Aliso: A Journal of Systematic and Floristic Botany

Volume 10 | Issue 4

Article 3

1984

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Carlquist, Sherwin (1984) "Vessel Grouping in Dicotyledon Wood," *Aliso: A Journal of Systematic and Floristic Botany*: Vol. 10: Iss. 4, Article 3.

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VESSEL GROUPING IN DICOTYLEDON WOOD:
SIGNIFICANCE AND RELATIONSHIP TO
IMPERFORATE TRACHEARY ELEMENTS

Sherwin Carlquist

Abstract.—A hitherto unappreciated correlation exists between nature of vessel grouping and nature of imperforate tracheary elements in wood of dicotyledons at large: families and genera with true tracheids (large fully bordered pits common on both radial and tangential walls) have solitary vessels. Presence of true tracheids as a subsidiary conductive system is hypothesized to render vessel grouping a superfluous adaptation. Vessel grouping does occur to various degrees in taxa with fiber-tracheids or libriform fibers; the degree of grouping is related to likelihood or seriousness of vessel failure by air embolisms because of either drought or frost. Grouping of vessels is regarded as a way of providing alternate conduits whereby water can be carried in the same pathways in case one or several vessels in a group are incapacitated by air embolisms. Presence of vascular tracheids, if sufficiently abundant, is held to be correlated with smaller degree of vessel grouping because vascular tracheids can form a subsidiary conductive system; small numbers of vascular tracheids do not affect vessel grouping patterns. Species which possess vasicentric tracheids possess a subsidiary conductive system ideally located around vessels and have solitary vessels or else (if vasicentric tracheids are less common) a low degree of vessel grouping. Species with very large vessels at the beginning of growth rings tend to have little grouping in the earlywood vessels but more grouping in latewood vessels; this dimorphism is held to relate to enhanced safety of latewood vessels, since earlywood vessels have little safety and the latewood is thereby the wood portion where safety mechanisms are concentrated. Fiber-tracheids do not have sufficient conductive capabilities to form a subsidiary conductive system; borders on pits of fiber-tracheids are rapidly lost during evolution, and such loss generally precedes appearance of septate or nucleated conditions or is simultaneous with it. Relative selective value of the various vessel grouping types (clusters, radial multiples, diagonal bands, tangential bands) as well as of larger aggregations remains a topic for more investigation, as does significance of grouping of primary xylem vessels.

INTRODUCTION

Transections of some dicotyledon woods reveal vessels distributed in scattered fashion, few in contact with each other. In other woods, groups of

vessels ("group" is defined here as vessels in contact, not merely close) are characteristically present. Little attention has been devoted to reasons for this diversity, and for why there should be various types of vessel groupings. Vessels may be grouped in clusters (groups about as wide radially as tangentially), radial multiples, or in tangential bands. Vessel groups, in turn, may appear to form larger patterns (termed aggregations here) which extend across rays and even growth rings (where present); in these larger aggregations, not all vessels are actually in contact with each other.

Questions corresponding to the above patterns need to be answered. (1) Why are vessels characteristically grouped in some families of dicotyledons but not at all in other families or genera? This question will be addressed on the basis of comparative studies and morphological data, and is the prime focus of the present study. (2) In those families in which vessel grouping occurs, what governs the degree of vessel grouping? The answer to this question proves to be related to the answer to the first question. However, in terms of selective factors the number of vessels per group in these families is highest in driest areas, lowest in the most mesic areas (Carlquist 1966). This can also be expressed in terms of more vessels per group in temperate areas than in tropical zones (Carlquist 1966; Baas 1973; Baas et al. 1983). (3) Why are vessels grouped in more than one way (clusters, radial multiples, diagonal bands, tangential bands)? While the data of the present study do not apply directly to the solution of this question, some preliminary comments are in order. (4) Why are vessels large in diameter more likely to be solitary than smaller vessels? (5) Do larger aggregations of vessels bear any relationship to smaller groups? If so, what explanations can be offered for this phenomenon?

In dealing with these questions, the present study examines the role of imperforate tracheary elements. The term "imperforate tracheary element" in this paper includes tracheids, fiber-tracheids, and libriform fibers. I realize that the apparently nonconductive nature of libriform fibers would lead some workers to prefer that libriform fibers not be included under the concept of imperforate tracheary elements. At the outset of this discussion, I must stress that the nature of imperforate tracheary elements in particular taxa is the basis for interpretations of occurrence or nonoccurrence of vessel grouping. The central hypothesis of the present paper is that imperforate tracheary elements, if well adapted for conduction (true tracheids, vasicentric tracheids, vascular tracheids) offer great safety to the conductive process. If a vessel in a tracheid-bearing wood is disabled, the conductive process can be transferred to nearby tracheids. This transfer cannot occur in woods in which fiber-tracheids and libriform fibers have been evolved as a mechanical system and no tracheids are present. In these more specialized woods, grouping of vessels offers another kind of safety, one in which disabling of any vessel is

rendered less serious because the conductive process can be transferred to an adjacent vessel.

MATERIALS AND METHODS

The genesis of this paper lies in study of wood of numerous dicotyledon families, some of which show vessel grouping whereas others do not. Integral to this survey is the wood slide collection at the Rancho Santa Ana Botanic Garden, a collection which incorporates a general survey of dicotyledons as well as slides developed for particular monographs. However, any hypothesis concerned with dicotyledons as a whole must draw data not from selected families but from all families. The data of Metcalfe and Chalk (1950) have been used as a starting point. Metcalfe and Chalk often do not use the term "tracheid"; they prefer "fibre" qualified with a description of size of pits, whether they are bordered or not, whether they are on all faces, and whether they are dense or sparse. Metcalfe and Chalk, despite the enormity of data contained in that compendium, does not offer information on wood of all families. Papers subsequent to Metcalfe and Chalk (1950) have been utilized. These include Ayensu and Stern (1964), Baas (1973), Baas and Zweypfenning (1979), Bailey and Smith (1942), Bailey and Swamy (1949), Baretta-Kuipers (1976), Carlquist (1960, 1966, 1969, 1975, 1976a, 1976b, 1976c, 1977a, 1977b, 1978a, 1978b, 1980a, 1981a, 1981b, 1981c, 1981d, 1981e, 1982a, 1982b, 1982c, 1983a, 1984a, 1984b, 1984c, Carlquist and DeBuhr (1977), Carlquist and Eckhart (1984), Carlquist et al. (1983, 1984), Carpenter and Dickison (1976), Dickison (1967, 1977, 1980, 1981), Dickison and Baas (1977), Dickison et al. (1978), Gibson (1973), Giebel and Dickison (1976), Gottwald (1983), Koek-Noorman and Puff (1983), Koek-Noorman and Rijkvorsel (1983), Outer and Vennendaal (1980, 1983), Parameswaran and Conrad (1982), Quirk (1980), Richter (1981), Stern et al. (1969), Styer and Stern (1979), Vliet et al. (1981).

New data on vessel grouping and on imperforate tracheary element type were needed for some families not covered by the above sources. Using the wood slide collection at the Rancho Santa Ana Botanic Garden, I made original observations on the following families: Aextoxicaceae, Aitoniaceae, Crassulaceae, Frankeniaceae, Gentianaceae, Greyiaceae, Gyrostemonaceae, Loasaceae, Malvaceae, Marcgraviaceae, Martyniaceae, Misodendraceae, Montiniaceae, Myricaceae, Pedaliaceae, Sarcolaenaceae, Scyphostegiaceae, Sphenostemonaceae, Stackhousiaceae, Stegnospermataceae, and Tovariaceae. The family names used in the present paper do not correspond to those used in any particular phylogenetic system, nor do they signify that segregate families should be recognized. Segregate families are used merely as a way of giving data on a larger number of taxa.

My data on some families differed somewhat from those of Metcalfe and

Chalk (1950). I found woods of *Marcgravia rectiflora* Triana & Planchon and *Norantea guianensis* Aublet (Marcgraviaceae) to have libriform fibers (with unusual pit shape, to be sure) rather than fiber-tracheids. In Myricaceae, *Gale hartwegii* Cheval and *G. palustris* Cheval proved to have small bordered pits on radial walls of fiber-tracheids rather than simple pits on imperforate tracheary elements as reported for *G. palustris* (as *Myrica gale* L.) by Metcalfe and Chalk. Bordered pits are reported here for imperforate tracheary elements of Malvaceae (*Hibiscus*, *Lavatera*); Webber (1934) had claimed bordered pits on tracheary elements (which should thereby be termed fiber-tracheids) in *Pavonia* and *Wercklea*, and doubtless other genera of Malvaceae will prove to have small borders on pits of fiber-tracheids. Although I reported tracheids in Gyrostemonaceae earlier (1978a), I now feel that these cells should be termed fiber-tracheids because pits are small and sparse compared with those of tracheids of families in the first list below. Baas (1973) is correct in saying that fiber-tracheids occur in *Ilex*, in my opinion; his criteria also include pit diameter and sparseness.

The term "tracheid" here connotes only "true tracheids," and vascular tracheids and vasicentric tracheids are not included in that category. Metcalfe and Chalk typically do not recognize the term tracheid; they often refer to "fibres" with abundant bordered pits. I am using the term tracheid for imperforate cells in which pits approach lateral wall pitting of vessels in pit density, pit diameter, and degree of border presence. Stages transitional between tracheids and fiber-tracheids are difficult to define, and the listings below (aside from errors they may contain) would not be exactly the same as those compiled by others.

Vessel grouping can be calculated in various fashions. Although various authors have used the percentage of vessels which are solitary, the number of vessels per group is preferred here, if only because it can express sensitively various degrees of grouping in a family in which vessels are mostly grouped. Number of vessels per group, for example, can markedly differentiate among species of *Olearia* (Fig. 14–16). No matter which measure is utilized, dimorphism in vessel grouping (e.g., solitary vessels in earlywood versus grouping in latewood, as in *Ulmus americana* L., Fig. 13) should be mentioned. In my papers, a solitary vessel counts as "1," a pair of vessels as "2," etc., and these figures are averaged. A wood in which solitary vessels and pairs of vessels are equal in number as seen in transection would thus have a mean figure of 1.5 for number of vessels per group.

Collections cited in legends of plates are located in the herbarium of the Rancho Santa Ana Botanic Garden unless otherwise indicated.

DATA SUMMATION

LIST 1. Families in which vessels are solitary (in pairs only by chance, most apparent pairs actually are overlapping ends of vessel elements as seen

in transection) and in which tracheids occur include: Actinidiaceae, Aextoxicaceae, Aristolochiaceae (part), Balanitaceae, Betulaceae (part), Bruniaceae, Buxaceae, Byblidaceae, Canellaceae, Caprifoliaceae (excluding Sambucaceae), Casuarinaceae, Cephalotaceae, Chrysobalanaceae, Clethraceae, Columelliaceae, Convolvulaceae, Cornaceae, Crossosomataceae, Daphniphyllaceae, Desfontainiaceae, Diclidanthaceae, Didymeleaceae, Dilleniaceae, Dioncophyllaceae, Dipsacaceae, Elatinaceae, Elaeagnaceae, Empetraceae, Epacridaceae, Escalloniaceae, Eucommiaceae, Eucryphiaceae, Eupteleaceae, Garryaceae, Gomortegaceae, Gonostylaceae, Goodeniaceae, Goupiaceae, Grubbiaceae, Hamamelidaceae (part), Humiriaceae, Hydrangeaceae, Hypericaceae, Illiciaceae, Koerberliniaceae, Krameriaceae, Lardizabalaceae (part), Linaceae, Medusagynaceae, Menispermaceae, Myrothamnaceae, Nepenthaceae, Oncothecaceae, Paracryphiaceae, Penaeaceae, Pentaphylacaceae, Phellinaceae, Polygalaceae, Quinaceae, Sarracenaceae, Saurauaceae, Schisandraceae, Simmondsiaceae, Sphaerosepalaceae, Sphenostemonaceae, Stachyuraceae, Stackhousiaceae, Staphyleaceae, Stegnospermataceae, Stilbaceae, Strasburgeriaceae, Symplocaceae, Theaceae, Trigonaceae.

LIST 2. Families in which vessels are solitary or grouped, and in which fiber-tracheids are present as the imperforate tracheary element type. Fiber-tracheids are defined as having pits smaller and sparser than those of tracheids, with tendencies toward reduction in pit borders (outline of pit aperture frequently less in diameter than the length of an elliptical pit aperture). Aceraceae (part), Aitoniaceae, Akaniaceae, Annonaceae, Aquifoliaceae, Aristolochiaceae (part), Austrobaileyaceae, Balanopaceae, Bataceae, Betulaceae (part), Bixaceae, Brassicaceae, Brunelliaceae, Calycanthaceae, Caparaceae, Caryocaraceae (part), Cercidiphyllaceae, Chloanthaceae, Cochlospermaceae, Combretaceae (part), Corylaceae, Cunoniaceae, Cyrillaceae, Degeneriaceae, Dichapetalaceae, Duckeodendraceae, Elaeocarpaceae (part), Erythroxylaceae, Fouquieriaceae, Grossulariaceae, Gyrocarpaceae, Hamamelidaceae (part), Himantandraceae, Ixonanthaceae, Lardizabalaceae (part), Lauraceae (part), Loasaceae, Loganiaceae (part), Lythraceae, Malvaceae (part), Meliaceae (part), Montiniaceae, Nyssaceae, Pittosporaceae (part), Platanaaceae, Ranunculaceae (part), Scrophulariaceae (part), Simaroubaceae (part), Stylidiaceae, Styracaceae, Turneraceae, Zygophyllaceae. *Duckeodendron cestroides* Kuhlman. (Fig. 5-7) is representative of this group.

LIST 3. Families in which vessels range from solitary to grouped, and in which libriform fibers are the imperforate tracheary element type present: Acanthaceae, Aceraceae (part), Amaranthaceae, Anacardiaceae, Bignoniaceae, Bombacaceae, Burseraceae, Cactaceae, Campanulaceae, Capparaceae (part), Caryocaraceae (part), Combretaceae (part), Connaraceae, Coriariaceae, Datisceae, Didiereaceae, Elaeocarpaceae (part), Fabaceae, Gentianaceae, Geraniaceae, Greyiaceae, Hernandiaceae, Julianiaceae, Lactoridaceae, Lamiaceae, Lauraceae (part), Lobeliaceae, Malvaceae (part),

Marcgraviaceae, Martyniaceae, Melianthaceae, Misodendraceae, Myristicaceae, Octoknemaceae, Oliniaceae, Onagraceae, Oxalidaceae, Papaveraceae, Pedaliaceae, Piperaceae, Pittosporaceae (part), Plantaginaceae, Plumbaginaceae, Primulaceae, Ranunculaceae (part), Sabiaceae, Salicaceae, Scrophulariaceae (part), Scyphostegiaceae, Scytotepalaceae, Simaroubaceae (part), Siphonodontaceae, Sonneratiaceae, Sterculiaceae, Tetrameristaceae, Tovariaceae, Tremandraceae, Ulmaceae, Urticaceae, Verbenaceae, Vochysiaceae.

LIST 4. Families in which vessels are nearly always grouped, and in which libriform fibers are present as the imperforate tracheary element type. Families in this category have an average number of vessels per group of 2.0 or above. Aizoaceae, Alangiaceae, Apiaceae, Araliaceae, Asteraceae, Avicenniaceae, Begoniaceae, Berberidaceae, Cannabaceae, Chenopodiaceae, Cneoraceae, Corynocarpaceae, Crassulaceae, Eupomatiaceae, Frankeniaceae, Globulariaceae, Halophytaceae, Hippocastanaceae, Lacistemaceae, Leitneriaceae, Loganiaceae (part), Malesherbiaceae, Malpighiaceae, Meliaceae (part), Moringaceae, Myoporaceae, Myrsinaceae, Nyctaginaceae, Pittosporaceae (part), Portulacaceae, Punicaceae, Resedaceae, Rhamnaceae, Rutaceae, Salvadoraceae, Sambucaceae, Sapindaceae, Stylobasiaceae, Surianiaceae, Tamaricaceae, Tiliaceae, Tremandraceae, Valerianaceae, Viscaceae, Vitaceae.

LIST 5. Families in which vessels range from solitary to grouped and in which imperforate tracheary elements range from tracheids to libriform fibers. The families in this list, if studied genus by genus, could be assigned to the listings above. Thus, this category merely represents a provisional compilation of large and mostly incompletely known families; however, some of them (Celastraceae, Myrtaceae) are known to have tracheids, so that certain genera could be assigned even to the first of the lists above. Asclepiadaceae, Boraginaceae, Caryophyllaceae, Celastraceae, Chloranthaceae, Ebenaceae, Ericaceae, Euphorbiaceae, Fagaceae, Flacourtiaceae, Gesneriaceae, Hypericaceae, Juglandaceae, Lecythidaceae, Loranthaceae, Magnoliaceae, Melastomaceae, Monimiaceae, Moraceae, Myrtaceae, Ochnaceae, Oleaceae, Passifloraceae, Phytolaccaceae, Proteaceae, Rubiaceae, Sapotaceae, Thymelaeaceae, Violaceae.

LIST 6. Families which can be broken into two parts: genera which have solitary vessels accompanied by tracheids, and genera which have grouped vessels accompanied by fiber-tracheids or libriform fibers. Thus, within a single family one can find a contrast between these conditions, and no genera with tracheids in which the vessels are grouped to any appreciable degree. In the listing below, the genera cited have solitary vessels plus tracheids, the remainder of each family the alternative condition: Apocynaceae (Plumeriaceae), Cistaceae (all except *Helianthemum* sect. *Eriocarpum*), Clusiaceae (excluding Hypericaceae, the "Group B" of Metcalfe and Chalk: *Calophyllum*, *Kayea*, *Mammea*, *Mesua*), Dipterocarpaceae (*Anisoptera*, *Cotylelob-*

Fig. 1-4. Wood sections of Polemoniaceae.—1-2. *Eriastrum densifolium* subsp. *mohavense* (Michener 3954).—1. Transection, showing solitary vessels.—2. Tangential section; bordered pits on tracheids evident.—3-4. *Huthia caerulea* (Eyerdam & Beetle 2240, UC).—3. Transection; vessels are in radial multiples.—4. Tangential section, showing simple pits in libriform fibers. (Fig. 1, 3, magnification scale above Fig. 1 [finest divisions = 10 μ m]. Fig. 2, 4, magnification scale above Fig. 2 [divisions = 10 μ m].)

ium, *Dipterocarpus*, *Dryobalanops*, *Marquesia*, *Monotes*, *Upuna*, and *Vatica*), *Hydrophyllaceae* (*Eriodictyon*, *Wigandia*), *Icacinaceae* (genera with scalariform perforation plates plus *Cantleya*), *Linaceae* (genera other than *Lepidobotrys*), *Myricaceae* (genera other than *Gale*), *Olacaceae* (*Heisteria*, *Liriosma*, *Ongokea*, *Phlebocalymma*, some species of *Ximenia*), *Opiliaceae* (all except *Lepionurus*), *Polemoniaceae* (*Eriastrum*, *Leptodactylon*, and *Phlox*), *Rhizophoraceae* (*Macariseae*: *Anopyxis*, *Blepharistemma*, *Cassipourea*, *Macaraisia*, and *Sterigmapetalum*), *Rosaceae* (all except *Prunoideae* and a scattering of species in other genera), *Santalaceae* ("Group A" of Metcalfe and Chalk: *Eucarya*, *Exocarpus*, *Osyris*, and *Santalum*; both tracheids and vasicentric tracheids may prove to be present), *Solanaceae* (*Fabiana*, a few species in other genera). *Zygophyllaceae* have been excluded from this list by virtue of this recognition of *Balanitaceae* (Parameswaran and Conrad 1982). Examples from this list are illustrated in the case of *Polemoniaceae*, in which *Eriastrum densifolium* (Benth.) Mason subsp. *mohavense* (Craig) Mason (Fig. 1-2) has solitary vessels plus tracheids whereas *Huthia caerulea* Brand (Fig. 3-4) has grouped vessels accompanied by libriform fibers. Exceptions of a minor sort may be found in the tracheid-bearing *Polemoniaceae*, in which the number of vessels per group can range from 1.2 to 1.4 or occasionally even higher (Carlquist et al. 1984). One reason for this slightly elevated figure for grouping is that earlywood vessels can be relatively large and numerous, considerably scarcer in latewood, so that chances of contact in earlywood are raised. In other species of tracheid-bearing *Polemoniaceae*, number of vessels per mm² is unusually high, so that grouping inevitably occurs to a greater extent than it would if vessels were fewer per unit transection. Thus these *Polemoniaceae* do not really constitute an exception to the central hypothesis of this paper.

DISCUSSION AND CONCLUSIONS

This review of vessel grouping in dicotyledon woods and the types of imperforate tracheary elements which occur in particular woods reveals correlations which may be expressed in a series of statements and hypotheses.

1. *If tracheids with fully bordered pits which are rather large, abundant, and present on both radial and tangential walls of tracheids, occur in wood of a dicotyledon, the vessels in that species are solitary.* This correlation is clear from the first list, the sixth list, and the fact that there are no taxa in which typical tracheids occur and in which vessels are also grouped. If the families in the fifth list were analyzed genus by genus, the same pattern would very likely emerge. The explanation for lack of vessel groupings in species with typical tracheids appears to be that vessel grouping represents a means of increasing safety in a wood where no subsidiary conducting system (tracheids) is present. If tracheids are present in a species, the presence of a

subsidiary conductive system thereby evidently reduces the selective value of vessel grouping to virtually nil.

2. *Fiber-tracheids do not constitute a subsidiary conductive system effective enough to forestall the evolution of vessel grouping.* The second of the lists above shows that in groups in which fiber-tracheids occur, some degree of vessel grouping may be present, as illustrated by *Duckeodendron cestroides* (Fig. 5-7). If fiber-tracheids represent poor conductive systems, then grouping of vessels becomes a feature of selective value. In case of failure of a vessel the water column of which is under high tension, adjacent vessels can take over the conductive function with minimal rerouting of the conductive pattern. In *Ilex*, Baas (1973) has designated the imperforate tracheary elements as fiber-tracheids; he is correct in this interpretation, in my opinion. In *Ilex*, degrees of vessel grouping occur with relation to latitude: more numerous vessels per group occur in *Ilex* of temperate latitudes (Baas 1973). Presumably vessel grouping in the temperate species represents greater likelihood of vessel failure, perhaps because of freezing; vessel failure because of drought seems unlikely because *Ilex* is not characteristically found in dry regions.

Fiber-tracheids do not appear to represent a class of cells which are optimal in selective value. The conductive value of tracheids and the mechanical value of libriform fibers, respectively, can be assumed to be optimal. If these are correct assumptions, fiber-tracheid occurrence would represent transitions between these optimal conditions. Fiber-tracheids do appear relatively infrequent compared to tracheids and libriform fibers, as the above lists suggest, and one may hypothesize that they represent an unstable transitional form.

3. *In families in which libriform fibers are the imperforate tracheary element type, vessels are never entirely solitary, but may range from solitary to grouped with the degree of grouping related to ecology.* The reader may wonder why, if vessels are solitary or essentially so in species with tracheids, there are woods in which libriform fibers are the imperforate tracheary element type and in which little grouping occurs. The answer appears to lie with adaptation of wood to drought or (in the case of freezing) physiological drought. Species with libriform fibers in highly mesic regimes probably experience little or no selection for grouped vessels. This would account for the species in the third list in which less grouping occurs. The families in that list would benefit from analysis of the ecological adaptations of species with relation to the range in grouping.

In some families in which libriform fibers occur, vessels are characteristically grouped and rarely solitary. These families are given in the fourth list above. The high average grouping in these families denotes they have a greater degree of safety: adjacence of vessels as a means of retaining conductive pathways even if some vessels are blocked by air embolisms seems present

Fig. 5-9. Wood sections of Duckeodendraceae and Ericaceae.—5-7. *Duckeodendron cestroides* (Darrah 431).—5. Transection, showing grouped vessels.—6. Radial section; pits on radial walls of fiber-tracheids are few and sparse.—7. Tangential section, showing absence of pits on tangential walls of fiber-tracheids.—8-9. *Arctostaphylos auriculata* (Everett 24549).—8. Transection; most vessels are solitary.—9. Portion of transection to show earlywood with

at least to some degree. Average number of vessels per group in these families exceeds 2.0. Asteraceae is typical of these families; the average number of vessels per group in that family is 3.62 (Carlquist 1966). The average figure for mesic species is 3.04, whereas that for species in dry areas (ca. 20–50 cm of rain per year) is 5.20, and that for desert species (below 25 cm of rainfall per year) is 8.37. The number of vessels per group in tropical Asteraceae is 2.64, but the figure rises to 5.68 in temperate species (Carlquist 1966). The higher figure is presumably a response to greater probability of vessel failure through drought or freezing in temperate latitudes. This phenomenon is particularly clear in individual genera, and is well illustrated by the genus *Olearia* (Fig. 14–16). Although vessels in *O. argophylla* F. Muell. look mostly solitary (Fig. 14), in fact the number per group in five collections of that species falls no lower than 2.1 (Carlquist 1960). *Olearia argophylla* grows in highly mesic areas: along streams and in wet gulches in Tasmania, Victoria, and New South Wales, Australia. Vessel grouping is much higher in a widespread species of open scrub areas of New Zealand, *O. avicenniaefolia* Hook. f. (Fig. 15). *Olearia muelleri* Benth. (Fig. 16) has an almost infinite number of vessels per group, and occupies excessively dry areas: limestone flats from interior Victoria to the Nullarbor Plain of Western Australia, where soil overlying the limestone is very thin and water availability is low much of the year. Numerous other examples could be cited. Elevation of number of vessels per group with increasing aridity or cold offers the opportunity for failure of many vessels without disruption of the conductive pathways (three-dimensional pattern of vessels in the wood), so that survival of only a few intact vessels in each group could suffice to maintain water supply to the leaves. If vessel groups were smaller and all vessels of a group failed, water would have to be rerouted somehow if the conductive system were to stay intact. Where libriform fibers are present, rerouting conduction via essentially nonconductive cells (the libriform fibers) is not possible to any appreciable degree, so vessel grouping is the only form of safety available to avoid rerouting. Tracheids, on the other hand, not only form a subsidiary conductive system in the stem so that rerouting of the major pathways is unnecessary, they interconnect vessels laterally in the stem so that alternative pathways are available at all times.

Superficial observation of wood transections suggests that vessels may not be arranged randomly: contacts between vessels in a species with solitary vessels are fewer than one would expect, for if vessels were arranged randomly, a small but steady proportion of vessels in such a species should be

← vessels above; vascular tracheids (pits occluded by deposits) accompany vessels in latewood, below. (Fig. 5, 8, magnification scale above Fig. 1. Fig. 6, 7, 9, magnification scale above Fig. 2.)

Fig. 10-13. Wood transections of Fagaceae and Ulmaceae.—10. *Lithocarpus densiflora* (Balls 23862); vessels solitary, scattered.—11. *Quercus rubra* (unvouchered); a margin of a growth ring with earlywood above; all vessels surrounded by vasicentric tracheids; libriform fibers appear as dark areas.—12. *Nothofagus antarctica* (unvouchered); vessels are in radial multiples.—13. *Ulmus americana* (unvouchered); earlywood with many vessels solitary, above; vessels grouped in tangential bands in latewood. (Fig. 10-13, magnification scale above Fig. 1.)

in contact with other vessels. Study is needed to see whether vessels in species with solitary vessels are arranged in a random or nonrandom fashion. In either case, one might hypothesize, however, that selection for grouping must have occurred at some points in the phylads with appreciable (e.g., nonrandom) grouping.

4. *Presence of vascular tracheids, much like the presence of true tracheids as the imperforate tracheary element type, may be correlated with lowered number of vessels per group, but a lowered number per group should be expected only in the immediate vicinity of the vascular tracheids and only if vascular tracheids are quite numerous.* Low number of vessels per group is evident in *Arctostaphylos auriculata* Eastw. (Fig. 8–9). In this, as in other species of *Arctostaphylos*, earlywood consists of vessels plus libriform fibers, whereas latewood (Fig. 9, below, indicated by dark contents in the pit cavities) consists of vessels plus vascular tracheids. In this species of *Arctostaphylos* tracheids appear to be confined to latewood and thereby to be vascular tracheids; however, some Ericaceae may, in fact, have vasicentric tracheids (e.g., *Arbutus*), although Metcalfe and Chalk (1950, 1983) do not list that family as having vasicentric tracheids. Lowering of number of vessels per group with relation to vascular tracheids was also noticed in *Malesherbia* (Carlquist 1984c). Four of the five species of *Malesherbia* studied had an average of 2.2 vessels per group. In *M. densiflora* Phil. presence of abundant vascular tracheids contrasts with lack of vascular tracheids in other species, and the number of vessels per group in *M. densiflora*, 1.6 is appreciably lower. Although Michener (1981) does not give figures on number of vessels per group in *Keckiella* (Scrophulariaceae), examination of his slides shows that vessels tend to be solitary in latewood, where vascular tracheids are abundant, whereas vessels are grouped in earlywood, where vascular tracheids are absent. Presumably presence of numerous vascular tracheids in a wood serves as a subsidiary conducting system much as presence of true tracheids does. Where vascular tracheids are confined only to the last several layers of latewood, they are not likely to interconnect very many vessels, so the number of vessels per group should not be expected to drop very much. This is true in *Ulmus americana* L. (Fig. 13); in my material, vascular tracheids are localized only in the last two or three latewood cell layers, and vessel groupings are not affected. This is also true in *Chimonanthus* (Carlquist, 1983b), in which vessel groupings are very large.

5. *Presence of vasicentric tracheids is correlated with lowered number of vessels per group in particular woods.* The phenomenon of vasicentric tracheids is not well understood in terms of systematic distribution or evolutionary pathways (Carlquist 1984a). However, the clearest instances of vasicentric tracheid occurrence exemplify minimal vessel grouping. Transections of wood of *Lithocarpus densiflora* (H. & A.) Rehd. (Fig. 10) reveal numerous small solitary vessels, a fact perhaps related to the evergreen nature of this species as contrasted with occurrence of ring-porous conditions in deciduous

Fagaceae. Although distribution of vasicentric tracheids in the wood of *Lithocarpus densiflora* is not evident from casual study of transections, viewing of longitudinal sections reveals that each vessel is sheathed by vasicentric tracheids. This is more clearly evident in ring-porous species of Fagaceae, such as *Quercus rubra* L. (Fig. 11) where one can easily distinguish between the thick-walled libriform fibers and the much thinner-walled vasicentric tracheids. In that species there are no vessels surrounded wholly by libriform fibers: all are sheathed by vasicentric tracheids. The vasicentric tracheids tend to interconnect vessels as seen in transection, but the distribution is somewhat more a sheathing distribution than an interconnecting distribution, suggesting that vasicentric tracheids almost certainly serve as a way of substituting for a failed vessel rather than connecting one vessel with another. If vasicentric tracheids can substitute for a vessel they surround when it fails, the three-dimensional conductive pathways in the wood can remain intact and thus there is no selective value for a pattern of vasicentric tracheids in which they would interconnect vessels in a networklike pattern as seen in transection. The fact that solitary vessels in *Lithocarpus* and *Quercus* are related to presence of vasicentric tracheids is dramatized by comparing wood of those genera with that of *Nothofagus antarctica* Oerst. (Fig. 12). In that species of Fagaceae, vasicentric tracheids are lacking, septate fibers are the imperforate tracheary element type, and vessel grouping is prominent, exceeding 2.0 vessels per group. This contrast between species in a family with vasicentric tracheids and solitary vessels on the one hand and species without vasicentric tracheids but with grouped vessels on the other hand could be multiplied, showing that vasicentric tracheids, like true tracheids, are probably a subsidiary conductive system which renders negligible the selective value of grouping in vessels.

In the earlier discussion (Carlquist 1984a) the role of vasicentric tracheids as a subsidiary conductive system ideally placed to take over conduction from vessels they surround in case of failure of those vessels was stressed. The relationship between presence of vasicentric tracheids and lack of vessel grouping was not noted in that paper. Unfortunately these relationships cannot be documented so easily by lists because reports of vasicentric tracheids are not reliable. For example, the vasicentric tracheids claimed for Calycanthaceae prove to be vascular tracheids (Carlquist 1983b). The precise roster of genera and families in which vasicentric tracheids occur can be assembled only as a result of comparative studies on all families in which they have been reported. Some of these families are rather large (e.g., Myrtaceae, Rhamnaceae). For listing, see Metcalfe and Chalk (1950).

Once division of labor has resulted in presence of libriform fibers in a species, the only mechanism for increasing safety in conduction in a species, other than alteration in vessel dimensions (narrow vessels, for example) and more numerous vessels per mm² would be grouping of vessels or innovation

of vasicentric (and vascular) tracheids. Vasicentric tracheids represent a curious dimorphism in imperforate tracheary elements, and evidently only a few groups have been able to achieve this condition. Thus groups which lack vasicentric tracheids but which have libriform fibers as the imperforate tracheary element type may be expected to show various degrees of vessel grouping, depending on selective pressure for xeromorphy in wood structure.

6. *In woods in which libriform fibers are the imperforate tracheary element type, notably wide vessels are frequently solitary, whereas narrower vessels are more often grouped.* This observation can at present be supported only by examples, not by a survey of dicotyledons as a whole. One example shown here is *Ulmus americana* (Fig. 13). As noted above, vascular tracheids in my material of this species are limited to that last several layers of latewood and are too few in quantity to affect vessel grouping. A suitable hypothesis for why vessels tend to be less grouped in earlywood, more grouped in latewood of a ring porous species can be expressed as follows. Failure of vessels may be expected during the dry months, but is not serious because the latewood represents a subsidiary conductive system which can substitute for earlywood during that season. However, failure of latewood vessels would be much more serious, since no further reserve of conductive tissue is then available, and therefore various kinds of safety in latewood, such as vessel grouping, which are not present in earlywood may be expected. Note should be taken that the kind of dimorphism represented by *Ulmus americana* is by no means shared by all ring-porous species, and alternative distributions of grouped versus solitary vessels may be found in various types of growth rings. If one reviews transections of wood of dicotyledons with libriform fibers which are native to wet tropical areas, one frequently notes, however, that vessels are both large and often in small groups—sometimes solitary. The latter suggests lack of selection for safety despite the high vulnerability of wide vessels, and suggests that vessel failure rarely occurs in these species.

7. *Vining species typically have very wide vessels. Grouping of vessels in vines is also typically low, or apparently so.* Conductive systems of vines are probably rarely under stress; xylem tensions are low and positive pressures may occur (Scholander et al., 1955). Consequently, the safety conferred by vessel grouping is not of selective value. An exception to this is found in the latewood of *Akebia* (Carlquist 1984b). Probably *Akebia* experiences tension in latewood, possibly because of frost, so that safety does indeed play a role; such vessel grouping does not occur in Lardizabalaceae native to areas with little or no frost. In the case of vines, the transectional area is so predominantly devoted to vessels compared to wood of nonvining species that even if all imperforate tracheary elements in vines were tracheids, they could not constitute a subsidiary conductive system which could approach the high-volume capacity one would imagine characteristic of the numerous wide vessels. Consequently, although *Akebia* represents an exception, most

vines seem to have a minimum of mechanisms for safety in case of disabling of large vessels.

One must take into account that vessels in vines are not as solitary as they may seem at first glance. Because of vessel dimorphism (Carlquist 1981c), wide vessels in vines may be accompanied by narrow vessels.

8. *When imperforate tracheary elements lose maximal conductive capabilities in the shift from tracheids to libriform fibers, loss of borders is followed by, rarely preceded by, a septate or nucleate condition (either of which signals a nonconductive nature for the cell).* Lauraceae are a convenient example. Those genera with bordered pits on imperforate tracheary elements have nonseptate imperforate tracheary elements. Those genera with septate imperforate tracheary elements have simple pits on those imperforate tracheary elements (Metcalf and Chalk 1950). A similar situation obtains in Rubiaceae, judging from the data of Metcalf and Chalk.

A few exceptions to this principle may be found. In Lardizabalaceae, septate tracheids have been reported (Carlquist 1984b), but these are few in number and transitional to fiber-tracheids and probably are not significant in the water-conduction economy of these vines, in accordance with the comments in the preceding section. Presence of tracheids of suboptimal conductive capacity in *Akebia* may explain why vessels are grouped in latewood in that genus. Septate tracheids or fiber-tracheids have been reported in *Aphloia myrtiflora* Galpin of the Flacourtiaceae (Metcalf and Chalk 1950), and septate fiber-tracheids with minimal bordering on pits characterize Lythraceae according to Baas and Zweypfenning (1979). The number of these exceptions and the minor ways in which they are exceptions suggest that development of septate or nucleate fibers does indeed follow evolution of a minimally conductive imperforate tracheary element.

In fiber-tracheids, pits on radial walls seem generally more abundant than those on tangential walls, judging from the descriptions for pertinent families by Metcalf and Chalk (1950).

9. *Grouping of vessels in radial multiples is about as common as grouping in clusters. Somewhat less common are diagonal bands and tangential bands. The selective value of the pore cluster can be hypothesized to be a minimization of distance between any two vessels in a group; this arrangement minimizes the chance that an embolized vessel would break the vessel group into two halves disconnected by the air embolism.* If a radial multiple of vessels were one vessel wide and a vessel in the middle of the radial multiple were embolized, such a break in the conductive continuity would happen. However, radial multiples may have a potential advantage which overrides that potential disadvantage. Because of the sequential arrangement of vessels in a radial multiple from inside to outside, the conductive pathway represented by the innermost vessel in the series can be maintained if disabling proceeds centrifugally in a stem, as it generally has been shown to do. Radial multiples do not intersect rays, which would interrupt flow.

Tangential bands of vessels often occur with relation to growth rings: simultaneous initiation of a large number of vessels at the beginning of a growth ring makes adjacency a statistical likelihood. However, tangential bands not related to growth ring activity do occur in some groups such as Asteraceae (Fig. 15), Malvaceae, and Proteaceae (Fig. 17). Tangential banding can be regarded as a way of achieving very large vessel groups. This feature is not common in dicotyledons, however, except for what may be seen in earlywood of many species. Diagonal bands of vessels may be similar to radial chains in their effect, but have a potential advantage in interconnecting the three-dimensional conductive patterns of the wood with more numerous interstices.

Interestingly, Aloni and Zimmerman's (1983) report on the effect of auxins on vessel size and density illustrates tangential bands of vessels induced by auxin treatment. Tangential bands may prove to be related to particular auxin concentrations and their patterns in the plant body. Further studies are needed to demonstrate, for example, whether degree of grouping, when it changes from earlywood to latewood, is related to auxin levels. If tangential bands are primarily related to auxin levels, one could imagine that the morphogenetic pathway to tangential bands is simpler than in the case of the other types of groupings.

10. *Larger aggregations of vessels which include several groupings built into patterns which extend across rays may be seen in some dicotyledon woods (e.g., Fig. 16, 17). Although a pattern which continues across a ray does not offer the potential safety of a group uninterrupted by a ray, the interconnection of vessel groups, even when mediated by rays, can be hypothesized to offer a positive feature to the conductive system and to be better than isolated groups of vessels separated from each other only by libriform fibers.* The patterns of tangential bands of vessels illustrated by Aloni and Zimmerman (1983) include instances in which bands extend across rays. Therefore one should investigate the possibility that large aggregations of vessels may bear a relationship to auxin activity within a plant.

11. *Grouping of vessels occurs in primary xylem of stems, roots, and leaves. The reasons for grouping of vessels (or tracheids) into vascular bundles may be much like the reasons for grouping of vessels in wood. Although an earlier account stressed resistance to tension (Carlquist 1980b), which does appear correlated with the thicker helices on walls of primary xylem in plants with xeromorphic wood, the role of redundancy by means of groupings in primary xylem elements as a safety device may be overriding.*

12. *Adaptations by xylem to conditions of drought and freezing appear to be pervasive themes in wood of dicotyledons. In group after group, mechanisms to counter interruption of conduction have occurred in parallel fashion.*

As with other adaptations of dicotyledons, the multiplicity of parallel adaptations to drought and freezing suggests that these mechanisms are effective, but have limits which can be exceeded by extreme conditions,

Fig. 14–17. Wood transections of Asteraceae and Proteaceae.—14. *Olearia argophylla*, (McVaughten 163, A); vessels are sparse, in small groups.—15. *Olearia avicenniaefolia* (C.S.I.R.O. 12072), showing a growth ring; vessels in tangential and other groupings.—16. *Olearia muelleri* (C.S.I.R.O. 97145); extensive groupings of vessels evident.—17. *Persoonia longifolia* R. Br. (Carlquist 6058); latewood near bottom of photographed; remainder in earlywood. (Fig. 14–17, magnification scale above Fig. 1.)

limits not likely to be breached where conditions are uniformly mesic and above freezing. Attrition of individuals, populations, and eventually species to extremes of drought and cold may occur continually. Therefore these niches would never be saturated and adaptations such as vessel grouping would be expected to occur repeatedly and continually in numerous groups of dicotyledons independently.

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Footnote

This study was aided by a grant from the National Science Foundation, DEB 81-09910.