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DIAGONAL AND TANGENTIAL VESSEL AGGREGATIONS IN WOOD:
FUNCTION AND RELATIONSHIP TO
VASICENTRIC TRACHEIDS

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ABSTRACT

The list of families with diagonal ("dendritic" or "flameliike" of other authors) patterns of vessel aggregation is similar to the list of families that have vasicentric tracheids. This paper attempts to deal with apparent exceptions. Because of recent reports of vasicentric tracheids, the families with diagonal vessel aggregations are all also on the list of families with vasicentric tracheids with the exception of four families. Genera of those four families are studied to see if a relationship between vasicentric tracheids and diagonal vessel aggregations does hold. Of the families not on both lists, Leitneriaceae (*Leitneria*), Melastomataceae (*Mouriri*), and Moraceae (*Maclura*) do prove to have vasicentric tracheids in appreciable numbers. Small numbers of vasicentric tracheids and small degrees of vessel aggregation occur in *Asimina* (Annonaceae), *Morus* (Moraceae), and various Araliaceae. Vessels may not appear diagonally grouped if libriform fibers accompanying them are few, or if vessels are separated by large numbers of vasicentric tracheids. Diagonal grouping appears most marked in woods from drier and colder localities. Extensive diagonal vessel aggregations are apparently a reliable indication of vasicentric tracheid presence, but only a portion of the woods with vasicentric tracheids have diagonal vessel aggregations. By having few, large, and intersecting aggregations of vessels mixed with vasicentric tracheids, a wood has greater potential safety (failure of fewer water columns by air embolisms) in space (within wood) and time than a wood with smaller, more numerous vessel groupings. Vessel grouping and vasicentric tracheid presence are considered additive in their safety effects. Key words: dendritic vessel groupings, diagonal vessel groupings, ecological wood anatomy, flameliike vessel groupings, pore groupings, wood anatomy.

INTRODUCTION

As seen in transection, certain woods demonstrate vessel (pore) aggregations that run diagonally and may be extensive, forming patterns that continue across rays. These are conspicuous in woods of Calycanthaceae (Carlquist 1983), certain Fabaceae (Cozzo 1950), several genera of Oleaceae (Patel 1978), some Sapotaceae (e.g., Kukachka 1978*a*), and a few other families listed below. Metcalfe and Chalk (1950, p. 1351) term these "dendritic" patterns. Other terms given for these patterns are "flameliike" (Record 1942) and "echelon" (Kukachka 1978*a*). My term "diagonal aggregation" is, as far as I can tell, identical to the usages of these authors, but has been devised because it is less ambiguous. Diagonal aggregations connote any moderate to extensive pore grouping that extends across a transection in a direction between tangential and radial. "Dendritic" implies a dichotomous branching of the bands, which may more often anastomose, and "flameliike" is not used here because the image it conveys may not evoke all instances of this phenomenon. Also considered here are vessel aggregations that are tangential or nearly so rather than diagonal in orientation. These tangential aggregations are not bands of earlywood vessels, but instead are formed after the large earlywood

vessels. Some instances with tangential bands of vessels have been termed an "ulmiform" pattern. In *Ulmus* and other Ulmaceae, earlywood vessels are not grouped and are not associated with vasicentric tracheids, but throughout most of each growth ring, vessels are narrow and grouped into tangentially oriented aggregations in which vasicentric tracheids also are present. This pattern has also been observed in genera and families listed by Record (1942). In Proteaceae such as *Persoonia* (Carlquist 1984, fig. 17), tangential bands of vessels occur throughout the wood without any relationship to earlywood or latewood; in Proteaceae the term "ulmiform" has not been used for this phenomenon. The term "aggregation" as used here refers to larger groupings than such terms as "pore multiples," "pore clusters," etc., imply and was consistently used to designate these larger groupings in an earlier paper (Carlquist 1984).

While investigating vasicentric tracheids, I noticed that diagonal vessel aggregations occur conspicuously in many of the species that have vasicentric tracheids (Carlquist 1985, note added in proof). However, not all taxa listed as having vasicentric tracheids have diagonal aggregations of vessels. Looking at the list given by Metcalfe and Chalk (1950) for families with diagonal vessel aggregations, I found four families not on my list of families with vasicentric tracheids (Annonaceae, Leitneriaceae, Melastomataceae, and Moraceae). The correlation between these phenomena is sufficiently conspicuous so that an attempt is made to examine the exceptions and to see if they really are exceptions. The present paper is an attempt to resolve the relationship between diagonal vessel aggregation presence and the presence of particular tracheary element types.

The tangential (ulmiform) vessel aggregations are included in the present investigation because that phenomenon may be related to the one under consideration to the extent that some of the tangential bands tend to be diagonal. Some families known to have tangential pore bands are known to have vasicentric tracheids. In some families with vasicentric tracheids, vessel aggregations more nearly tangential than diagonal are frequent.

MATERIALS AND METHODS

Wood samples of pertinent genera were selected from the Rancho Santa Ana Botanic Garden wood collection (RSAw) or collected locally. Sections were prepared on a sliding microtome and stained in a safranin-fast green combination. Transections reveal the presence of diagonal vessel aggregations well. Longitudinal sections are indicative, not decisive, in demonstrating presence of vasicentric tracheids because small perforation plates might be on portions of elements cut away; consequently macerations are required for confirmation (Carlquist 1985). Macerations were prepared by means of Jeffrey's Fluid and stained in safranin. The definitions of the IAWA Committee on Nomenclature (1964) are employed here, although that compendium is somewhat vague on the definition of vasicentric tracheid. The part of the Committee definition considered essential here is the criterion that a vasicentric tracheid is associated with a vessel. Any tracheid associated with a vessel in a wood that also contains fiber-tracheids or libriform fibers (sensu IAWA Committee on Nomenclature 1964) is a vasicentric tracheid, and such a wood lacks true tracheids. The term vascular tracheid is reserved for tracheids formed only at the end of growth rings (and therefore not surrounding vessels) in woods that have fiber-tracheids or libriform fibers. A detailed account

of this terminology and the reasons for it have been given elsewhere (Carlquist 1986). There is no standardized set of terms for the vessel (pore) groupings under consideration in this paper, and the terms used earlier (Carlquist 1984) have been employed here.

Dr. William L. Stern is acknowledged for his help in providing some of the wood samples, for sponsoring my visit to Florida that led to the collection of the *Leitneria* wood sample, and for reading the manuscript and offering helpful suggestions.

RELEVANT TYPES OF VESSEL AGGREGATION

1. *Extensive Diagonal Aggregations of Vessels*

As shown by *Leitneria* (Fig. 1–2), diagonal bands of vessels may be oriented in various directions ranging from tangential to radial. *Leitneria* exemplifies this type well in terms of the tendency for the vessel aggregation pattern to continue across rays, because vessel groupings in *Leitneria* extend across uniseriate rays (Fig. 2). Most examples of this type have somewhat more numerous vessels per mm² than does *Leitneria*.

2. *Vessel Aggregations Indefinite in Extent Because of Abundance of Narrow Vessels and Vascentric Tracheids*

In *Berberis* (*Mahonia*) *nervosa* Pursh (Fig. 3–5), relatively few libriform fibers are present. Consequently, vessel aggregations are, in fact, indefinite in extent. This situation has also been illustrated for *Clematis ligusticifolia* Nutt. (Carlquist 1985). However, species of *Berberis* other than *B. nervosa* have more abundant libriform fibers, groups of which separate the aggregations of vessels and vascentric tracheids, and therefore diagonal aggregation of vessels becomes apparent. *Berberis haematocarpa* Woot. and *B. nevinii* Gray fall into this category and have transectional appearance much like that figured here for *Dendromecon* (Fig. 6).

3. *Less Extensive Diagonal Vessel Aggregations*

Dendromecon rigida Benth. ssp. *rhamnoides* (Gray) Greene (Fig. 6) is representative of this condition. The diagonal bands of vessels (which also contain vascentric tracheids) mostly do not extend across rays.

4. *Diagonal Vessel Aggregations Containing Vessels Well Separated by Large Numbers of Vascentric Tracheids*

This condition is well shown by many Fagaceae such as *Chrysolepis sempervirens* (Kell.) Hjelmqv. (Fig. 7). By appearing as light areas (in contrast to the denser areas, which are libriform fibers), the abundance of vascentric tracheids is evident. At first glance, one might not think of this as an example of vessel aggregation at all, but it clearly is and Metcalfe and Chalk (1950) have included Fagaceae in their list of species with diagonal vessel aggregations. There are some dicotyledonous woods in which vascentric tracheids are very similar to libriform fibers in transection, and thus the interconnection of vessels by vascentric tracheids is less evident; some species of *Eucalyptus* exemplify this.

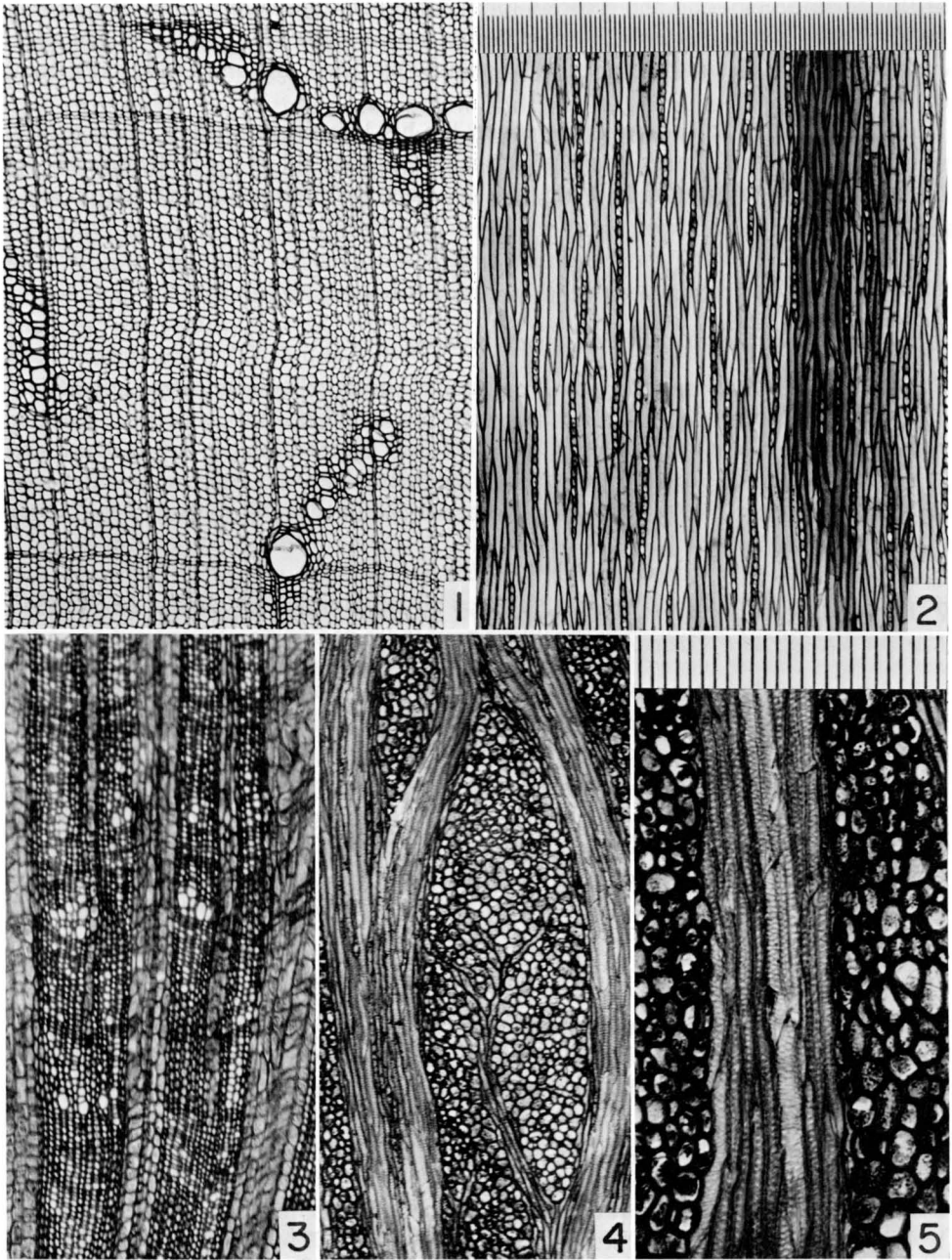


Fig. 1-5. Wood sections of Leitneriaceae and Berberidaceae.—1-2. *Leitneria floridana*, Carlquist 15639.—1. Transection; vessel aggregations at various diagonal angles can be seen.—2. Tangential section; dark cells at right are vessels and vascentric tracheids.—3-5. *Berberis nervosa*, Bissing 262.—3. Transection; diagonal patterns of vessel aggregation are not evident.—4. Tangential section; wide rays intercalated into the axial xylem.—5. Portion of tangential section showing axial xylem comprised wholly of narrow vessels plus vascentric tracheids. (Fig. 1-4, magnification scale above Fig. 2 [finest divisions = 10 μ m]; Fig. 5, scale above Fig. 5 [divisions = 10 μ m].)

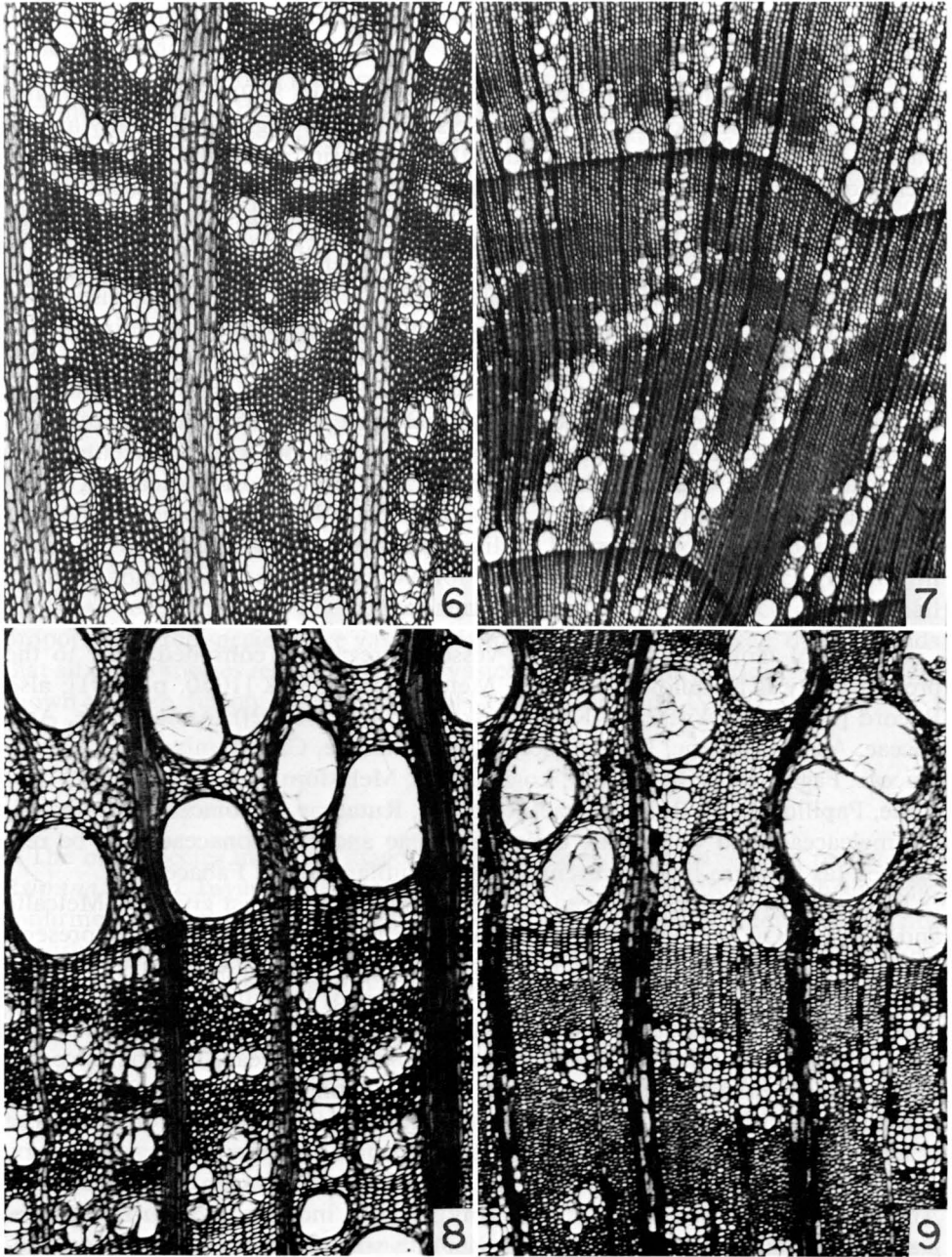


Fig. 6-9. Wood sections of Papaveraceae, Fagaceae, and Moraceae.—6. *Dendromecon rigida* ssp. *rhamnoides*, Thorne 34845. Transection; diagonal vessel aggregations present not indefinite in length, many are less than the width between two rays.—7. *Chrysolepis sempervirens*, Carlquist s.n. Transection; vessels are in diagonal aggregations, embedded in extensive zones of vasicentric tracheids.—8. *Morus alba*, ZTw 41. Transection; earlywood vessels are solitary, latewood vessels grouped but not into extensive aggregations.—9. *Maclura pomifera*, UN 262. Transection; latewood vessels are in diagonally-oriented aggregations that tend to be more nearly tangential than radial in direction. (Fig. 6-9, magnification scale above Fig. 2.)

5. *Tangential to Somewhat Diagonal Aggregations of Vessels in Latewood ("Ulmiform" Grouping)*

This condition is represented by a few Moraceae (Fig. 8, 9) as well as by many Ulmaceae. In these taxa, earlywood vessels are neither aggregated to any appreciable degree nor are they intermixed with vasicentric tracheids. The balance of each growth ring contains tangential bands composed of narrow vessels; in Ulmaceae, these bands contain vasicentric tracheids. In *Morus*, the latewood contains vessel groupings that do not form extensive tangential bands; there are extensive tangential grouping patterns that continue across rays in *Maclura* (Fig. 9).

6. *Tangential Aggregations of Vessels Present in Earlywood as Well as in Latewood*

This condition (not illustrated here) has been cited for various Proteaceae (Carlquist 1984). Several tangential bands are formed per year. Vasicentric tracheids are mixed with vessels in the bands. In the case of Proteaceae, fiber-tracheids are present between the bands, and the difference between earlywood and latewood vessels with respect to diameter is not very great.

TAXA INVESTIGATED

The list of families with diagonal vessel aggregations compiled prior to the present study is as follows (list from Metcalfe and Chalk [1950, p. 1351]; also Record [1942] and Yatsenko-Khmelevsky [1954, p. 71–72]): Annonaceae, Araliaceae, Asclepiadaceae, Berberidaceae, Boraginaceae, Caesalpiniaceae, Calycanthaceae, Fagaceae, Leitneriaceae, Loganiaceae, Melastomataceae, Moraceae, Oleaceae, Papilionaceae, Rhamnaceae, Rosaceae, Rutaceae, Sapotaceae, Solanaceae, Thymeleaceae, and Ulmaceae. Caesalpiniaceae and Papilionaceae may be recognized (as they are in the present paper) as subfamilies of Fabaceae.

The list above appears different at first glance from the list given by Metcalfe and Chalk (1950, p. 1351) of families in which vasicentric tracheids are present. However, if the more recent and much larger list of families with vasicentric tracheids (Carlquist 1985) is consulted, only four of the families with diagonal vessel aggregations have not yet been reported also to have vasicentric tracheids: Annonaceae, Leitneriaceae, Melastomataceae, and Moraceae. For the purposes of the present investigation, Araliaceae is also of concern because of the genera mentioned by Metcalfe and Chalk (1950) in their textual account of Araliaceae as having diagonal vessel aggregations (*Acanthopanax*, *Aralia*, *Fatsia*, *Kalopanax*, *Pseudopanax*, and *Textoria*). Only one (*Pseudopanax*) was on my 1986 list of Araliaceae with vasicentric tracheids (my list also includes *Hedera* and *Tetrapanax*). The family Leitneriaceae consists of a single species. Annonaceae, Melastomataceae, and Moraceae are large families, but diagonal vessel aggregations have been reported only in a small number of genera: *Asimina* (Annonaceae); *Memecylon* and *Mouriri* (Melastomataceae); and *Broussonetia*, *Maclura* p.p., *Morus* p.p., and *Prainea* (Moraceae). The listing for Moraceae is based upon data from Record and Hess (1943).

The reverse kind of exception (taxa with vasicentric tracheids but with no diagonal or tangential vessel aggregation) does exist, and such instances are discussed below. No special investigation involving making new slides of woods of

these taxa was necessary because those materials were assembled for my 1985 review of vasicentric tracheids.

In the case of families that appear on both lists, the assumption has been made that the genera with diagonal vessel aggregations do all have vasicentric tracheids. This assumption proves to be justified in the instances known to me. However, one can also use as an example the extensive study by Cozzo (1950) on papilionate Fabaceae. Cozzo studied 89 species in 48 genera. Cozzo reports in detail about vessel arrangement ("ordenacion") and vasicentric tracheid presence or absence. The majority of genera studied by Cozzo have neither vasicentric tracheids nor any special grouping of vessels. Definite diagonal or tangential vessel aggregations and definite vasicentric tracheid presence are reported by Cozzo in the genera *Adesmia*, *Anarthrophyllum*, *Coronilla*, *Cytisus*, *Genista*, *Laburnum*, *Sarothamnus*, *Sophora*, *Spartium*, *Sutherlandia*, *Ulex*, and *Wisteria*. Weaker vessel grouping tendencies, combined with lesser degrees of vasicentric tracheid presence, are reported by Cozzo in *Amorpha*, *Caragana*, *Colutia*, *Glycyrrhiza*, *Indigofera*, *Pso-ralea*, *Robinia*, *Sesbania*, and *Virgilia*. Because transections are figured photographically for all genera by Cozzo, one can check on his vessel grouping designations. Cozzo did not prepare macerations, so his reports of degree of vasicentric tracheid abundance are not reliable for all genera. However, the correlation in Fabaceae seems clear. If one selects another large family in which only a small proportion of the species have vasicentric tracheids, Pittosporaceae, one also finds that all of the species reported to have vasicentric tracheids (Carlquist 1985) were shown to have diagonal aggregations of vessels (Carlquist 1981).

RESULTS

Annonaceae

The only species in which diagonal vessel aggregations have been reported is *Asimina triloba*. Investigation of my material (USW 8639, RSAw) of this species confirmed that small diagonal aggregations of vessels occur in latewood (but not in earlywood). These diagonal aggregations are really not much different from pore clusters, which are also present in this species. Very narrow vessels as well as vessels of medium diameter are present in large numbers in the latewood.

Araliaceae

Aralia spinosa L. (US 12014, RSAw) does not have either diagonal or tangential vessel aggregations in my interpretation, although radial multiples are present and latewood vessel groupings are large; no vasicentric tracheids were observed in macerations.

Fatsia japonica Decne. & Planch. (cult. Claremont) has larger vessel aggregations than appear at first glance: the many narrow vessels and vasicentric tracheids appear like libriform fibers in diameter and wall thickness, but their nature is revealed from pitting. Vessel grouping can be diagonal, as claimed by Metcalfe and Chalk (1950), or oriented radially or tangentially. *Fatsia japonica* matches *Hedera helix* L. (Carlquist 1985) in having rather abundant vasicentric tracheids.

Hedera helix (cult. Claremont) has appreciable numbers of vasicentric tracheids; it also characteristically has diagonal vessel aggregations.

Kalopanax ricinifolium Miq. (US 13363, RSAw) has prominent extensive di-

agonal to tangential vessel aggregations in all portions of growth rings. Vasicentric tracheids occur in small but appreciable numbers, and like those figured earlier for *Hedera* (Carlquist 1985) have wider diameters than do vasicentric tracheids in dicotyledons at large.

Pseudopanax lessonii (DC.) Koch (cult. former Vavra Estate of UCLA) has some diagonal vessel aggregations, but radial multiples are more common. Vasicentric tracheids occur in small but appreciable numbers.

Tetrapanax papyrifera Koch (cult. Claremont) has large pore multiples; a few of these form short diagonal bands. Vasicentric tracheids are present but not abundant.

Leitneriaceae

Leitneria floridana Chapm. (Carlquist 15639, RSAw) proves to have both tangential and diagonal bands of vessels (Fig. 1). It also has large numbers of vasicentric tracheids mixed with vessels (Fig. 2), although no worker has reported the vasicentric tracheids hitherto. The vasicentric tracheids are more numerous than the vessels themselves. Tangential vessel bands are somewhat more common than diagonal bands in my material, although direction varies greatly within a section.

Melastomataceae

Examination of sections of *Mouriri guianensis* Poir. (USw 6613, RSAw) reveals occasional vasicentric tracheids near each vessel; vessels are large and diffusely distributed in the wood. In *M. princeps* Naud. (USw 10745, RSAw), vessels are narrower, more numerous, and often aggregated into pore multiples some of which are oriented diagonally; vasicentric tracheids are occasionally adjacent to vessels. These findings are in accord with the results of Welle and Koek-Noorman (1981, p. 366), who report the presence of "tracheids" (not further designated as vasicentric) in the New World Melastomataceae in general: "Sporadically one or two tracheids were found in macerations. We have no indication that their presence is of any diagnostic or taxonomic value. Therefore their occurrence is not reported in the generic descriptions." The tracheids in my macerations of *Mouriri* are rather more numerous than "one or two," and are (as seen in sections) characteristically adjacent to vessels. The vasicentric tracheids are sufficiently numerous that they must have physiological significance.

Moraceae

Maclura pomifera L. ("UN 263," collector unknown, RSAw) has large tangential bands of vessels in latewood (Fig. 9). These latewood bands are composed of narrow vessels mixed with vasicentric tracheids. Vasicentric tracheids have not been reported previously for Moraceae, although Greguss (1959) did figure such a cell in his drawings of macerated wood cells of *Maclura pomifera*. *Morus alba* L. (ZTw 41, RSAw) has latewood pore clusters less well developed than are the vessel groupings of *Maclura pomifera*. In *Morus alba* pore clusters do not form long tangential lines in the wood. Most are tangentially oriented but some run diagonally (Fig. 8). My material of *Broussonetia papyrifera* Vent. (cult. Vavra Estate) contains little latewood, very likely because of the moist conditions in

cultivation. The latewood vessels correspond in grouping to those figured for *Morus alba* (Fig. 8).

CONCLUSIONS AND HYPOTHESIS

The present investigation shows that several families reported to have diagonal vessel aggregations but not reported to have vascentric tracheids do, in fact, have vascentric tracheids in appreciable to large numbers in the same genera in which diagonal vessel aggregations have been reported. Genera in this category include *Leitneria* (Leitneriaceae), *Mouriri* (Melastomataceae), and *Maclura* (Moraceae). In Araliaceae, also investigated because vascentric tracheids had not been reported in some genera found to have diagonal bands of vessels, vascentric tracheids were present in appreciable numbers in *Fatsia*, *Hedera*, *Kalopanax*, and *Pseudopanax*.

Taxa in which diagonal (or some other kind of) vessel groupings are so limited in size that they probably should not be cited as representing diagonal vessel aggregations proved to lack vascentric tracheids or to have them in such limited numbers that no physiological significance should be attributed. Species in this category include *Asimina triloba* (Annonaceae), *Aralia spinosa* (Araliaceae), and *Morus alba* (Moraceae). These species are not really exceptions to the concept that plants with diagonal vessel aggregations also have vascentric tracheids. Obviously in any evolutionary phenomenon that is occurring in numerous phylads (as is true of vascentric tracheid origin), there will be groups in transition. These transitions, rather than invalidating ideas about evolutionary phenomena, reinforce them. *Aralia*, *Asimina*, and *Morus* may be regarded as at the threshold of vascentric tracheid and diagonal vessel aggregation origin.

Two main questions need to be answered: (1) why do some phylads have vascentric tracheids but lack prominent diagonal vessel aggregations? and (2) what is the selective advantage of diagonal vessel aggregation, in particular, and types of vessel aggregation, in general, in taxa that have vascentric tracheids?

With respect to the first question, one can compare related taxa in all of which vascentric tracheids occur but in only some of which diagonal vessel aggregations are evident. Araliaceae, a family in which vascentric tracheid presence is incipient, is instructive in this regard. The three genera with more numerous vascentric tracheids and more prominent diagonal aggregations of vessels (*Fatsia*, *Hedera*, and *Kalopanax*) occur at the ecological limits of the family. *Hedera* is remarkably resistant to drought and frost. *Fatsia* occurs as far north (central Honshu: Ohwi 1965) as any woody evergreen araliad. *Kalopanax* is deciduous, but is montane and occurs in Hokkaido, Manchuria, and Sakhalin (Ohwi 1965), very likely the most northerly range for a deciduous tree araliad.

The species of *Pittosporum* with more abundant vascentric tracheids and clear diagonal vessel aggregation patterns occur in areas where unusual degrees (considering the range of the family) of cold (*P. tobira* (Thunb.) Ait. f., southern Japan; *P. divaricatum* Cockayne, alpine New Zealand) or drought (*P. phillyreoides* DC., Nullarbor Plain of Australia) can occur. However, a better source of evidence may be found in those large families in which vascentric tracheids are universal or nearly so.

In Sapotaceae, the most conspicuous and clearly defined diagonal vessel aggre-

gations are to be found in species from drier and cooler areas at the northern limits of the family: *Bumelia*, notably *B. lanuginosa* (Michx.) Pers. from as far north as Missouri (Kukachka 1978a); *Paralabatia*, from the West Indies (Kukachka 1980); and *Manilkara*, from Florida and the West Indies (Kukachka 1981a). This is also true in the Southern Hemisphere of the genera *Chloroluma* of Argentina and Paraguay (Kukachka 1978b) and *Gayella* of Chile (Kukachka 1981b).

The list of families in which diagonal bands of vessels are reported is likely to grow, and discrepancy between the two lists will surely lessen somewhat, although there very likely will always be more families on the vasicentric tracheid list than on the diagonal vessel aggregation list. The family Myrtaceae should certainly be added, since both Metcalfe and Chalk (1950) and Vliet and Baas (1984) report "oblique" patterns of vessels. The comments above on Pittosporaceae make addition of that family necessary. Illustrations by Moseley (1948) of wood transections of *Casuarina* show that Casuarinaceae must be included in the list of families with diagonal vessel aggregation. In Asteraceae, *Chrysothamnus* should be added (Carlquist and Hoekman 1985). Some species of *Artemisia*, such as *A. tridentata* Nutt., have prominent diagonal vessel aggregations. In these bands, vasicentric tracheids are not abundant, but very narrow vessel elements (many with only one perforation plate) are common. Very narrow vessels probably provide nearly the resistance to air embolism formation and spread conferred by vasicentric tracheids, and should not be overlooked in this regard. *Artemisia* is interesting in that it appears to represent an instance in which vasicentric tracheid origin is following, rather than preceding (as seems likely in most other instances, such as Sapotaceae), development of diagonal vessel aggregations.

The value of large aggregations of vessels in taxa that have vasicentric tracheids is suggested by ecological distribution of species with both features, as noted above for Araliaceae and Sapotaceae. A net increase in resistance to air embolism formation and spread by having both features rather than either feature alone is very likely achieved. One can imagine that the ultimate safety in a vessel-bearing dicotyledonous wood would be represented by species in which true tracheids form the groundmass of the axial xylem, as in many Rosaceae (e.g., *Cercocarpus*). True tracheids are regarded as relictually present in phylads with primitive wood, whereas vasicentric tracheids represent an innovation in phylads in which tracheids have been lost in favor of fiber-tracheids or libriform fibers (Carlquist 1986). In woods with true tracheids, minimal three-dimensional disruption of the conductive pathways would occur if any particular vessel is embolized by drought or frost. No matter which vessel is embolized, true tracheids adjacent to it presumably remain intact and continue conduction. The least safety is achieved in woods in which nonconductive imperforate tracheary elements (fiber-tracheids or libriform fibers) form the groundmass of the axial xylem and in which vessels are solitary. Should any one vessel embolize, a portion of the three-dimensional conductive pattern is lost. Grouping of vessels in woods with a nonconductive groundmass increases the safety by offering redundancy: should one vessel in a group embolize, others in the group may remain intact, essentially preserving the conductive pathway.

Vasicentric tracheids offer an alternative to vessel grouping. Vasicentric tracheids are theoretically superior to vessel grouping in that vasicentric tracheids

are more resistant to embolism formation and spread than are vessel elements. Vasicentric tracheids lack perforations and thereby air bubbles theoretically cannot spread from one tracheid to another. In fact, in a vessel grouping, if all vessels are of the same diameter, all ought to embolize at about the same time. If a vessel is surrounded by vasicentric tracheids, the vessel would embolize well in advance of the vasicentric tracheids (which might remain intact indefinitely). Narrower diameter of vasicentric tracheids could also account for this (see below). Thus, a secondary conducting system, intact until all or most vessels are embolized, is available when vasicentric tracheids are present. Vasicentric tracheids do have the potential disadvantage of conducting a given water volume more slowly than vessel elements, but under conditions when vessels are embolized, slow rates of conduction are likely to prevail. One should remember that narrow vessels may potentially offer safety if they occur intermixed with wider ones, since they ought to embolize later than the wider ones. Several authors have presented evidence that narrow vessels embolize less readily than wider ones (Huber 1935; Zimmermann and Brown 1971; Ellmore and Ewers 1985).

A diagonally or radially arranged group of vessels in contact with each other has the potential advantage that should older vessels in such a file embolize, intact newly formed vessels can supplant the older ones, maintaining the three-dimensional conductive pathways intact in time and space.

When vasicentric tracheids are present in addition to vessels in diagonal or radial aggregations, the advantages propounded in the two preceding paragraphs would presumably be combined. However, radial vessel groupings do not intersect each other, whereas there is a great likelihood that adjacent diagonal vessel aggregations will intersect, because the diagonal slant varies and often adjacent bands run almost perpendicular to each other. Intersecting diagonal bands create an effectively continuous system of conductive cells around the entire stem, one which is unlikely to be disabled because vasicentric tracheids in those bands would represent a second and greater degree of safety than the vessels. Strands (appearing as islands in transection) of nonconductive cells (fiber-tracheids, libriform fibers) are enclosed within the matrix formed by intersecting bands of vessels and vasicentric tracheids but do not disrupt that matrix.

Thus, a species with vasicentric tracheids and vessels in intersecting diagonal bands represents an evolutionary re-creation of the ultimate safety present in those primitive woods in which vessels are scattered within a background of true tracheids. In either of these two "ultimate safety" systems one can imagine, for example, destruction at a given point on a stem of seven-eighths of the conducting cells of a stem; but because of the presence of tracheids, the conductive pathways can fan out above and below the damaged area. In a system without tracheids adjacent to vessels, this can occur only to the extent there are interconnections among vessels, and at best that would be a less effective way of rerouting conduction, because interconnections might be few and the "second line of resistance" to embolism represented by tracheids would not parallel the vessels at all points.

Tangential aggregations of vessels mixed with vasicentric tracheids (ulmiform patterns) potentially ought not to confer such a great degree of safety. If a cambium lays down libriform fibers between one tangential vessel band and a succeeding vessel band, water could not be conveyed from one band to the other unless in three dimensions the bands form a reticulate pattern, as indeed they may. Tran-

sections may be misleading in this respect. Moreover, if one looks at tangential bands, as shown here for *Maclura* (Fig. 9) or illustrated by Ellmore and Ewers (1985) for *Ulmus*, one sees that they often are not perfectly tangential but are diagonally oriented to varying degrees. Tangential bands of vessels without much three-dimensional intersection or diagonal orientation tendency very likely are rare in dicotyledons, since they would represent a conformation less optimal than that of diagonal vessel aggregations.

LITERATURE CITED

- Carlquist, S. 1981. Wood anatomy of Pittosporaceae. *Allertonia* 2:191–246.
- . 1983. Wood anatomy of Calycanthaceae: ecological and systematic implications. *Aliso* 10: 427–441.
- . 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 woody flora of southern California and similar regions; review of vasicentric tracheids. *Aliso* 11:37–68.
- . 1986. Terminology of imperforate tracheary elements. *IAWA Bull.*, n.s. 7:75–81.
- , and D. A. Hoekman. 1985. Ecological wood anatomy of southern Californian woody plants. *IAWA Bull.*, n.s. 6:319–347.
- Cozzo, D. 1950. Anatomía del leño secundario de las leguminosas papilionoideas Argentinas silvestres y cultivadas. *Rev. Inst. Nac. Invest. Cienc. Nat., Ciencias Botánicas* 1:223–361.
- Ellmore, G. S., and F. W. Ewers. 1985. Hydraulic conductivity in trunk xylem of elm, *Ulmus americana*. *IAWA Bull.*, n.s. 6:303–307.
- Greguss, P. 1959. *Holzanatomie der Europäischen Hölzer und Sträucher*. Akademiai Kiadó, Budapest. 330 p.
- Huber, B. 1935. Die physiologische Bedeutung der Ring- und Zerstreutporigkeit. *Ber. Deutsch. Bot. Ges.* 53:711–719.
- IAWA Committee on Nomenclature. 1964. Multilingual glossary of terms used in describing woods. Verlagsanstalt Buchdruckerei Konkordia, Winterthur (Switzerland). 138 p.
- Kukachka, B. F. 1978a. Wood anatomy of the neotropical Sapotaceae. I. *Bumelia*. *For. Prod. Lab. Res. Pap. FPL* 325:1–9.
- . 1978b. Wood anatomy of the neotropical Sapotaceae. VI. *Chloroluma*. *For. Prod. Lab. Res. Pap. FPL* 330:1–5.
- . 1980. Wood anatomy of the neotropical Sapotaceae. XVI. *Paralabatia*. *For. Prod. Lab. Res. Pap. FPL* 360:1–5.
- . 1981a. Wood anatomy of the neotropical Sapotaceae. XX. *Manilkara*. *For. Prod. Lab. Res. Pap. FPL* 371:1–13.
- . 1981b. Wood anatomy of the neotropical Sapotaceae. XXIII. *Gayella*. *For. Prod. Lab. Res. Pap. FPL* 374:1–3.
- Metcalfe, C. R., and L. Chalk. 1950. *Anatomy of the dicotyledons*. Clarendon Press, Oxford. 1500 p.
- Moseley, M. F. 1948. Comparative anatomy and phylogeny of the Casuarinaceae. *Bot. Gaz. (Crawfordsville)* 110:231–280.
- Ohwi, J. 1965. *Flora of Japan* (ed. by F. G. Meyer and E. H. Walker). Smithsonian Institution, Washington, D.C. 1067 p.
- Patel, R. 1978. Wood anatomy of the dicotyledons indigenous to New Zealand. 11. Oleaceae. *New Zealand J. Bot.* 16:1–6.
- Record, S. J. 1942. Keys to American woods. *Trop. Woods* 72:19–35.
- , and R. W. Hess. 1943. *Timbers of the new world*. Yale Univ. Press, New Haven. 640 p.
- Vliet, G. J. C. M. van, and P. Baas. 1984. Wood anatomy and classification of the Myrtales. *Ann. Missouri Bot. Gard.* 71:783–800.
- Welle, B. J. H. ter, and J. Koek-Noorman. 1981. Wood anatomy of the neotropical Melastomataceae. *Blumea* 27:335–394.
- Yatsenko-Khmelevsky, A. A. 1954. Research and methods of anatomical investigation of woody plants (in Russian). *Isdatel'stvo Akademii Nauk SSR, Moscow*. 337 p.
- Zimmermann, M. H., and C. L. Brown. 1971. *Trees. Structure and function*. Springer-Verlag, New York. 336 p.