidence that latewood vessels maintain columns while earlywood vessels fill with air during water stress (Ellmore and Ewers 1985). In chaparral shrubs, 62.2% of species have moderate to well-marked growth rings. This figure is more startling when one takes into account the nondeciduous nature of most chaparral shrubs. Nondeciduous shrubs in a climate as mild as that of southern California would be expected to show less growth ring expression; a sampling of cultivated shrubs from southern California shows that growth rings are minimal under these circumstances. One should note in passing that in chaparral shrubs, even the earlywood vessels are narrow when compared, for example, to the earlywood vessels of deciduous wet-forest trees.

Grouping of vessels is a curious phenomenon the significance of which has been clarified recently (Carlquist 1984). For many years, wood anatomists had known that in some woods, vessels are grouped, while in others, they are solitary. As long ago as



may occur separately, but if more than one occurs, effect is additive



may occur separately, with both safety additive

Table 3. Wood features in the southern California flora (for full explanation of conventions, see Carlquist and Hoekman 1985).

	VDiam*	VEL	Helic	V/G	Bars
True tracheids present	26.5	281	38.0	1.33	2.59
True tracheids absent	37.9	218	43.6	4.63	0.19
Desert scrub	25.9	190	56.0	2.62	0.00
Alpine	20.9	266	33.3	2.53	4.75
Chaparral	20.2	261	56.1	4.76	0.12
Coastal sage	34.5	188	42.4	7.55	0.00
Riparian	50.7	418	20.0	1.77	6.75

* Explanation of columns: VDiam, mean vessel diameter, μm ; VEL, mean vessel element length, μm ; Helic, percentage of species in category bearing helical thickenings in vessels of secondary xylem; V/G, mean number of vessels per group, where a solitary vessel = 1.0, a pair = 2.0, etc.; Bars, mean number of bars per perforation plate per species in category.

1685, Grew in *Anatomy of Plants* figured woods of oak with solitary vessels of wood of "wormwood" (*Artemisia*) with grouped vessels. The key to this phenomenon turns out to be the presence of tracheids versus fiber-tracheids or libriform fibers in a wood. If a wood has tracheids, it has a background of conductive cells. Should any vessel in the wood embolize, the tracheids around the vessel can continue to conduct, so the three-dimensional pattern remains relatively unimpaired. In a wood with fiber-tracheids or libriform fibers, however, vessels occur in a background of nonconductive cells. Should a particular vessel embolize, there is no sheath of conductive cells around it to maintain the conductive pathways. In woods with fiber-tracheids or libriform fibers, therefore, an advantage is gained by grouping of vessels; if one vessel in a group fills with air, its intact neighbors can maintain the conductive pathways. Therefore, one should expect to see increased grouping of vessels with xeromorphy in woods with fiber-tracheids or libriform fibers, but no increased grouping of vessels in woods with true tracheids. This is true, in fact (Table 3). Either true tracheids or abundant vasicentric tracheids deter vessel grouping (the latter is the case in oaks). The average number of vessels per group (where a solitary vessel = 1.0, a pair in contact = 2.0, etc.) in chaparral shrubs is 4.76. This is pronounced, and when one realizes that about a quarter of chaparral shrubs have true tracheids and thus ought not to group vessels appreciably, one can see that the remainder of chaparral shrubs clear-

ly are taking advantage of this feature. Vessel grouping is next highest in the southern California floristic area in desert shrubs (2.62 vessels per group), but that is not surprising because desert shrubs do represent the driest possible habitats.

For many years, wood anatomists have noticed that vessels tend to have helical sculpture ("helical thickenings," "spirals") in areas that are cold or dry or both. This was noted for chaparral and desert shrubs by Webber (1936). A systematic sampling (Carlquist and Hoekman 1985) quantitatively validates her observation; helical sculpture is reported in 56.1% of chaparral shrubs and 56.0% of desert shrubs of southern California. Although no figure is available for the world flora, the figure probably lies below 20%, and helical sculpture is rarely encountered in woods from, for example, Amazonian forests. Helical sculpture has been hypothesized to be a mechanism for increasing the surface area of vessel walls, and thereby increasing water bonding to vessel walls and deterring interruption of water columns (Carlquist 1982). In addition to ecological distribution of woods with helical sculpture in vessels, support can be found in distribution within a wood. Latewood vessels have helical sculpture to a much more pronounced extent than do early-wood vessels.

A very pronounced trend in evolution of dicotyledon woods as a whole as well as those in dry areas is the shortening of vessel elements (Fig. 4). Vessel elements are notably short (Table 3) in chaparral shrubs (261 μm), although even shorter ones

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Figure 4. Schematic representation of evolutionary trends that are hypothesized to add conductive safety to wood. In the case of a wood that has already evolved vasicentric tracheids, vessels may become narrower or may be grouped into extensive diagonal aggregations. In other woods (upper left) in which libriform fibers (or, alternatively, fiber-tracheids) accompany vessels but no vasicentric tracheids are present, a wide range of features that could increase conductive safety could be evolved: narrowness of vessels, increased denseness of vessels, grouping of vessels, presence of growth rings, helical sculpture presence in vessels, decreased length of vessel elements, and presence of vascular tracheids. As the bracket at right indicates, presence of more than one of these features is believed to have an additive effect on conductive safety.

Table 4. Relative percentage of species with wood features of conductive significance in the southern California flora (for full explanation of conventions, see Carlquist and Hoekman 1985).

Perforation plates simple	94.7
True tracheids present	23.7
Growth rings (strong or weak) present	66.9
Helical sculpture present	38.2
Vasicentric tracheids present	33.3
Vascular tracheids present	13.0

can be found in desert shrubs (190 μm) and coastal sage shrubs (188 μm). To put these figures into perspective, the average vessel element length in dicotyledonous woods as a whole is 649 μm (Metcalfe and Chalk 1950, appendix). Why vessel element length should shorten phyletically and ecologically is not entirely clear. One current hypothesis is that air bubbles can be trapped within individual vessel elements because the constriction formed by the perforation plate, even when the plate is simple, deters spread of air bubbles into adjacent vessel elements. This theory can be said to have been originated by Slatyer (1967). Some experimental support can be found in the observations of Sperry (1985). If this theory is correct, shorter vessel elements would tend to localize air bubbles to a greater extent, so that shorter lengths of the conductive system would be disabled.

Turning to chaparral shrubs with vasicentric tracheids (Fig. 4, bottom), one can see that some additional adaptations are possible. Vessels can become narrower and denser. Growth rings can be formed in these species. If vasicentric tracheids are not abundant in a particular wood, extensive vessel groupings can form. Often, as shown in Figure 4, species with vasicentric tracheids tend to have diagonal bands of vessels as seen in transections of woods. The significance of these bands has recently been clarified (Carlquist 1987). Species in which diagonal aggregations of vessels occur have vasicentric tracheids, or, in a few instances, very narrow vessels (*Artemisia*). Thus, the species with diagonal bands are essentially a subset of the species with vasicentric tracheids. This subset tends to occupy drier sites than the species with vasicentric tracheids but without diagonal vessel aggregations. The diagonal aggregations are very characteristic of chaparral species of *Ceanothus* and *Quercus*, among others. The theoretical value of the diagonal vessel aggregations lies partly in the grouping of vessels. The groupings are indefinite in extent, and because the diagonal bands intersect, an interconnected network is formed. Thus, failure of vessels anywhere in a stem would result in minimal disruption of conduction, for the three-dimensional network otherwise remains intact. The presence of vasicentric tracheids in these diagonal bands offers,

throughout their extent, a series of cells that would embolize less readily than the vessels they accompany. Thus there are two levels of safety within the bands, and should numerous vessels embolize, the three-dimensional pathways would continue to be represented by functioning vasicentric tracheids.

ADDITIVE NATURE OF ADAPTATIONS

As indicated by the bracket at right in Figure 4, features interpreted here as adaptations can be additive. To be sure, there are some instances in which occurrence of some features locks out evolution of others in a species. For example, as mentioned above, species with true tracheids tend to show minimal grouping of vessels. Species with true tracheids also tend to show less shortening of vessel elements than species with fiber-tracheids or libriform fibers. However, a phylad with true tracheids could develop such adaptations as narrowness of vessels, high density of vessels, helical sculpture in vessels, and growth ring presence. Phylads with vasicentric tracheids could develop any or all of those four, plus vessel grouping, shortening of vessel elements, and grouping of vessels into diagonal bands. The occurrence of diagonal bands is apparently unlikely to occur in species with vascular tracheids rather than vasicentric tracheids. True tracheids, vasicentric tracheids, and vascular tracheids are regarded here as different; true tracheids are relictual, vasicentric and vascular tracheids represent "reinventions" of the tracheid. Phylads with vascular tracheids, however, can merge into vasicentric tracheid presence. As vascular tracheids become increasingly abundant in a phylad, as in the chaparral Lamiaceae, the tracheids pervade the latewood in such a way that many vessels are embedded among them, and thereby functionally vasicentric tracheids must be said to exist.

In chaparral shrubs, the number of wood adaptations for dealing with water stress in any given species probably represents the majority of adaptations possible for a phylad. In other words, the occurrence of one good adaptation, such as vasicentric tracheid presence, apparently does not preclude in any way the addition of another feature, such as helical sculpture in vessels, or more than one feature.

What governs which features occur in which species? If we look at the data of Table 4, we see different percentages of species in the woody southern California flora as a whole have particular features. The table contains only presence-or-absence features; if a threshold value for certain other features such as narrowness of vessels, had been established, one might have added features of a strictly quantitative nature also. The feature at the top of the table, evolution of simple perforation plates from scalariform perforation plates, is almost so obvious it could have been omitted. Yet we must remember that for dryland species where there are strong seasonal differences in water availability and

thereby probably water conduction rates, simple perforation plates are virtually a necessity. Virtually no chaparral species have scalariform perforation plates, and those few that do have only one or several bars per plate. The next highest percentage is represented by growth rings. This is not unexpected, perhaps, if we consider that all woody species have the capability of varying vessel diameter and abundance, so very little new genetic information is needed to produce growth rings; mostly the evolution of growth rings represents ability to form wide vessels immediately upon onset of growth (and these earlywood vessels usually are long, consisting of more numerous vessel elements than latewood vessels and extending indefinitely along the length of a stem or root. As noted in Table 4, presence of true tracheids represents conservatism rather than innovation; a primitive feature is preferentially retained, despite other modifications in the wood. The percentage of woods with tracheids in the flora of southern California is rather high, higher than one would associate with such an area where dicotyledons with numerous specialized features are to be expected. Evidently, retention of true tracheids is so advantageous because of the safety of this cell type that phylads with true tracheids have been very successful. One should note, however, that the number of species per genus in the genera with true tracheids is relatively small, correlated with their relictual nature.

With the remaining features, the limiting factor appears to be one of developing genetic information. A remarkably large number of phylads have succeeded in developing vasicentric tracheids. By subtracting taxa with true tracheids and vascular tracheids, we found that 75% of the chaparral species studied that could evolve vasicentric tracheids have in fact evolved them. Considering the intricacy of re-evolving a cell type, yet retaining fiber-tracheids or libriform fibers also, I regard this as phenomenally high, and one might guess that only lack of the appropriate mutations has prevented the remaining 25% from acquiring vasicentric tracheids—certainly this feature is the most interesting single adaptation in the wood anatomy of chaparral species. The relatively low figure for vascular tracheids in the southern California flora (Table 4)—13%—can be interpreted not so much as a failure of acquisition of the right mutations, but as a signal that vascular tracheids are not as highly valuable in most phylads. Essentially a phenomenon related to the drought-deciduous habit of foliage, vascular tracheids are not adaptive in phylads with evergreen foliage. One can say that any group with vasicentric tracheids has physiological advantages over one with

vascular tracheids, and the percentage of vascular tracheid occurrence is accordingly lower.

LITERATURE CITED

- Carlquist, S. 1975. Ecological strategies of xylem evolution. Berkeley and Los Angeles: University of California Press.
- . 1982. Wood anatomy of Onagraceae: Further species; root anatomy; significance of vestured pits and allied structures in dicotyledons. *Annals of the Missouri Botanical Garden* 69:755–769.
- . 1984. Vessel grouping in dicotyledon wood: Significance and relationship to imperforate tracheary elements. *Aliso* 10:505–525.
- . 1985. Vasicentric tracheids as a drought survival mechanism in the flora of southern California and similar regions. *Aliso* 11:37–86.
- . 1987. Diagonal and tangential vessel aggregations in wood: Function and relationship to vasicentric tracheids. *Aliso* 11:451–462.
- Carlquist, S., and D.A. Hoekman. 1985. Ecological wood anatomy of the woody southern Californian flora. *International Association of Wood Anatomists Bulletin*, new series, 6:319–347.
- Ellmore, G.S., and F.W. Ewers. 1985. Hydraulic conductivity in trunk xylem of elm, *Ulmus americana*. *International Association of Wood Anatomists Bulletin*, new series, 6:303–307.
- Grew, N. 1685. *The anatomy of plants* (reprinted 1965). New York and London: Johnston Reprint Co.
- Huber, B. 1935. Die physiologische Bedeutung der Ring- und Zerstreutporigkeit. *Berichte der Deutschen Botanischen Gesellschaft* 53:711–719.
- IAWA Committee on Nomenclature. 1964. Multilingual glossary of terms used in wood anatomy. Winterthur, Switzerland: Verlagsanstalt Buchdruckerei, Konkordia.
- Metcalf, C.R., and L. Chalk. 1950. *Anatomy of the dicotyledons*. Oxford: Clarendon Press.
- Slatyer, R.O. 1967. *Plant-water relationships*. London and New York: Academic Press.
- Sperry, J.S. 1985. Xylem embolism in the palm *Rhapis excelsa*. *International Association of Wood Anatomists Bulletin*, new series, 6:283–292.
- Webber, I.E. 1936. The woods of sclerophyllous and desert shrubs and desert plants of California. *American Journal of Botany* 23:181–188.
- Zimmermann, M.H. 1982. Functional anatomy of angiosperm trees. In *New perspectives in wood anatomy*, ed. P. Baas, 59–70. The Hague: Martinus Nijhoff.
- Zimmermann, M.H., and C.L. Brown. 1971. *Trees. Structure and function*. Heidelberg and Berlin: Springer-Verlag.