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Sherwin Carlquist

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FURTHER CONCEPTS IN ECOLOGICAL WOOD ANATOMY,
WITH COMMENTS ON RECENT WORK IN
WOOD ANATOMY AND EVOLUTION

Sherwin Carlquist

Introduction

In recent years, work in wood evolution has featured an interesting mixture of comparative and experimental work, a consideration of anatomy, ultrastructure, and ecology, with modes of presentation stressing theoretical (or speculative), quantitative, and graphic elements. From the varied contributions, some concepts have moved closer to clarification, some are still quite imperfectly understood, and some have remained untouched. As in the development of any field, one wishes to comment on progress and, where possible, advance the process of evolutionary synthesis in wood evolution.

In this paper, a variety of topics have been selected for consideration:

1. Interpretation of the different types of growth rings as ecologically adaptive devices, together with a classification of growth rings on the basis of variations thus far known.
2. Comments on the problems of quantification and statistical significance in ecological wood anatomy.
3. A resumé of recent views on the vessel element as an adaptive structure, with an attempt to delineate what should and should not be inferred in describing the major trends of wood evolution as irreversible.
4. A review of the phenomenon of fiber dimorphism, with a discussion of the problems in applying this concept in dicotyledons.
5. A strengthening of concepts of pedomorphosis in dicotyledonous wood.
6. A review of recent work in scanning electron microscopy of woods.
7. An exploration of possibilities for ecological interpretation of primary xylem structure.

Growth Rings

One of the topics not covered in my (1975a) book with an appropriate degree of thoroughness is the occurrence and significance of growth rings. As a response to ecological conditions, a growth ring (or the absence thereof) can be a very sensitive adaptive device. Chowdhury's early work (1939, 1940, 1941) shows undeniable relationship between growth rings in particular species and the sequence of climatic events in the years those growth-

rings were produced. He does not pinpoint ecological adaptation exactly (e.g., the precise effect of rainfall, of temperature, etc.), but in the complicated climatic regime with which he is dealing that is not to be expected. The close correlation between growth rings and the sequence of climatic events has long been the basis for dendrochronology in the southwestern United States and other dry climates where seasonal occurrence of rainfall is the most important variable in formation of growth rings.

There are perceptible limits to alterability of cell types within a growth ring. With respect to tracheids or other imperforate cells, enlargement in a radial direction probably never exceeds about 2.0 times the tangential width of the fusiform initial from which it is derived. The radial diameter is most often much less than 2.0 times the tangential width. One can say that in growth rings where radial diameter of tracheids changes during a year, one might more aptly express the change not in terms of enlargement of the earlywood tracheids, but rather in terms of very narrow radial diameter of the latewood tracheids (e.g., Fig. 10). Tangential diameter of tracheids or other imperforate cells shows very little increase over the diameter of the fusiform cambial initials from which they were derived. Quantitative figures for changes in radial diameter and wall material within a growth ring are given for tracheids by Denne (1973) in a study which shows these variables to be correlated with shoot vigor in his material.

With respect to vessel elements, however, limits to increase in diameter compared with the fusiform cambial initials from which they were derived are almost indefinite, as the relatively huge diameter of vessels in vines, lianas, and certain markedly ring-porous trees (Fig. 22, 23) indicate. Vessel diameter seems to be closely correlated positively with volume of water conveyed and inversely correlated with "safety" of the conductive system (see Zimmermann 1971; Carlquist 1975a and the literature cited therein). Therefore, one should be able to use vessel diameter change within a ring as a sensitive indicator of ecological change within a season. Few works have attempted to express vessel diameter fluctuation within a single ring quantitatively, but at least one paper (Swamy, Parameswaran, and Govindarajalu 1960) can be cited in this regard.

Although vessel diameter changes are viewed as the prime source of fluctuations with which growth rings may be recognized, shift in the composition of cell types present at the beginning versus the end of a growth ring is also quite important. This has been recognized in a number of works, particularly with respect to parenchyma presence (Chowdhury 1953, 1964). The absence of vessels at the end of a growth ring has been cited (Carlquist 1978) and will be detailed further below.

Any of the above three sources of variability, singly or collectively, may be used to characterize types of growth rings. Other anatomical expressions seem of other anatomical significance: variation in tracheary element length

within growth rings (Swamy, Parameswaran, and Govindarajalu 1960) is a minor phenomenon perhaps related to differential intrusive ability, not water-conducting capabilities of cells.

One may be grateful for studies which delineate clearly which woods in a group or flora lack growth rings, which woods tend to have a growth ring of a nature other than annual, and which woods have annual growth rings. Tomlinson and Craighead (1972) are a good example in this respect. Studies which report environmental modifiability of growth-ring formation are all too few. In order to determine this, one must be able to study wood of a species grown in two environments—one preferably the native environment. Such a study was performed by Bissing (1976). Bissing found that *Helianthemum scoparium* Nutt. and *Leptodactylon californicum* H. & A. lost the diffuse-porous condition in favor of producing growth rings when cultivated in the Rancho Santa Ana Botanic Garden, compared with their native habitats. The reverse tendency occurred for *Lupinus albifrons* Benth., in which the Botanic Garden was judged to be more extreme, seasonal with relation to water availability and humidity, compared with the natural habitat. Forsaith's (1920) work is similar with relation to the effect of altitude.

Ecological correlations of the diffuse-porous and ring-porous conditions have been found by a variety of workers. Mowbray and Oosting (1968) and the workers they cite show that species in which growth begins early during the growing season are ring porous, whereas species which begin late are diffuse porous. Likewise, correlations have been found, not surprisingly, between the evergreen and the deciduous habit. Ring-porous dicotyledons are predominately deciduous, diffuse-porous dicotyledons evergreen, although exceptions may certainly be found (Chowdhury 1964; Tomlinson and Craighead 1972).

By way of developing hypotheses on growth-ring function, I would like to begin by offering a classification of growth rings. The formation of successive cambia, which often do not coincide with annual or seasonal phenomena, are not treated in this classification. Perhaps, most significantly, we must respect the statements by Chowdhury (1953) that cambial activity even in tropical climates may occur during a fraction of the year, and that physiological data are lacking, in any case. A categorization of growth rings may point to areas worth physiological study. However, one must stress, as is done elsewhere in this paper, that there is reason to believe that physiological measurements, despite their value may not always provide values closely parallel to the actual adaptations suggested by these structures. The peak velocities which wider vessels are capable of providing may only rarely be attained—perhaps never in particular plants or under particular experimental conditions. However, the selective advantage of a species may depend on capabilities of a structure only rarely maximally reached. The abun-

Figs. 1-5. Wood sections to show growth rings.—1. *Larrea tridentata* (Bissing 200, RSA). Large earlywood vessels visible above center.—2, 3 *Cistus purpureus* (Carlquist IV-8-1972, s.n., RSA).—2. Earlywood above center, latewood of preceding year below.—3. Higher magnification pit cavities filled with resin show that the imperforate tracheary elements are tracheids.—4. *Lepidospartum squamatum* (Carlquist 621, RSA). Large vessels at top are from

dance of narrow vessels in latewood may provide redundancy where exceptionally high tensions occur, resulting in blockage of many vessels by air embolisms, yet such blockages may not seriously lower conductive capacity. However, a technically well-equipped physiologist might have difficulty with a concept such as "seriously lower."

The following classification is offered as a way of comprehending all sources of variation evident to me from the slides and literature I have studied. Additional types are conceivable and may be entered as they come to light. One of the purposes of this classification is to demonstrate all degrees of distinctness of growth rings. Unlike Chowdhury (1964), I do not have criteria whereby growth rings are said to be present or counted as not present.

Type I. Little differentiation into growth rings; changes with season gradual:

A. Tracheids only present; gradual changes during the year evident, no sharp transitions. Examples: certain *Araucariaceae* (e.g., *Agathis palmerstonii* F. Muell., *Araucaria cunninghamii* Ait.: see Greguss 1952). Some *Araucariaceae* are devoid of growth-ring activity (*Araucaria montana* Brogn. & Gris), a few have well-marked growth-ring activity [*A. araucana* (Molina) Koch].

B. Vessels smaller in latewood, but not markedly so. Other cell types unaffected. Examples: *Larrea tridentata* Cov. (Fig. 1), *Cistus purpureus* L. (Fig. 2). In both of these examples, *tracheids* are the imperforate tracheary elements (note fully bordered pit pairs in tracheids of *Cistus*, Fig. 3).

C. Vessels approximately uniform in size, but parenchyma cells present seasonally in rings. Tomlinson and Craighead (1972) cite this condition for *Forestiera segregata* Krug & Urban (= *F. porulosa* Poir) although they do not claim the parenchyma to be a reliably annual production. Doubtless examples in which a wood is uniform but parenchyma bands formed annually in response to seasonal events could be found.

D. Vessels slightly diminished in size in latewood, but imperforate tracheary elements also appreciably diminished in size. This was observed in *Viola trachelifolia* Gingins (Fig. 6), where earlywood imperforate tracheary elements (fiber-tracheids) are radially wider than those in latewood.

E. Vessels slightly diminished in diameter in latewood, but imperforate

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earlywood, balance of section is a portion of latewood of the preceding ring.—5. *Aralia spinosa* (USw-12014). Top two thirds of photograph shows earlywood vessels. (Magnification scale for Figs. 1, 2, 4, 5 above Fig. 1 [divisions = 10 μ m]. Magnification scale for Fig. 3 above 3 [divisions = 10 μ m].)

Figs. 6-9. Wood sections to show growth rings.—6. *Viola trachelifolia* (Carlquist 1984, RSA). Earlywood above center.—7. *Eucryphia cordifolia* (USw-8461). Earlywood, with thinner-walled tracheids, above center.—8. *Evodia cucullata* (Yw-28318). Libriform fibers are thicker in upper half of photo, which shows latewood.—9. *Calodendron capense* (Yw-20300). Top quarter shows earlywood; latewood, featuring thick-walled fibers, in bottom three quarters. (Magnification scale for 6-9 above Fig. 1.)

tracheary elements appreciably thicker walled in latewood. This condition is illustrated by *Eucryphia cordifolia* Cav. (Fig. 7), in which tracheids are the imperforate elements, and by *Evodia cucullata* Gillespie (Fig. 8), in which the imperforate tracheary elements are libriform fibers.

Functional interpretations of Type I growth rings.—Two sources of variability are evident in the above kinds of growth rings: increased diameter in earlywood vessels, and alterations in wall thickness or diameter of imperforate tracheary elements. The significance of vessel diameter in Type I appears to be merely that of increasing moderately the flow(volume per unit time)-handling capacities of earlywood. The increase in number of vessels in latewood in the Type I growth rings is so slight as not to constitute an appreciable redundancy in vessels and thus increase the safety of latewood. In some, such as *Larrea*, *Krameria*, and *Cistus*, the imperforate elements are tracheids, and these tracheids, rather than narrower or more numerous vessels, are very likely the “back-up” system providing safety to the water-conducting system of the plant. Should the relatively few vessels in genera such as *Larrea* be blocked by air embolisms, huge numbers of tracheids stand available as alternate pathways. They would conduct slowly in comparison to vessels, but slow conduction rates in these xerophytes would likely be expected. However, only in such xerophytes as these would fluctuation in vessel number and diameter be the less important component in coping with seasonal change in water availability. Marked increase in vessel diameter in xerophytes is not to be expected, because these plants have limited transpiration at any season compared with broadleaved hardwoods. In the nonxerophytes of Type I, fluctuation in vessel diameter would, however, reflect moderate alteration in transpiration in a plant that transpires more, but in a less seasonal environment: subtropical and tropical plants which grow in moderately uniform conditions, for example.

Type II. Vessels absent; tracheids are differentiated into radially wider, with thinner walls in earlywood; and radially narrower, with thicker walls in latewood. This type of growth ring is so familiar as to need no description, and can be illustrated by the temperate Pinaceae. The quantified data of Denne (1973) illustrate well both the sharp drop in radial diameter of latewood tracheids and the equally sharp increase in wall material per unit area in latewood as compared to earlywood.

Functional interpretation of Type II growth rings.—Early in the season, especially as Denne (1973) notes, with larger or more vigorous shoots, wider tracheids would be capable of providing a greater volume of flow per unit time. One can hypothesize that production of wall materials in latewood might bear a relationship with greater availability of insolation later in the season, but this seems to me at first glance not a prime factor in determining wall thickness.

The distinctive feature of Type II growth rings is their duality: both wider, but not, usually, extraordinarily wider tracheids in earlywood with thinner walls; and narrower tracheids with thicker walls in latewood. In view of known high rates of transpiration of some conifers, as stressed by Zimmermann (1971), construction of capillaries with wider diameter, a feature aided not only by increase in radial diameter but by thinness of walls, would seem of selective advantage. The latewood features, that of having numerous conducting cells with narrow diameter and thick walls which would resist tensions in water columns is equally important: conifer wood has aspects of xeromorphy, and the numerous narrow latewood tracheids can be considered a parallel to the occurrence of numerous narrow vessels in latewood of xeromorphic dicotyledons with vessels. From this picture one cannot excise the advantage of thicker walls in latewood for mechanical strength.

However, one may note the tremendously narrow lumina of both earlywood and latewood tracheids in such a conifer as *Microstrobos* when compared with tracheids of conifers from less severe environments (Carlquist 1975a) is informative. The high proportion of wall material to tracheid diameter in *Microstrobos* suggests not so much selective advantage for mechanical support in this rather small alpine shrub, but perhaps an overriding selective advantage for tracheids which resist deformation during periods when water tensions in tracheids are extraordinarily high, such as when ground is frozen but sunlight permits transpiration. Rundel and Stecker (1977) have shown that increased tension in xylem water columns at progressively greater heights in *Sequoiadendron* trees are correlated with narrower tracheid diameters—not in portions of growth rings, but in xylem of particular trunk and branch samples irrespective of fluctuations within growth rings. Thus the possibility arises that wide tracheid diameters are of selective advantage in conifers unless particular conditions run counter to maximal flow requirements so strongly that an overriding selection for narrower and thicker-walled tracheids obtains. In shrubby conifers of extreme habitats, such as *Microstrobos*, or in very high branches on a tree such as *Sequoiadendron*, such an override would seem to occur. One is tempted to extend the interpretation to growth rings by saying that high tensions in late-season periods could be the selective factor for thicker-walled tracheids which have narrow radial diameter. However, the radial narrowness does clearly provide more tracheids per unit transection, and thus increases the tracheid number and therefore theoretically would increase the safety somewhat.

Although Winteraceae have little seasonality, growth rings may be found in the vesselless dicotyledons *Trochodendron* and *Tetracentron*. The possible evolutionary significance of growth rings in vesselless dicotyledons has been discussed at length earlier (Carlquist 1975a), but the significance of scalariform pitting in earlywood tracheids of these and whether this can be

considered a juvenilism, as Takhtajan (1969) suggests, is discussed below under the topic of paedomorphosis.

Type III. Vessels vary little in number from one portion of a growth ring to another, but are much larger in diameter in earlywood than in latewood. Imperforate tracheary elements consist of cells other than tracheids or fiber-tracheids, and vary little in diameter or wall thickness with respect to position in the ring.

A. Imperforate tracheary elements consist of libriform fibers. *Calodendron capense* Thunb. (Fig. 9) is an example of this mode of construction.

B. Imperforate tracheary elements consisting of nucleated fibers or septate fibers. *Aralia spinosa* L. (Fig. 5), which has septate fibers, qualifies as an example. The greatly larger diameter of earlywood vessels would easily permit this species to qualify as ring porous. *Juglans nigra* L. (Fig. 24) is also a clearly ring-porous species which falls into Type IIIB.

C. Imperforate tracheary elements are all libriform fibers with very thick walls. The libriform fibers of *Phoradendron tomentosum* (DC.) Englem. ex Gray (Fig. 25) have very thick walls and thus are tracheary elements corresponding to this description.

Functional interpretation of Type III growth rings.—Tracheids can be assumed to be conductive cells advantageous because of their inability to transmit air embolisms from one tracheid to another: air bubbles do not traverse pit membranes, but easily traverse perforation plates from one vessel element to another, disabling entire vessels easily. Because of this, and because they are narrow and tend for that reason alone to be large in numbers and therefore in "redundancy," a feature of value when conductive systems are partially disabled, the presence of tracheids in woods which also have vessels can be understood. The tracheids constitute a subsidiary conductive system. Tracheids are assumed to conduct considerably more water than libriform fibers because pit volume in libriform fibers is much smaller. Therefore, woods with Type IIIA might reasonably be supposed to have a poorer subsidiary conductive system than vessel-bearing woods in which the imperforate tracheary elements are tracheids (e.g., Type V) or in which vascular tracheids are abundant (Type VII). Therefore the design solutions of Type III woods differ but little from those Type I (excepting the tracheid-bearing woods in Type I). The difference is chiefly in the larger-diameter earlywood vessels of Type III, which mark them as potentially well adapted to temperate climates in which large volumes of water are conducted early in the season. Type III woods might also be expected in tropical situations in which trees are broad leaved, and in which an alternation between dry and wet seasons is reflected in wood structure. Type III woods would not be envisaged as advantageous in situations in which water availability dwindled markedly seasonally, because latewood vessels

do not show great redundancy and the subsidiary conductive system is not composed of tracheids. In Type IIIB, the occurrence of living or septate fibers would reduce to nil the tendency of imperforate tracheary elements to serve as a subsidiary conductive system. The IIIC species also would have a very poor subsidiary system because excessively narrow lumina provide minimal space for water columns in the libriform fibers.

Type IV. Vessels wide in earlywood; vessels numerous and of moderately small diameter present from just outside earlywood until the end of the latewood with little or no gradation in size toward end of ring. Imperforate tracheary elements are libriform fibers. Parenchyma not seasonal in production. Examples shown here are *Lepidospartum squamatum* A. Gray (Fig. 4) and *Olearia virgata* Hook f. (Fig. 17). *Lepidospartum squamatum* is unusual in having narrow vessels so abundant in all portions of the growth ring including a few mixed with wider vessels in the earlywood, as seen in Fig. 4, top. Perhaps the most marked example referable to Type IV, and an example which would be called a definitively ring-porous wood, is *Quercus alba* L. (Fig. 22). Chowdhury (1964) reports vessels wide but few and in earlywood in *Anogeissus* (Combretaceae), *Zizyphus* (Rhamnaceae), and *Mansonia* (Sterculiaceae).

Functional interpretation of Type IV growth rings.—The large earlywood vessels in this type suggest an accommodation to greater rates of sap flow at the beginning of the growth season. The presence of libriform fibers does not suggest subsidiary conductive capability by the imperforate tracheary elements. However, the numerous narrower vessels in the balance of the growth ring in these species suggest that vessels, in fact, are equivalent to a subsidiary conductive system because of their redundancy and safety. These narrower vessels do not suggest a markedly reduced conductive capacity of latewood compared with earlywood, but a greater safety for it. The occurrence of numerous narrow vessels at *any* point in the growth ring suggests a flexible system, and one is tempted to correlate it with habitats in which the growing season can turn suddenly and decisively hot and dry.

Type V. Vessels wide in earlywood, in general progressively narrower in latewood. Tracheids present as the imperforate tracheary element type. Parenchyma cells not produced in accordance with seasonal events.

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Figs. 10–13. Wood sections to show growth rings.—10. *Ephedra californica* (C. B. Wolf 10050, RSA). Top half of picture shows latewood grading downward into the vessel-free wood with which the growth ring ends.—11. *Myrica hartwegii* (C. B. Wolf 4807, RSA). At top, earlywood vessels, grading quickly downward to vessel-free wood below; earlywood of next

growth ring at bottom.—12. *Cercocarpus intricatus* (Wolf 7576, RSA). Earlywood above, grading upward toward latewood.—13. *Forsellesia nevadensis* (Thorne & Tilforth 43694, RSA). Earlywood above center, grading upward into latewood. (Magnification scale for 10–13 above Fig. 1.)

A. Vessels not present at all in latter portion of growth ring. Imperforate elements roughly uniform throughout the growth ring. An example may be seen in *Myrica hartwegii* S. Watson (Fig. 11).

B. Vessels few in latewood, especially in the last several cell layers of latewood. Imperforate elements roughly uniform throughout the growth ring. *Cercocarpus intricatus* S. Watson (Fig. 12) is a clear example, but *Cercidiphyllum japonicum* Sieb. & Zucc. (Fig. 15) also falls into this category.

C. Vessels not present at all in latter portion of growth ring. Tracheids narrower or thicker walled in latewood. *Ephedra californica* S. Watson (Fig. 10) is a clear example.

D. Vessels fewer in latewood than in earlywood, especially in the last several cell layers of latewood. Tracheids wider in diameter in earlywood than in latewood. *Forsellesia nevadensis* (Gray) Greene (Fig. 13) and *Lep-todactylon californicum*.

Functional interpretation of Type V growth rings.—Types VC and VD are variants on VA and VB respectively. The range of types within Type V shows a gamut from fairly uniform presence of vessels in latewood to complete absence of vessels in latewood. This latter condition, noted for a number of Bruniaceae such as *Lonchostoma esterhuyseniae* Dahlgren & Strid (Carlquist 1978), invites comparison to gymnosperm woods, since the latewood is vesselless. Even those species with a scattering of small vessels in latewood are functionally very similar: the latewood must operate on a near-vesselless basis. The possible significance of Type V growth rings seems to lie in accommodation of greater flow rates in earlywood combined with accommodation of greater safety in latewood. That statement could be made of other growth-ring types also. Type V is distinctive in that it involves a more primitive type of wood (imperforate tracheary elements all tracheids), and the paucity of vessels after the first earlywood vessels suggest that conductive rates for these species accommodate more moderate transpiration. Bruniaceae are microphyllous; *Ephedra* is leafless; and *Cercocarpus intricatus* and *Forsellesia nevadensis* are desert shrubs with small leaves and presumptive low transpiration rates. *Myrica hartwegii* on the other hand, grows in very wet places and is deciduous; that could be said of *Cercidiphyllum japonicum*, too. In these mesophytes, large volumes per unit time are probably never conducted because of high humidity throughout

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Figs. 14–17. Wood sections to show growth rings.—14. *Ceanothus leucodermis* var. *eglandulosus* (Wolf 2140, RSA). Earlywood above, grading upward into latewood.—16. *Cercidiphyllum japonicum* (USw-19679). Earlywood above, grading upward toward latewood; latewood near center is nearly free from vessels.—16. *Artemisia spinescens* (Carlquist 433, RSA). Entire growth ring. Interxylary cork near bottom, then, above it, numerous narrow vessels of

the earlywood grading into vessel-sparse latewood above.—17. *Olearia virgata* (J. M. Harris, s.m., WZw). Earlywood vessels above, grading abruptly upward into latewood; very narrow vessels predominate in growth rings, with a few wide vessels scattered through each ring. (Fig. 14–17, magnification scale above Fig. 1.)

Figs. 18–20. Wood sections to show growth rings.—18–20. *Arctostaphylos auriculata* (Wallace 1372, RSA).—18. Earlywood above middle, vascular tracheids and narrow vessels of latewood below center.—19. Radial section. Earlywood vessel, center; to the left of it, septate fibers of earlywood; to the right of it, narrow vessels and vascular tracheids of latewood.—20. Transection at high power, showing narrow vessels of latewood; the bordered pits are filled

the growing season, tendency to be an understory element, or relatively limited leaf surface during periods of physiological drought.

Type VI. Vessels more numerous as well as greater in diameter in earlywood than in latewood. Imperforate tracheary elements are libriform fibers and are approximately the same throughout the growth ring. Parenchyma bands not formed with relation to seasonal events. This type is probably less frequent than any of the types in which latewood vessels are not only smaller, but more numerous. Examples of Type VI shown here include *Ceanothus leucodermis* Trel. var. *eglandulosus* Torr. (Fig. 14) and, in an extreme way, *Artemisia spinescens* Eaton. Vessels few in latewood have been reported as a normal occurrence in a high-elevation eucalypt, *Eucalyptus delegatensis* R. T. Baker (Tupper 1913).

Functional interpretation of Type VI growth rings.—The presence of more numerous as well as smaller vessels in several growth-ring types would be expected as accommodations to safety in latewood; if so, the paucity of vessels in latewood of Type VI needs explanation. Presence of more numerous earlywood vessels (sometimes wider, Fig. 14; sometimes about the same diameter as latewood vessels, Fig. 16) in woods which do not have tracheids as imperforate tracheary elements can only be interpreted as accommodation of flow of more water per unit time in earlywood without an accompanying increase in safety in latewood. The numerous and narrow earlywood vessels in *Artemisia spinescens* may be an alternative form of safety. In such examples as *Ceanothus leucodermis eglandulosus* and *Eucalyptus delegatensis* the foliage may play a role in modifying transpiration, and should be investigated.

Type VII. Narrow vessels and vascular tracheids present in latewood, wider vessels and libriform fibers (or fiber-tracheids) present in earlywood. No parenchyma bands formed with relation to seasonal events. This type of growth ring is illustrated for *Arctostaphylos auriculata* Eastw. (Fig. 18–20). It also proves to be common in other species of this large genus of western North America. Superficial examination of transection such as the one shown in Fig. 18 would suggest that narrow thick-walled fibers are mixed with narrow vessels in latewood. However, at higher magnification

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with tannins, revealing them to be vascular tracheids rather than libriform fibers.—21. *Lepidodactylon californicum* (Bissing 96, RSA). Growth-ring margin two thirds of the way from top of photo, earlywood at bottom of that right; note tracheids thicker-walled in latewood. (Fig. 18, 21, magnification scale above Fig. 1. Fig. 20, scale above Fig. 3. Fig. 19, scale above Fig. 19 [divisions = 10 μ m].)

Fig. 22–25. Wood sections to show growth rings.—22. *Quercus alba* (USw-73914). Large earlywood vessel containing tyloses above; bottom third of photograph shows latewood of preceding year.—23. *Quercus borealis* (USw-2206). Large earlywood vessel in upper half; in latewood of preceding year, several thick-walled vessels may be seen.—Fig. 24. *Juglans nigra*

all of the fascicular xylem cells in latewood can be shown to have bordered pits (Fig. 20: bordered pits clearly evident because of the presence in them of tannins which stain deeply). The narrower of these cells with bordered pits lack perforations when viewed in radial section (Fig. 19, right). If the imperforate tracheary elements in such woods were true tracheids, one would expect true tracheids in the earlywood also. However, as one can see in transverse and radial sections of earlywood (Fig. 19, left third of photograph; Fig. 20, topmost row of cells, upper left), the wide septate fibers quite unlike tracheids prove to be the imperforate tracheary elements characteristic of this wood. This proves true of all species of *Arctostaphylos*. The other criteria for vascular tracheids are present: transition occurs from true vessel elements into vascular tracheids where vessels are so narrow that accommodation of a perforation on the end wall is unlikely. Vascular tracheids are the same length as vessel elements, whereas true tracheids are much longer than vessel elements. Vascular tracheids are not present, to my knowledge, in any wood in which the fascicular xylem contains any imperforate tracheary element other than libriform fibers, with the exception of parenchyma cells (some globular cacti have wood consisting of vascular tracheids plus parenchyma and no fibers: Gibson 1973).

Functional interpretation of Type VII growth rings.—Wider vessels in earlywood of these woods do not seem notably numerous, but do represent a moderate potential accommodation to greater flow. *Arctostaphylos* has relatively small sclerophyll leaves, so transpiration would not be as great as in a plant with thin, broad leaves, and only moderately wide earlywood vessels would be expected. The striking feature, the abundance of vascular tracheids in latewood, indicates a high degree of redundancy and safety, approaching a gymnospermous condition, in latewood. If Type VI suggests accommodation mainly to increased flow in earlywood, Type VII suggests almost the reverse, adaptation by latewood to times of water stress and probable high tension in water columns of xylem. These wood capabilities help to explain the remarkable radiation of *Arctostaphylos* in the dry regions of the southwestern U.S., a noteworthy development within a family often found in wet areas, Ericaceae.

Type VIII. Vessels much wider in diameter in earlywood than in latewood. Latewood vessels variously more numerous per unit area of transection

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(USw-21278). Earlywood contains two large vessels with tyloses; latewood of preceding year below center.—25. *Phoradendron tomentosum* (Wallace 23, RSA). Slightly wider vessels of earlywood above center; latewood of preceding year below center. (Fig. 22–25, magnification scale above Fig. 1.)

than earlywood vessels, but appreciably thicker walled. Imperforate tracheary elements are not tracheids. Axial parenchyma not produced seasonally in accordance with growth-ring formation. *Quercus borealis* Michaux (Fig. 23) is an example, as is *Fraxinus excelsior* L. (Yatsenko-Khmelevsky 1954). Type VIII may be considered a variant of Type V, as the pairing of two *Quercus* wood transections hints (Fig. 22, 23). Gibson (1977a) reports thinner-walled latewood vessels in cacti, seemingly a reversal of the pattern shown in Fig. 23. That may prove worthy of recognition as a distinct type of growth ring.

Functional interpretation of Type VIII growth rings.—Exceptionally wide vessels connote low safety, by which one means that they are few per unit area of transection and disabling of one disables a larger area of conductive tissue than would disabling of a narrower vessel. I have hypothesized (1975a) that wall thickness may be a factor in preventing wall deformation, and therefore disabling of a vessel. If a vessel is exceptionally wide, the wall would have to be excessively thick to prevent buckling of the wall. A narrower vessel, however, can achieve much greater resistance to buckling with a thickness that would not be resistant for a wide vessel. Wide vessels are formed in vines or in earlywood of ring-porous species or in certain monocotyledons (e.g., grasses) where vessels are not subject to great tension and may, on the contrary, often experience a positive pressure (e.g., vines, grasses). The potential resistance of thick-walled vessels to deformation under high tension is, in my opinion, illustrated by *Larrea tridentata* (Fig. 1), *Cistus purpureus* (Fig. 3), and *Krameria grayi* Rose & Painter (Fig. 39). In xerophytes such as these, one may assume that high tensions prevail throughout the year, as has indeed been reported for *Larrea* (Scholander et al. 1965). In a species such as *Quercus borealis*, we may have a latewood equivalent to the xeromorphic wood produced throughout the year by *Larrea*. Gibson (1977a) can offer no hypothesis for occurrence in certain cacti of vessels with walls thinner than those of earlywood vessels. One might hypothesize that in terms of resistance to tension, a thinner-walled narrow latewood vessel would be equivalent to a thicker-walled wider earlywood vessel, so that in effect, no actual change in vessel capability occurs. Indeed, no actual change in vessel capability with respect to tension resistance would be expected in cacti, where tensions are low and constant, and where the moderate degree of growth-ring activity present could be explained merely as accommodation of greater flow during peak periods of rainfall or transpiration. The essential "shutdown" of cactus transpiration by crassulacean acid metabolism is a mechanism which prevents high tensions from building in the xylem, presumably.

Type IX. Vessel elements wider in diameter in earlywood, narrower in latewood. Abundance of vessels in earlywood versus latewood varies some-

what. Imperforate tracheary elements approximately the same in diameter and wall thickness from one portion of a growth ring to another. Imperforate tracheary elements mostly tracheids or fiber-tracheids. Latewood vessels with scalariform perforation plates frequently. Earlywood vessels with simple perforation plates (or, in a few cases, fewer bars than the latewood vessels). Parenchyma bands not formed on an annual basis. One must stress that not all dicotyledons with scalariform perforation plates and marked growth rings show the pattern of having simple perforation plates in earlywood, scalariform ones in latewood. However, the number of species which do show this annual shift is striking. Examples which are shown here include *Vaccinium arboreum* Marshall (Fig. 26–30), *Arbutus texana* Buckley (Fig. 31), *Styrax officinalis* L. var. *fulvescens* (Eastw.) M. & J. (Fig. 32), *Sassafras albidum* Nees (Fig. 33), and *Laurus nobilis* L. (Fig. 34). Many authors report “mixed scalariform and simple perforation plates” without analysis of whether variation in plate morphology with respect to position within a ring occurs. The type of growth ring described above was apparently first reported by Bissing (1976) in *Styrax*. In most of the instances cited, the latewood vessel elements not only have more numerous bars per perforation plate, but the bars appear thicker. Some species in which the number of bars remains the same, but in which thickness of bars shifts with position in growth ring may be expected, judging from preliminary observations.

Functional interpretation of Type IX growth rings.—Wider vessels with simple perforation plates in earlywood seem, as in the other growth-ring types, a potential accommodation to flow of greater volumes per unit time earlier in the season. Does presence of scalariform perforation plates, often with thick bars, in latewood have a functional significance or is it simply retained because where flow rates are lower, it is not markedly disadvantageous? Scalariform perforation plates confer no “safety” compared with simple perforation plates, because air bubbles can cross either type of plate. However, the scalariform plates, possessing as they often do in these growth rings thick bars or networklike configurations (Fig. 28–30), may offer some potential for resisting deformation of a vessel. The presence of bars would not be a great disadvantage where slow rates of water movement prevail, as would be expected in latewood; absence of bars in earlywood vessels where conductive rates might be higher could be hypothesized. Earlier (Carlquist 1975a) the idea was advanced that where vessel elements have few but wide bars on perforation plates, as in *Rhizophora*, this might be an accommodation to high tensions, preventing deformation. Vliet (1976) has questioned this interpretation for *Rhizophora*, but he does not give his reasons. DeBuhr (1977) accepted this interpretation in Sarraceniaceae.

The presence of wide, thick bars between wide perforations, the presence of scalariform lateral wall pitting on vessels, and the gelatinous walls on wood cells of *Rhizophora* all seem potential accommodations to expansion

Fig. 26-30. *Vaccinium arboreum* (USw-19344), wood sections to show aspects of growth ring activity.—26. Transection, showing earlywood in top two thirds of photograph; latewood of preceding year below.—27-30. Perforation plates of vessel elements from radial section.—27. Simple perforation plate of earlywood vessel.—28. Scalariform perforation plate with some bar anomalies; bordered pits show in ray cell walls below.—29. Perforation plate with inter-

and contraction of a marked nature, preserving cell shape during these changes with minimal deformation. We know that stems actually shrink during periods of high transpiration to a measurable degree, so this does not seem so unlikely. Vliet (1976) says, "it is hard to accept this functional explanation. I know of no other mangrove genera with scalariform perforation plates." However, it is entirely plausible that ancestors of Rhizophoraceae may have had scalariform perforation plates, which specialized for reasons such as I offered, whereas other mangrove groups are mostly derived from ancestors with simple perforation plates. Expecting every mangrove to have the *Rhizophora* pattern in its wood is contrary to the obviously complex ways in which angiosperms evolve.

The fact that growth rings of Type IX exist may be an additional reason to suspect that the "primitive" vessel is potentially still high in selective value where flow rates are not rapid and moderate tensions occur occasionally. Modification of the scalariform perforation plate can be expected to feature removal of the bars where flow rates are a consideration, but retention and strengthening of bars on a perforation plate may well be a strategy for resisting high tensions, parallel to the thick walls of vessels in *Larrea*, etc., where flow rates are slower. These two strategies can occur within a single plant at different times of the year in the case of growth rings of the type just described.

Type X. Vessel elements narrowest in latewood, moderately wide in earlywood, but greatest in diameter in the middle of the ring. Imperforate tracheary elements are all libriform fibers. Axial parenchyma not formed in seasonal bands (although interxylary cork zones may be annual). Examples include *Artemisia tridentata* Nutt. (Fig. 41) and *A. filifolia* Torr. (Fig. 42), although other species of *Artemisia* have other growth-ring types, such as V and VI.

Functional interpretation of Type X growth rings.—If reasoning given in discussions of other growth-ring types is followed, peak flow capacity in the Type X *Artemisia* species would occur not at the beginning of the growth ring, but a little later, in midseason. A correlation with growth form is possible. During winter rains, desert and Great Basin species of *Artemisia* tend to leaf out on short shoots. Later, as rains continue, foliage continues to increase on short shoots but long shoots also form. Flow in xylem might be expected to increase with development of the long shoots. In south-

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connections between perforations, thick bars, borders on perforations.—30. Two perforation plates in adjacent vessels showing morphology of bars similar to that shown in Fig. 29. (Fig. 26, magnification scale above Fig. 1. Fig. 27–30, scale above Fig. 3.)

Fig. 31-34. Wood section to show aspects of growth ring activity.—31. *Arbutus texana* (USw-19051). Transection, earlywood begins just above center; latewood of preceding year in bottom half of photograph.—32. *Styrax officinalis* var. *fulvescens* (E. K. Balls 19107, RSA). Simple perforation plate of earlywood vessel (left) adjacent to scalariform perforation plate of latewood vessel (right).—33. *Sassafras albidum* (Stern, s.n., Yw). Earlywood vessel (blank

western North America where *Artemisia* and other shrubs with heteroblasty occur, the wettest portion of the growing season often is not the earliest, but the middle. In the hardwood forests of eastern North America, melting of snow insures maximal soil moisture at the beginning of the growing season, then rising temperatures tend to reduce soil moisture. Thus Type V growth rings would be correlated with the hardwood forests, Type X a strategy in accord with climates of the Southwest.

Type XI. Vessel elements fluctuating variously in diameter according to seasonal progression. Imperforate tracheary elements may be either tracheids, fiber-tracheids, or libriform fibers. Parenchyma formed seasonally as a band.

As stressed by Chowdhury (1964), occurrence of parenchyma bands at positions within the growth ring other than terminal or initial does not qualify for defining growth rings. Initial parenchyma and terminal parenchyma have been grouped by some authors as marginal parenchyma.

A. Initial plus terminal parenchyma present. This type is evidently rather scarce, because it is not included in the discussions of Chowdhury (1964), although that paper does, to be sure, refer primarily to tropical trees. As figures 35 and 36 show, *Robinia pseudo-acacia* L. exhibits presence of starch grains in at least the last six cell layers of the growth ring (Fig. 36, below center), as well as more than six layers of the earlywood which follows (Fig. 35; 36, above center). This instance of initial plus terminal parenchyma was easily discovered because the sections were prepared from liquid-preserved wood samples, in which starch grains are evident. Starch grains alone could not be used to determine parenchyma presence, but identification of parenchyma cells in radial section confirmed the occurrence described. Other examples are to be expected.

B. Layers of initial parenchyma present in growth ring. This type is shown here for *Parkinsonia aculeata* L. (Fig. 37). Chowdhury (1953) details occurrence of initial parenchyma in *Gmelina* (Verbenaceae).

C. Layers of terminal parenchyma present in growth ring. Terminal parenchyma is shown here for *Stanleya pinnata* (Pursh) Britton (Fig. 38) and *Krameria grayi* (Fig. 39). In Chowdhury's (1964) survey of tropical woods, he reports terminal parenchyma only for the family Magnoliaceae.

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area at left) with two scalariform perforation plates of latewood vessels at right. The earlywood vessels contain simple perforation plates only (not shown).—34. *Laurus nobilis* (Yw-40407). Two scalariform perforation plates from latewood. (Fig. 31, magnification scale above Fig. 31. Fig. 32–34, radial sections, scale above Fig. 3.)

Fig. 35–38. Wood sections to show growth rings. 35–36. *Robinia pseudo-acacia* (Carlquist, s.n.).—35. Transection showing earlywood with large vessel, containing tyloses, above; latewood of preceding year below.—36. Juncture between growth rings at higher magnification, latewood below center.—37. *Parkinsonia aculeata* (Carlquist, s.n.). Earlywood begins in upper half of photograph; latewood of preceding year in lower half.—38. *Stanleya pinnata* (Biss-

When only a single cell of parenchyma is present at the end of a growth ring, as in *Populus grandidentata* Michaux (Fig. 40), one could argue that such a layer could be either terminal or initial. However, Fig. 40 clearly shows the parenchyma layer to be the narrowest of the layers of the growth ring, and thus it must be called a terminal parenchyma layer.

Functional interpretation of Type XI growth rings.—The interpretation of terminal parenchyma as a reserve tissue for starch or other photosynthates seems the simplest explanation. Such storage would help initiate a rapid flush of growth, presumably mostly in springtime. This would not readily explain the occurrence of initial parenchyma, however: at first glance, this parenchyma seems to be available for storage when the shoot is leafing out and is not yet at maximal photosynthate production. However, neither terminal nor initial parenchyma bulks large in dicotyledons as a whole. Living (nucleated) fibers in wood (Wolking, 1969, 1970, 1971), vascular rays, axial parenchyma, parenchyma between bands of xylem in woods with successive cambia, and parenchyma accompanying interxylary phloem (Carlquist 1975b) all represent known sites of photosynthate storage in dicotyledon woods, and these are perhaps much more important than initial or terminal parenchyma for storage. Because rays are available for radial transport of photosynthates, initial parenchyma of the preceding year could serve as a storage site for production of new shoots. One could generalize from viewing growth rings of many woods under the microscope that there is much more investment in wall material (and therefore photosynthates) in latewood than in earlywood. The occurrence of initial parenchyma represents a minimal investment of photosynthates in wall material at the season when leaves are producing smaller quantities of photosynthates.

Type XII. Wood diffuse porous but initial parenchyma present. This type is tentatively presented because of Chowdhury's (1964) presentation of a table of diffuse-porous species which have initial parenchyma. These include Combretaceae, Fabaceae, Meliaceae, and Santalaceae. Whether or not this phenomenon represents growth-ring activity in the sense of the other types discussed here needs investigation.

Type XIII. The occurrence of cork bands (interxylary cork) demarcating growth rings is a special phenomenon, found mostly in certain desert shrubs

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ing 253, RSA). Latewood vessels in the parenchyma band, center; earlywood of succeeding year above the band. (Fig. 35, 37, 38, magnification scale above Fig. 1. Fig. 36, scale above Fig. 3.)

Fig. 39–42. Wood sections to show growth rings.—39. *Krameria grayi* (Bissing 1900, RSA). Growth ring plus portions of two others; bands of initial parenchyma at beginning of the two earlywood portions.—40. *Populus grandidentata* (Potzger 7286, RSA). Portion of transection at high magnification. A single layer of parenchyma (dark file of cells) between the latewood (below) and earlywood (above).—41. *Artemisia tridentata* (Carlquist 1701, RSA). Prominent

and cacti, shown here for *Artemisia tridentata* (Fig. 41). The related species *A. filifolia* (Fig. 42) lacks interxylary cork. Interxylary cork bands occur in conjunction with some form of growth-ring activity, and perhaps should not, therefore, be recognized as a separate growth-ring type. However, they are a distinctive feature in some species, and may have significance in channelling water in particular portions of the xylem. The reader can find the phenomenon reviewed by Ginzburg (1963), Moss (1934, 1936, 1940), Moss and Gorham (1953), and Waisel et al. (1972).

Experimental Evidence Concerning Growth Rings.—The data of Bissing (1976) is a form of evidence which can be regarded as experimental. Bissing collected wood samples of selected species cultivated in the Rancho Santa Ana Botanic Garden. He also collected wood samples for each of these species from the wild populations from which the Botanic Garden plants were derived (all cultivated material is supported by herbarium specimens from the population of origin). Climatic and ecological data are known rather precisely for the Botanic Garden, and climatic records can be consulted for the source areas for the various species. Bissing's results showed increase in ring porosity for the Garden material in only one case (*Lupinus albifrons*) for which the Garden was judged to be a more xeric habitat than the wild locality in some respects. The reverse, as one might expect, was more common. Growth rings were less marked or virtually absent in Garden material of *Calycanthus occidentalis* H. & A., *Leptodactylon californicum*, and *Rhamnus californica* Esch.: for these, the Botanic Garden was more mesic than the source areas.

Bissing found a small increase in vessel diameter in cultivated specimens compared with their wild representatives, seemingly validating the concept that greater water flow in xylem is related to greater water availability and that, in turn, a more rapid and prolonged growth season based on greater soil moisture is involved. Where vessels are wider in diameter, fewer per unit of transectional area can be accommodated, and Bissing found a clear decrease in vessels per sq. mm. of transection in the representatives from the more mesic habitat (i.e., the Botanic Garden in the case of most species, the wild for a few from highly mesic natural habitats). Narrower vessels tend to be more highly grouped. Consequently, Bissing's finding that the 16 species for which the Garden was the more mesic habitat mostly (12 of

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band of interxylary cork delimits bottom third of photograph; latewood below cork, earlywood above it.—42. *Artemisia filifolia* (Detweiler 23, Yw-26678). Earlywood in upper half; latewood of preceding year, lower half, terminates in large numbers of very narrow vessels. (Fig. 39, 41, 42, magnification scale above Fig. 1, Fig. 40, scale above Fig. 3.)

them) had a higher number of vessels per group in the Garden might be surprising: production of a greater volume of conductive tissues to accommodate greater flow of water per unit time is presumably the overriding cause. Suggestive of the Type IX growth-ring data above, as well as my earlier (1975a) correlation between fewer bars per perforation plate and greater xeromorphy, Bissing found that *Myrica californica* Cham. & Schl., *Platanus racemosa* Nutt., and *Rhododendron occidentale* (T. & G.) Gray showed a decrease in bars per perforation plate in the cultivated material. This was related to the fact that the Garden is more xeric than the wild for these species, according to Bissing.

Huber (1935) found that large earlywood vessels are likely to be formed when more water is available in the soil and air is relatively humid. This would accord with the idea that such "vulnerable" vessels correlate with lower tensions in water columns.

Growth Rings on a Floristic Basis: Desert Habitats.—Recent work on growth rings has perhaps covered tropical areas more thoroughly than temperate areas (Chowdhury 1939, 1940, 1941, 1965; Tomlinson & Craighead 1972). However, in compiling the above system, the apparent adaptations of wood anatomy in a highly xeric portion of the Californian flora, the Mojave Desert and nearby desert regions, came to mind. The point of citing woods in this area is to stress that essentially all of the woody plants in this region have well-marked mechanisms, evident in wood, for dealing with drought, and that many of these involve distinctive growth-ring phenomena. There are exceptions. Cacti are CAM plants and wood formulations of cacti which are markedly or even slightly succulent do not conform to patterns based on plants in which transpiration patterns are more normal. Likewise, C_4 photosynthesis characterizes the woody Chenopodiaceae (*Atriplex*, *Grewia*) and Zygophyllaceae (*Larrea*), and may be of overriding importance in that foliar patterns, not wood characteristics, are the prime tool for dealing with the environmental situation (Johnson, 1976) in C_4 species. Some desert shrubs are succulent (e.g., *Fouquieria*) or lose all of their leaves during the warmer part of the year, and thus are not dealing with stress conditions (e.g., *Lycium*). Where leaves and their physiology are buffers between the environment and the conducting system, one surely cannot expect wood patterns to be the same as in woody plants which lack these buffers. For this reason, wood of Asteraceae proved a sensitive indicator of and key to the environments in which they live (Carlquist 1966). Asteraceae of the Californian deserts are C_3 plants, with a single exception (Johnson 1976), so that their wood would reflect environmental patterns more directly than would wood of C_4 or CAM plants is not surprising. I stress these points because some recent authors find that evolutionary hypotheses are invalidated for them if alternate pathways produce exceptions.

In the case of Mojave woods, lack of strongly marked growth rings can be seen in shrubs which have thick-walled vessels in secondary xylem, tracheids as the imperforate elements, and various foliar devices to modify typical transpiration patterns. *Larrea* (Fig. 1) and *Krameria* (Fig. 39) illustrate these tendencies, and have moderate growth-ring activity.

Before I surveyed growth rings, I would not have guessed that presence of tracheids as imperforate elements, as in *Larrea* and *Krameria*, was so pervasive in woods of dry habitats. Surely only the high degree of safety of the tracheid as a subsidiary conductive element not subject to massive disabling by air embolisms as vessels are can explain the over-representation among the Mojave woods of tracheid-bearing woods. For example, *Rosa-ceae* (*Adenostoma*, *Fallugia*, *Purshia*) bulk very large in the California deserts, and have tracheids in addition to vessels in woods. As noted above under growth-ring Type V (*Cercocarpus*, Fig. 12), not only are tracheids the subsidiary element in woods of this family, they predominate greatly over vessels or are exclusively the type present in the last several layers of each growth ring in *Cercocarpus*. Such plants as *Ephedra* (Fig. 10) are classic in this regard, but one may also cite such desert genera as *Forsellesia* (Fig. 13) and *Crossosoma* of the Crossosomataceae as well as *Mortonia* of the Celastraceae as examples of Type V growth rings.

The presence of conifers (*Pinus*, *Juniperus*) in the Californian deserts probably relates to the safety inherent in their wood, as discussed under Type II growth rings. Type III growth rings lack such safety in latewood and are therefore not to be expected in desert areas, with few exceptions. Type IV, however, features numerous small-diameter latewood vessels which would confer safety and this type is present in the numerous Asteraceae and Lamiaceae which inhabit Californian desert regions. Type VI, although probably rare in dicotyledons at large, occurs in *Artemisia spinescens* (Fig. 16) and is very likely highly adaptive in the Californian deserts because the vessels of the earlywood are so numerous and narrow in diameter that addition of more such vessels in the latewood is of no great advantage. Type VII is probably rare in dicotyledons at large, but certainly must be one of the mechanisms whereby *Arctostaphylos* has occupied sub-desert and even some desert localities; vascular tracheids and narrow vessels (Fig. 18–20) occur in latewood in *Arctostaphylos*. Type VIII is not to be expected in desert areas because of its lack of latewood safety, and indeed apparently does not occur in deserts. Type IX is not to be expected in desert areas because woods with scalariform perforation plates even in latewood only probably represent too mesomorphic a formulation to correlate well with desert habitats, as far as we now know. Type X is exemplified by *Artemisia* (Fig. 41, 42) and indeed is to be expected in desert areas primarily: the huge numbers of very narrow vessels alone in these woods would provide a redundancy adapted to water stress. Type XII is a tropical type not found

in xeric areas as far as I know. Type XI growth rings, based on marginal parenchyma occurrence, can be expected in any type of habitat because they do not seem related to xeromorphy any more than to mesomorphy, and their occurrence in *Krameria* (Fig. 39) is not surprising. Type XIII, interxylary cork bands, is predominantly a desert phenomenon, as in *Artemisia tridentata* (Fig. 41) and certain other species of *Artemisia*, perhaps because xylem is so completely encapsulated and thereby dissociated from some environmental effects.

A scattering of desert shrubs have vascular tracheids (e.g., *Gutierrezia* spp., *Lepidospartum squamatum*, *Haplopappus* spp.: Carlquist 1960). Vascular tracheids have greater safety than vessel elements and occur in xeric habitats (Carlquist 1975a).

One may note that Californian deserts are exceptionally rich in one growth-ring type so obvious as to make mention essential, because it could easily be overlooked: the wood of annuals. In annuals, vessels can become progressively more numerous and narrower during the season; vessel elements also become shorter. This applies to annual stems of perennials also (e.g., *Aster spinosus* Benth.)

The above commentary on growth rings suggests that, as we may suspect from the work of Chowdhury (1964) and Tomlinson and Craighead (1972), there are all degrees of transition between diffuse-porous and ring-porous conditions. This variation is not merely in degree of growth-ring formation, but in the particular types present.

Quantification, Ecology, and Statistical Significance

Comments on the potential of the field of ecological wood anatomy seem necessary because there seems to be potential misunderstanding of how to obtain ecological evidence or data, how it can be quantified and whether quantification really means anything; how to relate this to plant structure; and about how to interpret plant structure when evolutionary tendencies are as complicated as they are in angiosperms, rife with parallelisms, reversions, and multiplicity of adaptations within a single parent plant.

One could, with justification, state that very few types of data in wood anatomy are statistically significant, or ever can be. For example, those who have one or two wood samples of a species, from disparate sources and of various sizes, and who calculate range, means, standard deviation and standard error for wood cell dimensions are unaware of the hollowness of these figures. Only rigorously sampled woods (the sampling monitored by statistical parameters) from plants where one can resample portions of an individual can produce statistical apparatus applicable broadly. However, if work that has used the plausible interpretations of data rather than followed

strict laws of statistical falsification were denied validity, much of our work in organismal biology would be found to have shaky foundations.

There is some tendency in presenting data on wood cell size to use numerical ranges for any particular feature rather than means (e.g., Vliet 1979). Means probably represent the best way of visualizing the functional nature of wood cells (e.g., Vliet 1979, fig. 5b). Ranges in quantitative wood features are very often so wide that no reasonable conclusion can be drawn from them (e.g., Vliet 1979, fig. 5b). Vliet's data do, however, tend to show when expressed as means that longer vessel elements occur in more mesomorphic situations. Where, for example, conductive cells are concerned, the extreme ends of ranges in sizes represent relatively few cells, and the conductive characteristics of the wood are, on the other hand, represented by the median in that the bulk of the wood cells, not the extremes, dictate a wood's capabilities.

One is sympathetic for the desire to use quantified ecological data, but unfortunately the easiest types of data to quantify do not yield the information one might wish. Graaff and Baas (1974) examine the relation of latitude and altitude to quantitative features of wood anatomy, continuing a comparison which can be dated back to Kanehira (1921). When woods from a wood collection are studied, as they were in the Graaff and Baas study, data on labels of voucher specimens permit relatively precise determination of altitude and latitude. But does this equate with ecology? If altitude and latitude were criteria, London should be more severe than St. Johns, Newfoundland, which is south of London. What we must look for, of course, are the ecological factors and ecological regimes themselves—and often ecological extremes account for plant structure and distributions, rather than modal ecological situations. Because xylem is a tool for transmitting, under tension or pressure, water from substrate to transpiring foliage, the factors directly related to this process are the important ones: rainfall and water availability in the soil; temperature; humidity; exposure to sun or shading; seasonal extremes; and others which, for example, collectively formed the basis for my (1966) listings which are very crude compared with what should ideally be done. Chowdhury (1939, 1940, 1941) was well ahead of his time in comparing actual ecological factors, graphed throughout a year, with the growth ring formed during that year.

However, one must realize that a plant is not a single tool but a group of them; foliar apparatus may diminish transpiration and thereby alter the wood formulation beyond what is normal in a particular climate, as is true for C_4 and CAM plants. If one collects data on xylem of *Sequoia* (Taxodiaceae), *Rhododendron* (Ericaceae), and *Myrica* (Myricaceae), all of which grow together in the redwood forests of northern California, one will see three different wood patterns. That does not invalidate the idea that the

three have xylem adapted to that environment, because the three *exploit* the environment in different ways. Quantification of wood features simply proves that the three woods are different; the biologist must explain why. Vliet (1979), commenting on my (1977a) paper on wood of florulas in Western Australia and on my (1977b) concepts of vulnerability and mesomorphy, stated that "even the data presented by Carlquist himself lend little support to the relevance of the artificial units 'vulnerability' and 'mesomorphy': the values he presented for different vegetation types in Australia are obviously not significantly different because of the wide range in variation type found within each vegetation type." There is the implication that each florula should conform to narrower ranges, and that florulas should not overlap with each other in quantitative wood characteristics, and that some kind of statistical significance should be obeyed before we can begin to think of wood anatomy as related to ecology, and use combinations of features to see how plants adapt to their environment. Vliet might well consider the statement of Baas (1976, p. 164): "each genus has its own individual pattern." We must be willing to deal with evolutionary complexities and compensations, parallelisms and multiple adaptations. The fact that wood patterns quantitatively follow ecological factors in the florulas of southwestern Australia so closely is much more significant to me than the fact that statistical separation among the florulas is not achieved.

Interestingly, the correlation between wood anatomy and ecology appears closer to Baas and Zweypfenning (1979) in the case of Lythraceae than to Vliet (1979) in the case of certain Combretaceae. The leaves of herbaceous Lythraceae are not adapted to limiting of transpiration; they lack the devices for doing so that Combretaceae have, such as the long-lived leaves of *Terminalia* which buffer the effect of the environment. Wood of Asteraceae correlates closely with habitat (Carlquist 1966 and the papers cited therein), and shows a considerable range of structure: the wood is evidently a relatively unbuffered tool for dealing with water relations in this family, whereas in other families (e.g., Cactaceae), wood is very much buffered. But this does not invalidate the functional hypothesis of wood evolution (Carlquist 1975a) at all. In the floristic assemblages of my 1977a paper, each plant within an assemblage has its own compromise of features which permit it to exploit each habitat and survive there. To expect identical features and strategies would be naive. The fact that wood data do correlate, albeit loosely, with each florula shows the surprising extent to which these strategies, although divergent, are fairly close for each area: plants with rain forest xylem don't grow in the deserts of Australia. Vliet (1979) finds my vulnerability and mesomorphy ratios not exceptionally low when he calculates them for mangrove Combretaceae, and decides my concepts are invalidated because his expectations are not met. Mangroves are unusual where water

stress is concerned because although water tensions may, as he claims, be high in mangroves (he does not cite data) at times, there is no shortage of water, and such a regime is undoubtedly related to lower vulnerability and higher mesomorphy ratios than would be true for a desert shrub.

The differences between lengths and diameters of vessel elements in roots as compared to those in stems seem to Gibson (1977a) not to be correlated with physiology, because gradients in tensions from top to bottom of a plant are not as sharp as the gradients in vessel data. The various portions of a plant differ in efficiency in conduction and in safety in the conduction system, however, and Zimmermann's (1978a, 1978b) statements on gradients in anatomy within a plant and their functional explanations may be followed. To expect precise correlation between measured tensions and vessel dimensions when factors other than tension (e.g., safety) are concerned would be unfortunate. Isolation of ecological factors is notoriously difficult. Even our measurements in ecology may, to an appreciable extent, be inapplicable. If, for example, we carefully measure the daily march in changes of tension in water columns of the xylem, do we measure the factors to which the xylem is adapted? The extreme tension for one hour for one day per year which was not measured could very likely dictate failure or success of a system such as this, rather than the typical rise and fall of tensions. Plants are optimal engineering structures, which means that in their natural habitats, their physiological systems rarely fail, and have, on the contrary, a margin of safety. Zimmermann's work rightly stresses such concepts as safety in conductive systems (by which Zimmermann means redundancy of vessels, so that an excessive number of vessels is never disabled), but safety cannot really be quantified, because we cannot know how many vessels are disabled for how long in a particular stem. I invented (1977b) a term, vulnerability, which is a very rough inverse equivalent to "safety" and illustrative of the problems of trying to define "safety."

Wide, short vessels characterize lianas, as is well known and has been stated many times (e.g., Ayensu and Stern 1964; Carlquist 1975a; Vliet 1979). However, wide but longer vessels may be found in lowland tropical forest trees. This latter observation has been admirably stressed by Baas (1976). The water-transpiring capacities of large-leaved trees in sunny lowland localities must be great, and the occurrence in such trees of wide vessels to match the high flow rates related to such transpiration represent a logical adaptation.

Large leaves in sunny lowland localities have a high heat-carrying capacity; if ground water is abundant, transpiration is active, and rates of flow feature large volume per unit time, this is an adaptive system. Large-leaved conifers with thin, horizontally displayed leaves (e.g., *Podocarpus blumei*) are mostly understory plants, however, probably related to the fact that

conifer xylem does not convey high volumes per unit time. Integrating leaf types and their physiological characteristics with xylem and with ecology at the same time represents a definite challenge for future research.

Our data on the characteristics of wood anatomy in terms of particular vegetation types is still quite rudimentary. For example, Styer and Stern (1979) thoughtfully compare their data for *Deutzia* to my (1975a) data for desert shrubs. However, data on montane shrubs of temperate to subtropical regions, areas where *Deutzia* itself grows, or even Arctic shrubs (although they are more extreme) as studied by Miller (1975) might have offered closer comparisons.

Incidentally, I should note that my data on vessel (and tracheid) diameters were derived in the way standard for wood anatomists: each vessel selected was measured at its widest point, and the measurement includes the wall. Unfortunately, this method of measurement is convenient for comparative work in wood anatomy, but it is not ideally suited to studies on functional anatomy of woods. Measurements of lumina of vessels (vessel diameter excluding walls) would be better for understanding wood on a functional basis. If vessels are relatively wide, wall thickness does not comprise an appreciable portion of their transectional area. Where vessels and tracheids are very narrow, however, thickness of walls represents an appreciable figure. Woods with tracheids only and woods with numerous narrow vessels have a smaller conductive area than data such as mine would indicate.

Relatively narrow thick-walled vessels or tracheids may be able to withstand enormous tensions, as in latewood of conifers or in the woods of *Larrea*, *Cistus*, and *Krameria*, without deformation. Although there is little experimental evidence on the ways in which woods resist tensions in water columns, one would assume that as optimal design structures, wall thickness is always more than enough, in any species, to prevent deformation under extreme conditions. I do not find that large amounts of cellulose (and lignin) in such thick walls represents merely deposition of excess photosynthates by the plant, a byproduct of the fact that thick-walled imperforate cells in the same woods as vessels serve mechanical functions to support the plant and resist torsion and shear. Since vessel wall thickness does range widely within dicotyledons, a functional explanation seems in order, and at present, wall thickness of cells actively involved in conduction appears to correlate well with probably or known water tensions measured in these plants.

In population biology, we can inquire into how natural selection is inducing genetic change and quantify this. However, at best we can study the effects of only a few genes over a short period of time, and situations must be unitary in their simplicity. How can we approach the "natural experiments" in which adaptations we see today were achieved millions of years ago, however? Shifts such as origin of vessels or loss of bars from the perforation plate cannot be duplicated under experimental circumstances.

The distribution of characters systematically, ecologically, and phytogeographically does yield information, albeit in a confusing fashion, on how natural selection acted in the geological past. However, these distributions do not describe evolution in any uniform ways, and no single method can be followed. The worker must be prepared to know a group quite thoroughly, so that parallelisms, reversions, compensations, multiple ways of adapting to a single ecological factor, and "invisible" adaptations such as crassulacean acid metabolism can be elucidated. Some workers have resorted to thinking of wood evolution as containing nonadaptive or capricious pathways, the "*patio ludens*" of Baas (1976), or, as in the case of Dickison (1977) an understandable feeling of bafflement. However, particular systematic groups have had complicated histories. A group with xeromorphic wood patterns can shift into very wet localities. For example, neither *Plantago* (Plantaginaceae) nor *Dubautia* (Asteraceae) have wood adapted to very wet places, yet several species of *Plantago* and one of *Dubautia* are endemic on perhaps the wettest mountain on earth (Carlquist 1970, 1974). *Dubautia* in the Hawaiian Islands has a series of species which show progression from probable dryland ancestry into wet forests (Carlquist, 1974). The Hawaiian species of *Euphorbia* have a similar history, and we have the evidence of a physiological feature: the chamaesyroid Euphorbias have C₄ photosynthesis around the world, but this adaptation to xeric habitats has been retained in the Hawaiian species, even those in rather moist forest (Pearcy and Troughton 1975). Baas (1976) claims that I have gone "much further than Bailey" in neo-Darwinistic interpretation, but one can ask why one should not progress further than Bailey? Actually, Bailey (1966) endorsed the correlations I found in my early work between ecology and wood anatomy. I do feel that looking for potential functions is a more productive method of inquiry than looking for null hypotheses or for random variation. Patterns of evolution are often extraordinarily complex, but the fact that some groups of plants do not illustrate evolutionary trends in their simplest form does not seem sufficient reason to find evolution an unworkable hypothesis.

The Adaptive Morphology of the Vessel Element

Zimmermann (1978a) says, "the length of vessel elements is functionally meaningless, as far as we know." Baas (1976) makes a similar statement. I (1975a) have offered explanations which Zimmermann and Baas presumably feel are insufficient, but clearly the distribution of vessel-element lengths within dicotyledons suggests that length of vessel elements and its change is clearly related to major and pervasive themes of evolution. This has been evident in the work of Bailey and Tupper, of Frost, of Kribs, of Barghoorn and of subsequent authors (see Carlquist 1961 or 1975a for full

citation of this period of work on wood evolution). Vessel-element length is not controlled by selective value of the imperforate elements which accompany them (Carlquist 1975a). An exception has been found in the case of *Stylidium* (Carlquist 1981), in which a short-term selection for longer fibers has probably occurred. There is no correlation in dicotyledons between habit and length of vessel elements and/or imperforate tracheary elements (Carlquist 1975a; Baas 1976). No suggestions other than mine (1975a) for phyletic shortening of vessel elements appear to have been offered, although there is general agreement that in each group of dicotyledons investigated, species in xeric habitats have vessel elements shorter than those in mesic habitats (e.g., DeBuhr 1977). Certainly the systematic and ecological patterns of vessel-element length are clear, but we have no experimental work on this topic, nor is it easy to imagine how that could be designed. If by "xeric habitats" we include areas with low humidity and with frost, we may have a broader definition which includes several sources of physiological drought. Perhaps then we can include *Ilex*; Baas (1976) was skeptical of the correlations earlier.

Simplification of the perforation plate phyletically with increasing xeromorphy, a theory I elaborated earlier (1975a) has been validated by various authors, such as Dickison et al. (1978) and Vliet (1979). Baas (1976), while agreeing in general, cites a few supposed exceptions, such as *Dillenia*, but Dickison (1979) says of *Dillenia*, "species from drier habitats possess vessel elements with predominantly simple perforation plates in response to adaptive selective pressures . . . the reduction in bar number within scalariform perforation plates in the drier habitat species is very apparent." Zimmermann (1978a) offers support in discussing why perforation plates tend to be simpler at lower levels in a plant body. This phenomenon is shown well in palms by Klotz (1977), who finds vessel types correlated with ecology in palms. My hypotheses (1975a) would suggest that more numerous bars per perforation as one goes from roots to stems to leaves of a palm would tend to correlate with higher tensions in a plant at higher levels, lower tensions at the plant base, during periods of active transpiration. Zimmermann (personal communication) tends to discount this explanation, because he feels that the scalariform perforation plate is not, as I have claimed, an effective means of preventing vessel deformation under tension. This is a point to be elucidated in future studies.

There are families of dicotyledons characterized wholly by long scalariform perforation plates (Carlquist 1975a, p. 152–153). Some of these appear very uniform, and no major ecological shifts within these groups occur. In these families there is very likely a simple explanation—the mesomorphic wood patterns cannot be modified evolutionarily and are limiting. The entire family Clethraceae has long scalariform perforation plates and is ecologically stereotyped (Giebel and Dickison 1976). Balanopaceae is also a uni-

formly mesic family with mesomorphic woods (Carlquist 1980). In the case of *Balanops*, neither vessel-element length nor number of bars per perforation plate vary much within the family. The number of bars per plate is slightly lower in *B. australiana* F. Muell., and may be correlated with the probability that this large tree may transpire large volumes of water per unit time, and selective pressure for correlatively high flow rates may account for simplification of the plate. *Balanops australiana* is still a rain forest tree. Only one species, *B. pancheri* H. Baillon, occupies a drier habitat, the lower slopes of serpentine hills in New Caledonia. It probably occurs in these zones not because of alterations in xylem (which is typical for the family) but because of alterations in the vegetative apparatus: smaller, narrower leaves; shrubby instead of arboreal habit; and shoots of short (2–3 yr perhaps) duration, innovated from roots continually instead of having a main trunk. Thus in *B. pancheri* shoots of limited size and duration can be innovated or die back in response to wet or dry periods.

Bissing (1976) compared woods of Californian native plants from wild localities and from plants of these same species, taken from those localities, cultivated in the Rancho Santa Ana Botanic Garden. Bissing judged the Botanic Garden to be drier (hotter in summer, with lower humidity and lower soil moisture) than the wild localities for three species with scalariform perforation plates: *Rhododendron occidentale*, *Myrica californica*, and *Platanus racemosa*. These were the only species in Bissing's study with scalariform perforation plates. One possible explanation, mentioned above for the Type IX growth rings and also for *Balanops australiana* (Carlquist 1980) would be that conduction of greater volumes per unit time is correlated with fewer bars per perforation plate. There are unpublished experimental data which tend to show that bars on perforation plates slow conductive rates not greatly but appreciably. Even a moderate lessening of conduction would constitute a selective force if this is true. That high transpiration rates raise flow rates and that this could either cause phenotypic modification (in the Bissing studies) or be a long-term selective factor for simplified perforation plates should be considered. Viewing ecological opportunities for dicotyledons at large, one can say that very likely at all times in their history, the number of drier niches available has been greater than the number of wetter niches, so that the predominant trend toward xeromorphy in wood of dicotyledons is understandable.

However, high tension in water columns might constitute a selective advantage for simplification of a perforation plate, not by removal of bars necessarily; retention of few but wide bars might also be an outcome. This hypothesis (Carlquist 1975a) was mentioned above in connection with Type IX growth rings. The ideas were formulated to account for the fact that the tribe Rhizophoreae of Rhizophoraceae have stabilized so remarkably with few but wide bars per perforation plates. These woods also have scalariform

lateral wall pitting on vessels and gelatinous walls on all cells, features which tend to reflect adaptation to high tensions in the wood, with correlative physical shrinkage and expansion. This hypothesis for such woods has been dismissed by Vliet (1976), who offers no alternative hypothesis for this fascinating and curious phyletic. DeBuhr (1977) accepts my hypothesis for similar phenomena in Sarracenaceae. The persistence of scalariform perforation plates in general and for the *Rhizophora* type in particular does not seem adequately explained by saying that in these cases, there is no positive selective value for removal of bars on the perforation plate.

Zimmermann (1978a) has offered a functional explanation for why scalariform perforation plates in dicotyledon vessels should be retained phylogenetically. He claims that like sieves, they prevent aggregation of air bubbles formed when wood thaws, and thus these bubbles are resorbed more readily and the wood restored to functional capability more securely. This appealing explanation does not seem to be supported by the fact that families which have scalariform perforation plates are mostly in frost-free regions (Carlquist 1975a, p. 152–153; Baas 1976). One high-latitude Arctic florula in which wood anatomy has been examined for 10 dicotyledon species (Miller 1975) shows that half have scalariform perforation plates, half simple ones. A genus cited by Zimmermann as an example of the scalariform condition in cold climates, *Salix*, is represented in Miller's florula only by species with simple perforation plates. The number of dicotyledon species with scalariform perforation plates which occur in areas completely free from frost is so large that Zimmermann's explanation, although theoretically possible, is inapplicable in the case of most woods with scalariform perforation plates.

Zweypfenning (1978) has presented an appealing hypothesis to account for function of vestured pits. His idea is that vestured pits resist aspiration and rupturing, and therefore would be of advantage in dry situations where high tensions could be expected. He appears to withdraw this explanation because, as he notes, exceptions to the ecological correlation could be found and might even bulk rather large. There does not need to be perfect correlation, just as the occurrence of flightless birds does not negate the function of feathers in flight. However, experimental work could be undertaken, particularly to see if rates of flow are the same in vestured as in nonvestured pits.

Balancing experimental work against interpretations suggested by systematic and ecological distribution of a character is indeed a fine art, the problems of which can be seen by examining such papers as Giordano et al. (1978). Jeje and Zimmermann (1979) show that wall sculpture such as helical striae on vessel walls may reduce flow resistance by as much as 40% compared with ideal capillaries. Helical sculpturing of this sort occurs primarily on vessel walls of dry-country shrubs with presumptively slow conductive rates (Webber 1936); it also occurs on walls of certain wood parenchyma

cells (Welle 1975), in tips of vessel-element tails, places where rapidity of conduction would seem of no selective value. It occurs in tracheids of some gymnosperms (Taxaceae; various Cupressaceae; a few Pinaceae) but most gymnosperm tracheids lack such sculpturing, and the ecological distribution of the sculpturing shows no pattern. The effect of spirals, vested pits, and warty lumen surface on flow rates as demonstrated experimentally offers further opportunities, but integrating this with an interpretation that involves phyletic evolution will evidently be one of the more difficult problems in wood anatomy.

Reversibility.—The “irreversibility” of the major trends of xylem evolution as stated by Bailey and others are probably misleading if read in an excessively narrow sense, and therefore are capable of being misunderstood. Baas (1973) has given a useful discussion of this concept. If we follow, say, vessel-element length in a single stem, one can see that it changes markedly with the years, or that markedly more vigorous individuals have vessel elements markedly longer, dwarfed individuals vessel elements markedly shorter than the average condition. This “noise level” is not what is involved in reversibility or irreversibility.

I have illustrated, as Baas notes, several instances in which vessel-element length has increased with ecological shift into wetter areas, as in *Dubautia* (Carlquist 1974).

The irreversibility Bailey had in mind was an “over all” kind of tendency, not what one sees at a taxonomically local level. We know now that shorter vessel elements tend to be associated with drier habitats, longer vessel elements with wetter ones (see Carlquist 1975a for a review). Given that, we can add the observation that predominantly angiosperms have evolved from tropical to temperate, from tropical to cold climates, from wetter to drier areas. Moist tropical areas have evidently been saturated since angiosperms originated. The number of adaptations and changes required for life in cold or dry areas is considerable, so that once the extreme niches have been reached, reversal of a large number of features becomes a statistical unlikelihood: there are already too many competitors for the mesic niches to promote the reversal of all of these characters. That reversal can occur if there is opportunity for radiation into mesic areas. Oceanic islands, which tend to receive a high proportion of immigrants from dry areas rather than from mature, wet forest, are one such example, and thus the Hawaiian composites, lobelioids, violas, and euphorbias, among many examples, have reversal in vessel-element length evolution (see Carlquist 1974). Other suddenly opened habitats, such as volcanic uplands near the equator (e.g., Mt. Kenya; Colombian páramos) can be cited, and these, too, have groups (*Espeletia*, *Senecio*) in which reversal in vessel-element length has occurred. However, in all of these, there is a mechanism, paedomorphosis (Carlquist

1962) whereby these changes have occurred, and if one examines this process one may decide that there is a special mechanism for this reversion. We must examine other features and other groups which do not represent a special phenomenon such as paedomorphosis.

Can number of bars on perforation plates increase, as well as decrease, as Baas (1973) suggests? Perhaps, but I would guess within what one could call "noise level" limits, upping number of bars to a portion of the range in a phylad, not exceeding the range in bar number which does exist in that phylad is possible. In any case, phyletic from simple back to scalariform perforation plates has not been demonstrated: once the genetic information for forming bars on perforation plates has been lost, it cannot be reacquired, evidently. The multiperforate perforations figured by Gottwald and Parameswaran (1964) for Dipterocarpaceae are what one would imagine if such a reversion did occur. The scalariform perforations of *Vitex lucens* Kirk, which run tangentially rather than radially and are thus anomalous (Butterfield and Meyland 1975) are perhaps more difficult to explain. There are, in dicotyledons, families in which secondary xylem and even metaxylem has only simple perforation plates but protoxylem has scalariform perforation plates (Bierhorst and Zamora, 1965). Thus, the "genetic information" has not been lost, and by paedomorphosis, or juvenilism, scalariform perforation plates in secondary xylem could be evolved in such a group. I know, however, of only one candidate for this phyletic, *Pentaphragma* (Carlquist 1975a). A large segment of dicotyledon families lacks bars on perforation plates in both secondary and primary xylem. I see no way in which reversion to the scalariform condition could occur in these groups. However, I cannot imagine selective forces which would supplant simple plates with scalariform ones in any case.

In addition to predominant phyletic toward colder and drier by angiosperm groups and in addition to inability to form structures for which genetic information has been lost such as scalariform perforation plates, Baileyan "irreversibility" connotes simultaneous evolutionary shift of numerous features within the secondary xylem, and of complex *correlation of a functional sort* among these features, the complexity so great that reversion no longer becomes possible to any statistically appreciable degree. As one portion of this enmeshing of characters with each other, one may cite increased division of labor in tracheary elements, leading to libriform fibers with minimal conductive and maximal mechanical function, and to vessel elements, with maximal conductive and minimal mechanical function. Phyletic to substitute intermediate fiber-tracheidlike cells is difficult to imagine, for both of the extreme cell types are optimal, and shifting the proportion of each within a wood is very easy. Likewise, specialization in ray parenchyma has occurred in a manner parallel to specialization in vessel elements. If the phyletic increasing procumbency of ray cells represent a more efficient pho-

tosynthate-conductive system in which more rapid flow rates of photosynthates can be achieved, and if a wood has developed a conductive system (wide vessels with simple perforation plates) to accomodate more rapid flow rates for water, it seems very unlikely that one system could revert without the other reverting also. As each adaptation is added to the whole, not only is retrograde evolution less and less likely statistically in such a system, reversion to suboptimal structural types would encounter strong negative pressure. By "suboptimal" one could read not so much "inferior" as "optimal in a limited range of situations." If one adds together all the trends of specialization discovered in wood by Bailey's students (see Carlquist 1961, 1975a), and asks what likelihood there is that these trends could reverse collectively or in groups even, one gets very low statistical odds, but I feel that the functional interrelationships of the features are of overriding significance. If irreversibility is related to complexes of interrelated features, interrelated on functional grounds, our progress in understanding irreversibility is understandably slow, since functional interpretation of wood structure is still a field in ferment. Students of wood evolution have not made clear statements on irreversibility in terms of each character and the degree to which reversibility is possible individually or in combination with other features. Such statements are probably neither possible nor very helpful, imagining they could be made, but we can reasonably expect better statements on irreversibility and the central role of the vessel element and its evolution to emerge over the next several decades.

Fiber Dimorphism

Study of certain Heliantheae prompted development of a theory of fiber dimorphism as the explanation for certain modes of axial parenchyma occurrence (Carlquist 1958). This idea was presented in graphic form later (Carlquist 1961). The concept of Arnold (1951) that nucleated fibers represent derivatives of libriform fibers is allied but not the same: the fibers with which he was dealing were monomorphic, and he is claiming that in some woods, nuclei persist in fibers whereas the fibers would have died sooner in ancestral types. In *Aeschynomene* (Fabaceae), libriform fibers have been supplanted, phylogenetically, by parenchyma cells in the axial xylem, but they are monomorphic. In my 1961 book, I stressed that fiber dimorphism occurred in certain cases only. Various workers appear to have been very perceptive in analyzing where this concept applies and where it does not. In addition to the *Dubautia*-*Argyroxiphium*-*Wilkesia* in Asteraceae, one might cite some legumes, judging from Cumbie's (1960) work, notably *Erythrina* and the tribe Phaseoleae. However, these legumes have not been analyzed in this regard. Baas and Zweypfenning (1979) cite fiber dimorphism convincingly for Lythraceae and demonstrate that fiber dimorphism in Me-

lastomataceae should be considered as originating independently from that in Lythraceae.

Where woods partly lack fibers as a result of succulence, one may suspect that fiber dimorphism is occurring; such phylads may ultimately show replacement of all fibers by parenchyma cells. Certainly *Brighamia* among the lobelioids can be cited in this regard (Carlquist 1962). Such succulents as *Talinum guadalupense* Dudley, *Carica candamarcensis* Hook. f., and *Crassula argentea* L. f., also discussed in that paper, show fibers supplanted by parenchyma. We do not know in these particular succulents whether ancestors went through a stage involving fiber dimorphism. In fact, I rather suspect they may not have because I do not happen to know representatives of these families with dimorphic fibers. However, the concept of fiber dimorphism does, on the basis of this reasoning, probably apply in cacti, in which various degrees of fiber presence or absence may be found, judging from the data and illustrations of Gibson (1973, 1977a, 1977b, 1978a, 1978b). We need additional data on which groups possess fiber dimorphism, which do not, and what the probable reasons for origin of dimorphic fibers are. Work on nucleated fibers, such as that of Wolkinger (1969, 1970, 1971) may give some useful hints on probable function of dimorphic fibers, since the two phenomena might be functionally similar.

Paedomorphosis

The term paedomorphosis was applied to characteristics of primary xylem which continue for prolonged periods into secondary xylem, sometimes for the entire life of a particular plant (Carlquist 1962). This theory was based on wood of cycads and, in dicotyledons, wood of annuals, rosette trees, stem succulents, "woody herbs," and other plants in which xylem accumulation is not in accordance with that of a typical woody plant in rapidity of accumulation or morphological features, or both. Groups such as the lobelioid Campanulaceae (Carlquist 1969) have species which illustrate this concept well, and indeed, the idea is an obvious one to those acquainted with growth forms such as those named. The idea has been accepted widely (Anderson 1972; Bailey 1966; Baas 1977, 1979; Cumbie 1963, 1967a, 1967b; DeBuhr 1977; Gibson 1973, 1977a, 1977b, 1978a; Koek-Noorman 1976; Takhtajan 1969; Walsh 1975). A functional dimension has been added to the original theory (Carlquist 1975a).

One element of the theory of paedomorphosis explains the occurrence of rays in which cells are predominantly or exclusively erect, ray types not even mentioned by Kribs (1935) and therefore probably not known to him, very likely because of his preoccupation with truly woody plants. Recently the paedomorphosis explanation of such rays and of other features referable to paedomorphosis has apparently become so thoroughly acceptable to

some authors that these features are cited and "paedomorphosis" mentioned without citation of the original concept (e.g., Baas and Zweypfenning 1979; Bridgewater and Baas 1978). Unfortunately in one reference (Bierhorst and Zamora 1965), the idea of paedomorphosis is incorrectly equated with Bailey's (1944) theory that phyletically, primitive features are eliminated from primary xylem later than they are from secondary xylem, so that primary xylem becomes a kind of "refugium" for more primitive features. Paedomorphosis is quite different: the tendency for primary xylem features (some of which are very likely rightly interpreted as primitive) to persist into secondary xylem, often for years or indefinitely, because of a change in the ontogeny.

However, one single reference (Mabberley 1974b) questions the theory of paedomorphosis. It does so on the basis of an astoundingly mistaken reading of the facts of plant anatomy. On the first page of Mabberley's paper is a salient misstatement: "the primitive characteristic [in the xylem of florally advanced families] include the occurrence of scalariform end-plates in vessel elements, features which are considered to be most like those of the tracheids thought to be antecedent to the vessel elements." Precisely the reverse is what I stated clearly in my 1962 paper: in these florally specialized families, the end walls of vessel elements uniformly bear simple perforation plates. These simple perforation plates are not infrequently found on vessel elements with scalariform *lateral wall pitting* in certain plants, and the theory of paedomorphosis both in its 1962 statement and its 1975a expansion explains why the most specialized perforation plates should be found combined with what is considered the most primitive lateral wall pitting (Frost 1931). Mabberley has confused perforation plates with lateral wall pitting. Mabberley (1974b, p. 978) quite mistakenly states, "Carlquist holds that in the xylem of such pachycauls, the presence of scalariform perforation plates is not primitive, but on the contrary advanced in being a feature of the primary xylem, characteristics of which are 'carried over' into the secondary xylem. This notion is the heart of Carlquist's 'Theory of paedomorphosis in dicotyledonous woods'." Thus we see that Mabberley's inability to distinguish between end-wall morphology and lateral-wall morphology in vessel elements is central to his attempt to contradict the theory of paedomorphosis, an unfortunate blunder which renders the entire paper meaningless. Because he fails to note the uniformly simple perforation plates of the woods concerned, he is forced to misstate my theory in a manner similar to the misstatement of Bierhorst and Zamora (1965) cited above.

In his attempt to discredit the paedomorphosis theory, Mabberley also cites a theoretical link between pith diameter and fusiform cambial initial length proposed by Philipson and Butterfield (1967). Baas (1976) and Koek-Noorman (1976) invalidate the Philipson and Butterfield theory both on the basis of studies of woods and on theoretical grounds.

The balance of Mabberley's (1974b) paper discusses growth-form considerations in such a way as to support his mentor, E. J. H. Corner, vocal proponent of primitiveness of pachycauly in angiosperms. One can welcome description and interpretations of pachycauls such as those of Hedberg and Hedberg (1979), based on comparative studies. One can also welcome physiological evidence which shows that upland arborescent chamaesyroid *Euphorbia* species in the Hawaiian Islands are derived from lowland herbaceous relatives (Pearcy and Troughton 1975). However, one cannot respect conclusions based on incorrect information and dependent on pen-and-ink drawings linked by arrows to denote alleged phyletic (e.g., Mabberley 1974a).

As a footnote to Koek-Noorman's (1976) paper, one should note that paedomorphosis is not in conflict with the "xeric conditions" in which *Rubia fruticosa* Ait. and *Crucianella maritima* L. grow. I hypothesized that milder conditions in which there is no marked annual cessation of growth is often correlated with paedomorphosis. *Rubia fruticosa* does, it is true, occupy lowland barrancas in the Canary Islands; I have seen it in these sites. These barrancas are drier than the laurel forests upland of them, but not nearly as dry as barrancas on mainland areas in the same latitude (e.g., Morocco). More importantly, mildness of climate for *Rubia fruticosa* is more a matter of freedom from frost in this insular climate. Lack of frost has permitted evolution of a long-lived shrub from what were probably short-lived ancestors, such as *Galium* represents. *Rubia fruticosa* also has aspects of succulence which minimize cessation of growth during the dry season. Similar considerations (perennation because of lack of frost) apply to *Crucianella maritima*.

We can wish, along with Gibson (1978a) that future considerations of paedomorphosis include details of first-order framework deposition of wall material on the vessels (the horizontally running bands) together with consideration of the second-order framework (vertically running strands of wall material). These considerations will very likely deal with the formation of vascular tracheids and vessel elements in cacti capable of shrinkage during periods of drought and therefore more deficient in the vertically running strands of wall material than the horizontally running strands (Gibson 1978b). Such considerations might even be important in analyzing other instances, such as the vessels of Vitaceae, which have scalariform lateral wall pitting which appears not so much a retention of a primitive feature but, whatever its evolutionary status, an accommodation to vessel function and physical characteristics of wide-diameter vessels.

The idea of Takhtajan (1969) that paedomorphosis is basic to origin of vessels in dicotyledon woods does not appear to be justified. That interpretation was an attempt to integrate the scalariform lateral wall pitting of vessels in woods showing paedomorphosis with the scalariform lateral wall pitting hypothesized by Frost (1931) as primitive in dicotyledons and the

scalariform pitting on earlywood tracheids of *Trochodendron* and *Tetracentron*. Woods which consist wholly of scalariformly pitted tracheids have insufficient mechanical support in arborescent plants unless the stems also contain special fiber zones, as in the tree ferns, or a massive sclerenchymatous cortex, as in the Lepidodendrales (Carlquist 1975a). Woods composed wholly of scalariformly pitted vessels must also contain imperforate tracheary elements with very strong walls or be, as in the case of *Vitis*, growth forms in which self-support is not a factor. The woods I described in paedomorphosis considerations are special growth forms in families with highly advanced floral features; these growth forms (e.g., succulents, rosette trees) show both in appearance and in anatomy what I (1975a) termed "release from mechanical strength." Such plants would be poor candidates for ancestors to the angiosperms. These growth forms are notably lacking in the families with floral features widely regarded as primitive. The wood of dicotyledon families such as Winteraceae, Theaceae, etc., is mechanically strong and does not fall into categories referable to paedomorphosis at all. Frost's concepts (1930a, 1930b, 1931) on origin of vessels still seem valid, and referable to the woody plants from which the concepts were derived.

Conifers and other groups in which circular bordered pits are present exclusively have no division of labor (except for *Gnetum* and *Ephedra*) into vessels and imperforate tracheary elements. In conifers, this pattern has become so pervasive that circular bordered pits are even formed on helical elements in the primary xylem (Bierhorst 1960). *Cordaitea* did have scalariformly pitted tracheids in metaxylem; this pattern yields to circular bordered pits in the secondary xylem, a fact which shows both the selective value of this pitting type for arborescence and the possibility that scalariform pitting of metaxylem may have been widespread in early seed plants, as it probably was in angiosperm ancestors. Rather than paedomorphosis, wood of early angiosperms shows three solutions to the mechanical problem of forming a wood strong enough to support a shrubby or arboreal growth form: (1) division of labor between scalariformly pitted earlywood tracheids and circularly pitted latewood tracheids in a vesselless wood, as in *Trochodendron*; (2) formation only of circular bordered pits in a wood without vessels and without seasonality, as in Winteraceae; (3) division of labor between vessels and a mechanically strong system of imperforate tracheary elements, the latter with circular bordered pits or with pits reduced in borders during phyllis. All of these solutions show selection for optimal mechanical strength, whereas paedomorphosis examples do not. Thus, Takh-tajan's suggestion must be disregarded.

Electron Microscopy in the Study of Wood Anatomy

Within the past two decades, comparative anatomy of woods has been indubitably advanced with the aid of electron microscopy. I shall discuss

scanning electron microscopy primarily. Most of the features which relate the comparative studies of wood, the focus of this paper, involve structures in a size range most appropriately studied by scanning electron microscopy rather than transmission electron microscopy. Light microscopy continues to be the easiest method of observation for most features of interest for comparative studies.

For scanning electron microscopy, extremely well-cut sections lacking scratches or tears are required. Given this requirement, several crucial advantages are currently being realized: (1), three-dimensional representation of objects hitherto shown as two-dimensional in light photomicrographs; (2), increased depth of focus; (3), high resolution, especially valuable for such items as vestured pits and porosities in pit membranes, beyond the resolution capabilities of light microscopes. The implications of these capabilities for comparative work are that for the first time we will have accurate representations of particular objects. Crystals have been figured most inadequately in much literature, and scanning electron microscopy can correct this deficiency. Vestured pits have been identified with difficulty with the light microscope; with both scanning and transmission electron microscopy we can now see not merely presence or absence of the vesturing but varied types. Optical sections of objects in wood will continue to be useful. If time and equipment are available, transmission electron microscopy can excel in these cases, as shown by Côté and Day (1962).

Items particularly well resolved by both types of (particularly scanning) electron microscopy can be listed by category (references are representative, not a full citation):

1. Vestured pits: Cassens 1980; Côté 1967; Côté and Day 1962; Kučera, Meylan, and Butterfield 1977; Meylan and Butterfield 1972, 1978; Miller 1977; Vliet 1978, 1979; Welle 1980.
2. Silica bodies: Gottwald 1980; Welle 1976.
3. Spiral thickenings on wall surfaces: Parham and Kaustinen 1973; Welle 1975.
4. Warts on inner wall surfaces: Côté 1967; Parham and Baird 1974.
5. Starch grains: Baas and Zweypfenning 1979.
6. Crystals: Vliet 1979.

One trend, which seems likely to be followed, is the presentation of entire wood sections (e.g., at least equivalent to a growth ring) as well as magni-

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Fig. 43–46. Vascular bundles from sections of leaves.—43–44. *Trematolobelia macrostachys* (Carlquist 612, RSA).—43. Transection of leaf vein; vessels are few and wide.—44. Longisection of leaf vein. Helical bands of tracheary elements are thin and relatively sparsely distributed along lengths of the tracheary elements.—45–46. *Cercocarpus intricatus* (C. B.

43

44

45

46

Wolf 7576, RSA).—45. Transection of major leaf vein; phloem at extreme left, tracheary elements grade smaller toward the phloem.—46. Longisection of leaf vein; bands in tracheary elements are thick, some interconnected by strands of secondary wall material. (Fig. 43–46, magnification scale above Fig. 3.)

fications of details. Meylan and Butterfield (1978) present a visually compelling case for the use of this method in comparative studies.

Functional Anatomy of Primary Xylem

If one studies the Dixon-Ashkenazy theory of ascent of sap, one immediately sees that during transpiration, tensions are least in the roots of a tree, highest in the leaves, and that a gradient between the top and bottom of a plant occurs. If one is dealing with smaller plants such as grasses, root pressure can suffice for much of the supply of water, and frequent disabling of vessels by air embolisms is not disadvantageous, since vessels can be cleared of these nightly. Such plants may, as a consequence, have vessels adapted to only mild tension or pressure in the sap of xylem.

However, in trees or shrubs in which high tensions develop in water columns, not only do tensions increase with height in the plant, the highest tensions should be in veins of leaves. Although wood seems a strong tissue capable of resisting tensions, we ordinarily do not think of leaf veins as mechanically strong. However, they obviously are strong in terms of resisting tension.

If we look at transections of vascular bundles of leaves of most mesic plants, we see groups of tracheids or vessel elements. These vessel elements are fairly large in diameter, as shown for *Trematolobelia macrostachys* Zahlbr. (Fig. 43). The bundles are small in that only small numbers of tracheary elements are grouped together. The bands of these tracheary elements are thin (Fig. 43, 44) and well spaced (Fig. 44) with no cross-connections between them.

Formation of tracheary elements in fascicles rather than singly offers the option of mutual support and therefore better capability for withstanding tensions (Carlquist 1975a). Leaf veins are a superb example of this, because if distribution of water into a leaf were the prime factor in grouping of tracheary elements, they would be minimally grouped, fanning out throughout a leaf.

Another feature which should be considered in relation to leaf veins is the significance of helical thickenings on tracheary elements. Presence of helical thickenings in metaxylem is a feature we associate with stems and roots, where elongation is occurring. However, in many leaf veins, the secondary wall matures after areoles are already expanded, and in cleared or sectioned mature leaves, we see little or no evidence of stretching of the gyres as we often do in stems and roots. Granting that these observations are valid, another explanation of helical thickenings in tracheary elements of leaves needs explanation. Helical thickenings are more common in leaves than in stems, in fact, for stems frequently have metaxylem which bears scalariform or transitional pitting. The explanation which might be tendered is that he-

lical structure allows for expansion and contraction; these changes would occur constantly in leaves in accordance with the daily cycle. Adaptation to expansion and contraction is characteristic of the vessels and vascular tracheids of globose cacti (Gibson 1973) and of the stems of many Crassulaceae. The helices in mesomorphic leaves such as *Trematolobelia* could accommodate expansion and contraction, certainly, but one would not expect these wide elements with thin helical bands to withstand strong tensions, and strong tensions probably never occur in the foliage of this cloud-forest shade plant.

We see quite another story if we look at leaves of desert or sclerophyll plants. *Cercocarpus intricatus* (Fig. 45, 46) is a typical example. All tracheary elements are narrower than those of *Trematolobelia*. Metaxylem elements are at first larger than protoxylem elements, but later metaxylem and the secondary xylem elements (Fig. 45) are notably small in diameter. They form very large groupings, so mutual support would be appreciable. Thickening bands are wide; some of these are interconnected by strands (the "second-order framework" of Bierhorst and Zamora 1965). These bands could potentially withstand much greater tensions than those of *Trematolobelia*. This is particularly true if one compares the thickness of the bands to the diameters of the tracheary elements, for narrower elements are much stronger than wider ones, given the same helical band thickness.

Such isolated observations are, one can say with justification, meaningless. We do, however, need more observations of leaf bundles to integrate knowledge of their anatomical structure into knowledge of tensions these leaves experience. We have little or no comparative data in this respect. One must take into account the fact that leaves vary in duration: the leaves of *Cercocarpus intricatus* persist through the summer, whereas leaves of other desert shrubs fall as temperatures rise, and thus do not experience excessively high tensions.

Despite the fine surveys of Bierhorst (1960) and Bierhorst and Zamora (1965) of primary xylem of (chiefly stems of) vascular plants, our understanding of the functional nature of primary xylem in stems and roots is rudimentary. If we look at the Bierhorst and Zamora (1965) data for angiosperms, we note that primary xylem is less specialized in morphology of end walls of tracheary elements than secondary xylem. Many groups with only simple perforation plates in secondary xylem have only tracheids in primary xylem (e.g., Pittosporaceae). The list of dicotyledon families with vessel elements with simple perforation plates in both primary and secondary xylem is much smaller than the list of dicotyledons in which vessel elements have simple perforation plates in secondary xylem, regardless of what those in primary xylem are like.

These facts can be expressed phyletically as retention of more primitive xylem in primary xylem than in secondary xylem, but one must, for func-

tional interpretations, go beyond that plausible statement and ask why this situation occurs. Evolutionary expressions in angiosperms usually do not remain unchanged over long periods of time unless they are performing functions optimally.

The presence of tracheids exclusively in the primary xylem of a species which has vessel elements in the secondary xylem (e.g., Pittosporaceae) could connote a great degree of safety. Primary xylem conductive systems do not consist of large numbers of elements in young stems, usually, so having tracheids only could provide the safety which having vessel elements exclusively could not. One might guess that safety of conductive elements is a more critical item in primary xylem than in secondary xylem, where the redundancy of conductive cells (both vessel elements and subsidiary conducting cells) is relatively enormous, and the vulnerability of vessels is not as serious a problem.

Many dicotyledons which have only simple perforation plates in secondary xylem have scalariform perforation plates in metaxylem (Bierhorst and Zamora, 1965). Of what value would these scalariform plates be in primary xylem? Are they merely relicts in which the bars do not represent a serious obstacle to flow? Zimmermann's (1978a) hypothesis that scalariform perforation plates are sieves for keeping air bubble size small (and bubbles therefore easily resorbable when thawing occurs) appears inapplicable to primary xylem. Freezing is unlikely to occur when stems are actively growing and when primary xylem is functioning. If scalariform perforation plates are a way of resisting deformation under tension in secondary xylem (Carlquist 1975a), that hypothesis might be applied to primary xylem as well.

The papers by Bierhorst (1960) and Bierhorst and Zamora (1965) illustrate a remarkable amount of structural diversity. Too much of this diversity is constant within the plant body, too characteristic of particular species, and too widespread systematically to be dismissed as mere nonadaptive chance formations. Looking for relationships between morphology of primary xylem tracheary elements and their functional capabilities should be potentially a very rewarding task.

Literature Cited

- Anderson, L. C. 1972. Studies on *Bigelovia* (Asteraceae), II. Xylary comparisons, woodiness, and paedomorphosis. *J. Arnold Arb.* 53:499-514.
- Arnold, C. A. 1951. Some observations on the anatomy of the common geranium. *Pap. Michigan Acad. Sci.* 37:3-11.
- Ayensu, A. S., and W. L. Stern. 1964. Systematic anatomy and ontogeny of the stem in Passifloraceae. *Contrib. U.S. Nat. Herb.* 34:45-73.
- Baas, P. 1973. The wood anatomical range in *Ilex* and its ecological and phylogenetic significance. *Blumea* 21:193-258.

- . 1976. Some functional and adaptive aspects of vessel member morphology. *Leiden Bot. Ser.* 3:157–181.
- . 1977. The peculiar wood structure of *Leptospermum crassipes* Lehm. (Myrtaceae). *I.A.W.A. Bull.* 1977/2:25–30.
- . 1979. The peculiar wood structure of *Vaccinium lucidum* (Bl.) Miq. (Ericaceae). *I.A.W.A. Bull.* 1979/1:11–16.
- , and R. C. V. J. Zweypfenning. 1979. Wood anatomy of the Lythraceae. *Acta Bot. Neerl.* 28:117–155.
- Bailey, I. W. 1944. The development of vessels in angiosperms and its significance in morphological research. *Amer. J. Bot.* 31:421–428.
- . 1966. The significance of reduction of vessels in the Cactaceae. *J. Arnold Arb.* 46:288–292.
- Bierhorst, D. W. 1960. Observations on tracheary elements. *Phytomorph.* 10:249–305.
- , and P. M. Zamora. 1965. Primary xylem elements and element associations of angiosperms. *Amer. J. Bot.* 52:657–710.
- Bissing, D. R. 1976. The effect of cultivation on the expression of anatomical features of the wood of selected dicotyledons. Doctoral thesis, Claremont Graduate School. Claremont, Calif. 117 p.
- Bridgewater, S. D., and P. Baas. 1978. Wood anatomy of the Punicaceae. *I.A.W.A. Bull.* 1978/1:3–6.
- Butterfield, B. G., and B. A. Meylan. 1975. Simple to scalariform combination perforation plates in *Vitex lucens* Kirk (Verbenaceae) and *Brachyglottis repanda* J. R. et G. Forst. (Compositae). *I.A.W.A. Bull.* 1975/3:39–42.
- Carlquist, S. 1958. Wood anatomy of Heliantheae (Compositae). *Trop. Woods* 108:1–30.
- . 1960. Wood anatomy of Astereae (Compositae). *Trop. Woods* 113:54–84.
- . 1961. Comparative plant anatomy. Holt Rinehart & Winston, New York. 146 p.
- . 1962. A theory of pedomorphosis in dicotyledonous woods. *Phytomorph.* 12:30–45.
- . 1966. Wood anatomy of Compositae: a summary, with comments on factors controlling wood evolution. *Aliso* 6(2):25–44.
- . 1969. Wood anatomy of Lobelioideae (Campanulaceae). *Biotropica* 1:47–72.
- . 1970. Hawaii. A natural history. Natural History Press, New York. 463 p.
- . 1974. Island biology. Columbia University Press, New York & London. 660 p.
- . 1975a. Ecological strategies of xylem evolution. University of California Press, Berkeley. 259 p.
- . 1975b. Wood anatomy of Onagraceae, with notes on alternative modes of photosynthate movement in dicotyledon woods. *Ann. Missouri Bot. Gard.* 62:386–424.
- . 1977a. Ecological factors in wood evolution: a floristic approach. *Amer. J. Bot.* 64:887–896.
- . 1977b. Wood anatomy of Onagraceae: additional species and concepts. *Ann. Missouri Bot. Gard.* 64:627–637.
- . 1978. Wood anatomy of Bruniaceae: correlations with ecology, phylogeny, and organography. *Aliso* 9:323–364.
- . 1980. Anatomy and systematics of Balanopaceae. *Allertonia* 2:191–246.
- . 1981. Types of cambial activity and wood anatomy of *Stylidium* (Stylidiaceae). *Amer. J. Bot.* (in press).
- Cassens, D. L. 1980. Vested pits in the New World *Pithecellobium* (sensu lato). *I.A.W.A. Bull.*, n.s., 1:59–64.
- Chowdhury, K. A. 1939. The formation of growth rings in Indian trees. *Indian Forest Rec.*, n.s., Util. 2:1–39.
- . 1940. *Ibid.*, Part II. *Indian Forest Rec.*, n.s., Util. 2:41–57.
- . 1941. *Ibid.*, Part III. A study of the effect of locality. *Indian For. Rec.*, n.s., Util. 2:59–75.

- . 1953. The role of initial parenchyma in the transformation of the structure diffuse-porous to ring-porous in the secondary xylem of the genus *Gmelina* Linn. Proc. Nat. Inst. Sci. India 19:361–369.
- . 1964. Growth rings in tropical trees and taxonomy. J. Indian Bot. Soc. 43:334–342.
- Côté, W. A., Jr. 1967. Wood ultrastructure. An atlas of electron micrographs. Univ. Washington Press, Seattle. 54 p.
- , and A. C. Day. 1962. Vestured pits—fine structure and apparent relationship with warts. Tappi 45:906–910.
- Cumbie, B. G. 1960. Anatomical studies in the Leguminosae. Trop. Woods 113:1–47.
- . 1963. The vascular cambium and xylem development in *Hibiscus lasiocarpus*. Amer. J. Bot. 50:944–951.
- . 1967a. Developmental changes in the vascular cambium in *Leitneria floridana*. Amer. J. Bot. 54:414–424.
- . 1967b. Development and structure of the xylem in *Canavalia* (Leguminosae). Bull. Torrey Bot. Club 94:162–175.
- DeBuhr, L. E. 1977. Wood anatomy of the Sarraceniacae; ecological and evolutionary implications. Pl. Syst. Evol. 128:159–169.
- Denne, M. P. 1973. Tracheid dimensions in relation to shoot vigour in *Picea*. Forestry 46:117–124.
- Dickison, W. C. 1977. Wood anatomy of *Weinmannia* (Cunoniaceae). Bull. Torrey Bot. Club 104:12–23.
- . 1979. A note on the wood anatomy of *Dillenia* (Dilleniaceae). I.A.W.A. Bull. 1979/2–3:57–60.
- , P. M. Rury, and G. L. Stebbins. 1978. Xylem anatomy of *Hibbertia* (Dilleniaceae) in relation to ecology and evolution. J. Arnold Arb. 59:32–49.
- Forsyth, C. C. 1920. Anatomical reduction in some alpine plants. Ecology 1:124–135.
- Frost, F. H. 1930a. Specialization in secondary xylem in dicotyledons. I. Origin of vessel. Bot. Gaz. 89:67–94.
- . 1930b. Specialization in secondary xylem in dicotyledons. II. Evolution of end wall of vessel segment. Bot. Gaz. 90:198–212.
- . 1931. Specialization in secondary xylem in dicotyledons. III. Specialization of lateral wall of vessel segment. Bot. Gaz. 91:88–96.
- Gibson, A. C. 1973. Comparative anatomy of secondary xylem in Cactoideae (Cactaceae). Biotropica 5:29–65.
- . 1977a. Wood anatomy of opuntias with cylindrical to globular stems. Bot. Gaz. 138:334–351.
- . 1977b. Vegetative anatomy of *Maihuenia* (Cactaceae) with some theoretical discussions of ontogenetic changes in xylem cell types. Bull. Torrey Bot. Club 104:35–48.
- . 1978a. Wood anatomy of platyopuntias. Aliso 9:279–307.
- . 1978b. Dimorphism of secondary xylem in two species of cacti. Flora 167:403–408.
- Giebel, K. P., and W. C. Dickison. 1976. Wood anatomy of Clethraceae. J. Elisha Mitchell Sci. Soc. 92:17–26.
- Ginzburg, C. 1963. Some anatomic features of splitting of desert shrubs. Phytomorph. 13: 92–97.
- Giordano, R., A. Salleo, S. Salleo, and F. Wanderlingh. 1978. Flow in xylem vessels and Poiseuille's law. Can. J. Bot. 56:333–338.
- Gottwald, H. 1980. 'Louro preto' found to be the first silica-bearing *Cordia* (*Cordia glabrata*, Boraginaceae). I.A.W.A. Bull., n.s., 1:55–57.
- , and N. Parameswaran. 1964. Vielfache Gefässdurchbrechungen in der Familie Dipterocarpaceae. Zeit. für Bot. 52:323–334.

- Graaff, N. A. van der, and P. Baas. 1974. Wood anatomical variation in relation to latitude and altitude. *Blumea* 22:101–121.
- Greguss, P. 1952. Die Xylotomie der Araukariaceen. *Acta Biol. Acad. Sci. Hungaricae* 3:443–541.
- Hedberg, I., and O. Hedberg. 1979. Tropical-alpine life-forms of vascular plants. *Oikos* 33:297–307.
- Huber, B. 1935. Die Bedeutung der Ring und Zertstreutporigkeit. *Ber. Deutsch. Bot. Ges.* 53:711–719.
- Jeje, A. A., and M. H. Zimmermann. 1979. Resistance to water flow in xylem vessels. *J. Exp. Bot.* 30:817–827.
- Johnson, Hyrum B. 1976. Vegetation and plant communities of southern California deserts—a functional view. In J. Latting [ed.], *Plant communities of southern California*. Calif. Native Plant Soc. Spec. Publ. 2:125–164.
- Kanehira, R. 1921. Anatomical characters and identification of Formosan woods with critical remarks from the climatic point of view. Bureau of Productive Industries, Taihoku, Taiwan. 317 p.
- Klotz, L. H. 1977. A systematic survey of the morphology of tracheary elements in palms. Doctoral Thesis, Cornell University. Ithaca, N.Y.
- Koek-Noorman, J. 1976. Juvenile characters in the wood of certain Rubiaceae with special reference to *Rubia fruticosa* Ait. I.A.W.A. Bull. 1976/3:38–42.
- Kribs, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. *Bot. Gaz.* 96:547–557.
- Kučera, L. J., B. A. Meylan, and B. G. Butterfield. 1977. Vestured simple perforation plates. I.A.W.A. Bull. 1977/1:3–6.
- Mabberley, D. J. 1974a. Branching in pachycaul senecios: the durian theory and the evolution of angiospermous trees and herbs. *New Phyt.* 73:967–975.
- . 1974b. Pachycauly, vessel elements, islands and the evolution of arborescence in 'herbaceous' families. *New Phyt.* 73:977–984.
- Meylan, B. A., and B. G. Butterfield. 1972. Three-dimensional structure of wood. Syracuse Univ. Press, Syracuse, N.Y. 80 p.
- , and ———. 1978. The structure of New Zealand woods. D.S.I.R. Bull. 222 New Zealand Department of Scientific and Industrial Research, Wellington. 250 p.
- Miller, H. J. 1975. Anatomical characteristics of some woody plants of the Angmagssalik District of southeast Greenland. *Medd. om Grønland* 198(6):1–30.
- Miller, R. B. 1977. Vestured pits in Boraginaceae. I.A.W.A. Bull. 1977/3:43–48.
- Moss, E. H. 1934. Rings of cork in the wood of herbaceous perennials. *Nature* 133:598.
- . 1936. The ecology of *Epilobium angustifolium* with particular reference to rings of periderm in the wood. *Amer. J. Bot.* 23:114–120.
- . 1940. Interxylary cork in *Artemisia* with reference to its taxonomic significance. *Amer. J. Bot.* 27:762–768.
- , and A. L. Gorham. 1953. Interxylary cork and fission of stems and roots. *Phytomorph.* 3:285–294.
- Mowbray, T. B., and H. J. Oosting. 1968. Vegetation gradients in relation to environment and phenology in a southern Blue Ridge gorge. *Ecol. Monogr.* 38:309–344.
- Parham, R. A., and W. M. Baird. 1974. Warts in the evolution of angiosperm wood. *Wood Sci. & Tech.* 8:1–10.
- Parham, R. A., and H. Kaustinen. 1973. On the morphology of spiral thickenings. I.A.W.A. Bull. 1973/2:8–14.
- Pearcy, R. W., and J. Troughton. 1975. C_4 photosynthesis in tree form *Euphorbia* species from Hawaiian rainforest sites. *Plant Phys.* 55:1054–1056.

- Philipson, W. R., and B. G. Butterfield. 1967. A theory on the causes of size variation in wood elements. *Phytomorph.* 17:155-159.
- Rundel, P. W., and R. E. Stecker. 1977. Morphological adaptation of tracheid structure to water stress gradients in the crown of *Sequoiadendron giganteum*. *Oecologia* 27:135-139.
- Scholander, P. F., H. T. Hammel, E. D. Bradstreet, and E. A. Hemmingsen. 1965. Sap pressure in vascular plants. *Science* 148:339-345.
- Styer, C. H., and W. L. Stern. 1979. Comparative anatomy and systematics of woody Saxifragaceae. *Deutzia*. *Bot. J. Linnean Soc.* 79:291-319.
- Swamy, B. G. L., N. Parameswaran, and E. Govindarajalu. 1960. Variation in vessel length with one growth ring of certain arborescent dicotyledons. *J. Indian Bot. Soc.* 39:163-170.
- Takhtajan, A. 1969. Flowering plants. Origin and dispersal. Trans. by C. Jeffrey. Oliver and Boyd, Edinburgh. 310 p.
- Tomlinson, P. B., and F. C. Craighead, Sr. 1972. Growth-ring studies on the native trees of sub-tropical Florida, pp. 39-51. In A. K. M. Ghouse and M. Yunus [eds.], Research trends in plant anatomy—K. A. Chowdhury commemoration volume. Tata McGraw Hill Pub. Co. Ltd., New Delhi.
- Tupper, W. W. 1913. An unusual seasonal growth ring in *Eucalyptus*. *Pap. Michigan Acad. Sci.* 13:217-219.
- Vliet, C. J. C. M. van. 1976. Wood anatomy of the Rhizophoraceae. *Leiden Bot. Ser.* 3:20-75.
- . 1978. Vestured pits of Combretaceae and allied families. *Acta Bot. Neerl.* 27:273-285.
- . 1979. Wood anatomy of the Combretaceae. *Blumea* 25:141-223.
- Waisel, Y., N. Lipschitz, and A. Kuller. 1972. Patterns of water movement in trees and shrubs. *Ecology* 53:520-523.
- Walsh, M. A. 1975. Xylem anatomy of *Hibiscus* (Malvaceae) in relation to habit. *Bot. Gaz.* 136:30-40.
- Webber, I. E. 1936. The woods of sclerophyllous and desert shrubs and desert plants of California. *Amer. J. Bot.* 23:181-188.
- Welle, B. J. H. Ter. 1975. Spiral thickenings in the axial parenchyma of Chrysobalanaceae. *Acta Bot. Neerl.* 23:397-405.
- . 1976. On the occurrence of silica grains in the secondary xylem of the Chrysobalanaceae. *I.A.W.A. Bull.* 1976/2:19-29.
- . 1980. Cystoliths in the secondary xylem of *Sparattanthelium* (Hernandiaceae). *I.A.W.A. Bull.*, n.s., 1:43-48.
- Wolking, F. 1969. Morphologie und systematische Verbreitung der lebenden Holzfasern bei Sträuchern und Bäumen. I. Zur Morphologie und Zytologie. *Holzforschung* 23:135-144.
- . 1970. Morphologie und systematische Verbreitung der lebenden Holzfasern bei Sträuchern und Bäumen II. Zur Zytologie. *Holzforschung* 24:141-151.
- . 1971. Morphologie und systematische Verbreitung der lebenden Holzfasern bei Sträuchern und Bäumen. III. Systematische Verbreitung. *Holzforschung* 25:29-30.
- Yatsenko-Khmelevsky, A. A. 1954. Osnovii i Mdogii Anatomicheskogo Issledovaniya Arvesinii. *Isdatelestvo Akademii Nauk SSSR, Moscow.* 337 p.
- Zimmermann, M. H. 1971. Transport in xylem, pp. 169-220. In M. H. Zimmermann and C. L. Brown [eds.], *Trees: Structure and function*. Springer Verlag, New York.
- . 1978a. Structural requirements for optimal conduction in tree stems, pp. 517-532. In P. B. Tomlinson and M. G. Zimmermann [eds.], *Tropical trees as living systems*. Cambridge Univ. Press, Cambridge.

- . 1978b. Hydraulic architecture of some diffuse-porous trees. *Can. J. Bot.* 56:2286–2295.
- Zweypfenning, R. C. V. J. 1978. A hypothesis on the function of vestured pits. *I.A.W.A. Bull.* 1978/1:13–15.