A THEORY OF PAEDOMORPHOSIS IN DICOTYLEDONOUS WOODS

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Introduction

The broad patterns of wood evolution have now become well established. These trends of evolution, based on the vessel element and its specialization, have been termed the "major trends of xylem evolution" (Carlquist, 1961). The key to the discovery of these trends was the investigation of Bailey & Tupper (1918) into the significance of vessel-element and tracheid length. Bailey & Tupper concluded that tracheids preceded vessel elements phylogenetically, and that longer vessels elements, which in general show numerous resemblances to primitive tracheids such as those of ferns, are more primitive than short vessel elements.

The natural consequence of these conclusions was investigation of features associated with great length of vessel elements. Such investigations were carried out first on dicotyledons, and utilized samples of dicot woods at large. Characters positively associated with long vessel elements can be said to be primitive; progressively lower statistical correlation indicates advanced expressions, and negative correlation the most advanced conditions. The studies of Frost (1930a, 1930b, 1931) showed that primitive dicot vessel elements are long, have highly oblique (nearly vertical) end walls with numerous bars on each perforation, have scalariform lateral-wall pitting, and tend to be angular in transsectional view. Independent con-
firmation of these expressions was given in monocots by Cheadle (1943). Specialization in vessel elements is expressed by decrease in length; loss of bars, leading to a simple perforation plate; breakup of scalariform pits into rows of opposite, finally alternate, pits; and tendency for the vessel to be round in transsectional outline.

In dicots, trends of specialization in axial and ray parenchyma were explored by Kribs (1935, 1937) and Barghoorn (1940, 1941a, 1941b). Conclusions of interest to the present study include the tendency of rays to specialize by losing their heterogeneity (presence of both erect or square and procumbent cells), resulting in homogeneity (procumbent cells only, or more rarely, erect cells only). Barghoorn (1941b) showed that in a few cases, predominance of erect ray-initial cells and their elongation results in elimination of rays by conversion of ray initials to fusiform initials. For summary of the above and other papers on wood evolution, and for an elaboration of the principles which underlie them, the reader may consult Carlquist (1961).

The purpose of the present study is not to present negations to these well-established trends of wood evolution. In the writer's experience these trends, although they have needed minor modification by various workers (see Carlquist, 1961), are fully justified. However, exceptional cases, which do not at first seem to follow the major trends of xylem evolution, may cause botanists to question the validity of these trends. The woods in the present study are such exceptional cases, and must be explained. This explanation takes the form of revealing that juvenile characteristics — those of the primary xylem — have been protracted into the secondary xylem. One may term this process paedomorphosis, in accordance with the term of de Beer (1930), since some woods appear to be permanently juvenile. Others appear to lose their juvenile qualities slowly, while typical woody dicots would be expected to mature rapidly. No one has suggested that all woods develop mature patterns at the same rate. Existing literature, on the contrary, suggests just the reverse. Thus, a unified concept of juvenilism or paedomorphosis in woods is needed to explain phenomena which have not been explained as yet. If some woods are permanently or for a long period in a state of juvenility, they are not truly comparable with woods which have attained a mature pattern, and the significance of this to comparative and evolutionary studies seems considerable. Also, juvenilism may take different forms in different groups of dicots.

Work on trends of wood evolution has emphasized statistical correlations. If the present cases are, as the writer believes, alterations of ontogeny of secondary xylem in various groups, statistical correlations cannot be applied to reveal this nature. The only ways in which ontogenetically altered woods can be perceived and analyzed are: (1) selection of woods which appear both from growth form of the plant and from exceptional conditions in wood anatomy, to be examples of paedomorphosis; these examples should be from various groups; (2), analysis of the ontogeny of woods in these species; this can be done by tracing changes on radia sections, beginning at the pith, in woods which show accumulation of xylem over a period of years long enough to have produced, in a "normal" woody plant, a semblance of a mature condition; and finally (3), comparison of these woods with woods of true herbs. Obviously annual herbs would be most definitive for showing modes of wood anatomy in herbaceous plants.

Materials and Methods

The usual techniques for sectioning of woods have been used. Softer woods were sectioned by paraffin techniques. Because the theoretical nature of the paper does not seem to demand publication of precise sources of materials, these are not given. Listing of sources and voucher specimens for the species used, however, will be sent by the author on request.

The Theory

Typically, in woody dicots, the beginning of secondary growth is accompanied
by changes toward mature histological patterns of wood anatomy. In plants with a tendency toward, or away from, an herbaceous habit (or in fact, in herbs) juvenile characteristics are present for the life of the plant or are slowly lost. Rosette trees, woody herbs, and stem succulents are among the plants which would be expected to show these trends. Primary xylem is more primitive than secondary xylem, and is a sort of refuge for primitive characteristics because, as Bailey (1944) has shown, advanced features have originated in the secondary xylem and progressed, phylogenetically, into the primary xylem. If woods are permanently juvenile, therefore, at least some features of their secondary xylem are more primitive than one would expect for a particular species. Differential rates of evolution cannot account for all of the phenomena of wood anatomy discussed below. For example, lateral-wall pitting of vessels evolves more rapidly than the perforation plate (Frost, 1930b), yet nearly all of the woods in Table 1 have simple perforation plates, combined with scalariform or scalariform-transitional wall pitting.

Juvenile features are held to be retained in secondary xylem because these plants are adjusted to, or are tending toward, a habit other than truly woody. Truly woody plants attain mature wood patterns more quickly because they do not terminate their existence as herbs or herblike plants.

Juvenile characteristics retained in secondary xylem may be retained differentially. For example, longer vessel elements and scalariform-transitional pitting appear both to be juvenile characteristics but may not necessarily occur together in a wood showing paedomorphosis (e.g. Neurolepsa lobata). Differential occurrence of characters is shown clearly in Table 1.

Because many dicots have some aspects of herb-like structure, even if they are not herbs, retention of a few juvenile characters in secondary xylem may be expected in a variety of species.

**Primary Xylem**

The features listed below often typify primary xylem in dicots as a whole. These characteristics have been noted by such authors as de Bary (1884), Bailey (1944) and Bailey & Tupper (1918). Characters of primary xylem have been considered routine by most plant anatomiasts, so little has been done to detail typical or variant modes of construction in primary xylem.

**Vessel Length** — The graphs of Bailey & Tupper (1918) show clearly the great length of protoxylem elements. Metaxylem elements are also long, but are intermediate in length between those which begin secondary growth and at least the later-formed protoxylem elements (see broken lines, Fig. 1).

**Vessel-Element Shape** — Prominently overlapping end walls in primary xylem were observed in many species with nearly transverse end-walls in the secondary xylem. This characteristic is found with considerable frequency in metaxylem elements in particular. This observation is in agreement with the findings of Bailey (1944). As seen in transsectional outline, vessels in primary xylem are often round. This is probably related to the fact that primary xylem vessels are often surrounded by parenchyma. Where vessels are grouped, however, they tend to assume compressed, polygonal shapes in primary xylem of many species.

**Lateral-Wall Pitting of Vessels** — The ontogenetic sequence from annular through helical, scalariform and scalariform-transitional pitting is familiar. For the purposes of this paper, attention is called to: (1) the presence of scalariform, or scalariform-like pitting in tracheary elements formed just internal to the secondary xylem; and (2) the widening of pit apertures. Wideness of pit “apertures” is not merely related to helical and annular elements (where it is probably related to stretching of elements). Wide apertures also occur in scalariformly-pitted vessels which seemingly cannot be stretched appreciably.

**Other Xylem Elements** — Fibers are present in primary xylem of some dicot species. They are most often thin-walled and rather wide in diameter. In other cases, parenchyma cells may be present to the exclusion of vertical elements other than vessels or tracheids. Abundance of
<table>
<thead>
<tr>
<th>Family and species</th>
<th>Habit</th>
<th>Vessel-element length, average, µm</th>
<th>Type of curve for vessel length</th>
<th>Vessel-element end-walls highly oblique</th>
<th>Vessels angular in tran-section</th>
<th>Intervascular pitting scalariform</th>
<th>Vessel-parenchyma pitting scalariform</th>
<th>Wide apertures present on pits of vessels</th>
<th>Rays wide and high</th>
<th>Ray cells mostly or all square to erect</th>
<th>Libriform fibers thin-walled</th>
<th>Libriform fibers relatively wide in diameter</th>
<th>Axial parenchyma exceptionally abundant</th>
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Under Habit, h = herb, rt = rossette tree or rosette shrub; ss = stem succulent; wh = woody herb. Under Vessel-element length, average, figure for a species is shown in bold face if the average length is markedly greater than is characteristic for the family to which it belongs (comparisons from Metcalfe & Chalk, 1950, and the writer's wood-slide collection). In other columns, + = presence of character; - = absence of character; 0 = does not apply (for example, libriform fibers are entirely absent in Brighamia).
parenchyma, or presence of parenchyma-like fibers, then, characterizes primary xylem of many dicots.

Pith Rays — Pith rays are most frequently wider and higher than rays of the secondary xylem. During cambial activity, large rays are typically broken up into smaller rays in many woody species. In addition, pith ray cells, in general, tend to be taller (more erect) than ray cells of the secondary xylem. This may be the result of elongation in pith ray areas, similar to the elongation in procambium or even vascular tissue (which accounts, in part, for the great length of primary xylem elements).

Juvenile Characteristics in Secondary Xylem

The species listed in Table 1 are among those which show juvenile characteristics in secondary xylem. Many more species could undoubtedly have been selected, and some others are mentioned in the text. Anatomical features are discussed in the same order as under “Primary Xylem” above.

Vessel-Element Length — Perhaps the most interesting evidence of permanent juvenility, or paedomorphosis, is the nature of vessel-element length in the species studied. While studying rosette-trees in Compositae and Lobeliaceae, I repeatedly observed that vessel elements were longer than one might expect, considering the phylogenetic advancement of those families. Bailey (1957) warns that fluctuations in vessel-element length — fluctuations unrelated to phyletic shortening of elements — occur within a group, but does not detail reasons why one should expect this. Bourée (1957) notes that vines often have longer vessel elements than would be expected, and xerophytes shorter elements than might be predicted.
Figs. 2-12.—Portions of lateral walls of vessels, from tangential sections, to show pitting (intervascular pitting unless otherwise mentioned). Fig. 2. Phoenicoseris regia. Fig. 3. Senecio praeox. Fig. 4. Macropiper excelsum. Fig. 5. Begonia coccinea. Fig. 6. Begonia coccinea, vessel-parenchyma pitting. Fig. 7. Carica candamarossis, vessel-parenchyma pitting. Fig. 8. Cereus gigantea. Fig. 9. Scabiosa kauaiiensis. Fig. 10. Brighamia insignis; vessel at left, transfusion cells associated with vessels at right. Fig. 11. Brighamia insignis. Fig. 12. Sedum praecultum. Fig. 2, × 280. Figs. 3-11, × 210. Fig. 12, × 106.
The latter group has shorter elements, according to Boureau, as "the result of an important reduction brought on secondarily by the environment in the dimensions of cambial initials, in spite of an evident primitive condition." One wonders if shortening of vessel elements in xerophytes might be better explained by saying that phyletic shortening of elements is hastened in such environments. Likewise, shortening of elements (governed by shortening of cambial initials) has apparently been accelerated in herbs. If vessel elements are longer than one "would expect", however, the explanation is not so easy. For example, Scaevola kauaiensis has markedly longer vessel elements than any of ten other woody species of that genus, but there is no reason to think that this feature is primordially retained in this isolated Hawaiian endemic.

After analysis of many cases, the most logical explanation for greater vessel-element length in species such as those of the present study appears to be that vessel-element length is a carry-over from the great vessel-element lengths characteristic of primary xylem. If we examine the change in length over a period of time, the reason for this interpretation will become more apparent. As shown in Fig. 1, the "normal" pattern, illustrated by Eriobotrya japonica, shows a marked drop prior to initiation of secondary growth. This is followed by a rapid increase in length. Increase in length slows during successive increments of growth. This type of curve applies to all tracheary elements in all woods so graphed by Bailey & Tupper (1918). Later, Bailey (1923) showed that "highly specialized dicotyledons" have a similar curve, but one which levels off more rapidly during secondary growth. Bailey also reported in this paper that "highly specialized dicotyledons with stoyed cambium" show a flat curve after the onset of secondary growth. Thus, cambial initials do not increase in length after the beginning of secondary growth in these species.

The type of curve found in Talinum guadalupense (Fig. 1) is surprising in view of the above. Beginning with protoxylem, there is a steady and progressive decrease in vessel-element length. Another type of curve is represented by Macropiiper excelsum. In this type, the decrease in vessel-element length takes place rapidly, and levels off soon, so that a nearly flat curve is obtained. Although the curve for Macropiiper is not unlike that reported by Bailey for species with stoyed cambia, Macropiiper does not have a stoyed cambium. Table 1 shows that the types of curves found in Talinum and Macropiiper characterize all of the species studied except Trematolobelia macrostachys. The "normal" curve for Trematolobelia may perhaps be explained by the monocarpic nature of this rosette tree, since a definite point of maturation is reached in flowering and events in wood histology may reflect this discrete destiny.

The hollow and flat curves may be considered as equivalent to the descending (primary xylem) portion of the curve shown for Eriobotrya. Thus, the "herb" phase must be protracted for many years — perhaps for the life of the plant — in the woods listed in Table 1. If this is true, one would expect wood of herbs to show this pattern. Analysis of a number of species of annual herbs showed that this is true. In Compositae, for example, the following annuals which accumulate considerable secondary xylem were observed to have a flat (Macropiiper-type) curve: Dicoria canescens, Gnaphalium californicum, Helianthus annuus, Heterotheca grandiflora, Lactuca scariola, and Silybum marianum. The hollow (Talinum-type) curve was observed in the following woody annual Compositae: Ambrosia hispida, Blepharisonia plumosa, Centaurea ragusina, C. solstitialis, Cirsium californicum, Erechites hieracifolia, and Madia salvia. The Eriobotrya-type of curve was not observed in any of the annuals examined.

One may well ask what the significance of rapid stabilization, or continued decrease, in vessel-element length may be. In either case, there is no increase in length following commencement of secondary growth, as there apparently is in truly woody plants. The immediate cause is lack of elongation of fusiform cambial initials. Moreover, decrease in length of cambial initials must take place in species with the Talinum-type curve. The physiological advantage, if any, of this
behavior is not evident. One might say that herbs and herb-like plants are not destined to develop mechanically significant wood, and thus have an incomplete cycle of cambial-initial length changes, and that the terminal stage of initial elongation found in woody plants is dropped out, or better, never initiated. This would be an adjustment, in wood histology, to decrease in significance of mechanical tissues. Such an explanation, however, seems more a form of words than a true explanation. Obviously, many truly woody species have very short fusiform cambial initials. Interestingly, few of the species studied here possess any appreciable degree of storying.

**Vessel-element Shape** — The tendency of vessels in the species studied to have highly inclined end walls on vessel elements, or to have vessel elements with markedly caudate tips is very pronounced. Table 1 reveals that this feature is by no means without exception. In some, such as the Compositae, end walls are more oblique than those of the majority of the family. Although many dicot species do not seem to have markedly overlapping end walls in primary xylem elements, the fact that markedly oblique end walls occur in metaxylem of some highly advanced species seems reason for entertaining the possibility that this character in secondary xylem may be a juvenile one.

As noted by Bailey (1957), vessels angular in transectional outline may be present in some highly specialized woods as well as some very primitive ones. This feature appears to bear some relation to juvenile conditions, for angular vessels are found in at least some primary xylems, and are characteristic of many of the woods listed in Table 1. Such vessels are illustrated in *Wunderlichia mirabilis* (Fig. 20).

**Lateral-wall Pitting of Vessels** — Most of the species selected as Table 1 possess mostly scalariform or scalariform-transitional pitting on vessels. Some of these, such as *Macropiper excelsum* (Fig. 4), *Begonia coccinea* (Figs. 5, 6) and *Brighamia insignis* (Figs. 10, 11) have nearly perfect scalariform patterns. More often, however, as in *Phoenicosperis regia* (Fig. 2), *Senecio praecox* (Fig. 3), *Carica candalmarcensis* (Fig. 7), *Cereus gigantea* (Fig. 8) and *Scevola kauaiensis* (Fig. 9), pitting is both scalariform and scalariform-transitional. In the latter species, pits are horizontally widened, and may be broken into segments less wide than a wall surface. To the list of species with such pitting in Table 1 may be added a number of Umbelliferae. These are mentioned because woods of this family appear frequently to be examples of paedomorphosis.

The data of Rodriguez (1957) reveal that at least 21 Umbelliferae have scalariform or scalariform-transitional vessel pitting. These Umbelliferae may well have retained such pitting from primary xylem, not from secondary xylem of primitive woods, as Rodriguez seems to believe. Perforation plates of Umbelliferae, as well as all of the species listed in Table 1, are simple. This contrasts sharply with the data of Frost (1930b, 1931) which indicate that in dicots as a whole, lateral-wall pitting evolves more rapidly than perforation-plate morphology. The Umbelliferae with scalariform pitting include some highly advanced species, such as *Sanicula deserticola*. Moreover, one would expect scalariform pitting to be abundant in the related but generally more primitive family Araliaceae, if scalariform pitting in Umbelliferae were a primitive character. This is, in fact, not true, according to the data of Rodriguez (1957). Many other examples of scalariform pitting may be found in highly advanced families such as Passifloraceae (*Soyauxia*), Fouquieriaceae, and Cochlospermaceae (*Metcalfe & Chalk, 1950*). Scalariform pitting in woods of some Cycadaeaceae appears best explained as a retention of primary xylem pitting patterns (I. W. Bailey, personal communication). Although there are doubtless some examples of species which have simple perforation plates combined with a primitively-retained lateral-wall pitting (e.g. perhaps *Clusia rosea*), occurrence of this condition in mature woods merely as a result of differential rates of evolution of the two portions of vessels would be expected to be extremely infrequent.

One may see that scalariform and scalariform-transitional pitting is related to primary xylem patterns ontogenetically. Comparison of Figs. 13 and 14 shows that
Figs. 13-16 — Figs. 13, 14. *Talinum guadalupense*. Portions of radial sections of secondary xylem; Fig. 13 is from near the pith; Fig. 14 is from near the cambium. Figs. 15, 16. *Plantago princeps*. Fig. 15. Radial section showing pith (left) and secondary xylem which originates in an interfascicular region. Fig. 16. Tangential section of secondary xylem, to show the rayless condition and the strong tendency for striping in the libriform fibers. Figs. 13, 14, × 164. Fig. 15, × 91. Fig. 16, × 67.
pitting patterns in *Talinum guadalupense* change hardly at all from near the primary xylem (Fig. 13) to near the cambium (Fig. 14), a distance of 12 mm. Other examples of this were repeatedly observed.

Vessel-parenchyma pitting differs little from intervacular pitting in the species of the present study. In a few cases (see Table 1), intervacular pitting may be alternate, while scalariform-transitional types occur on intervacular walls, or vice versa. Often, pit apertures are wider, and pit borders are narrower in vessel-parenchyma pitting than in intervacular pitting. Examples of this are shown in *Begonia coccinea* (Figs. 5, 6) and *Carica candamarcensis* (Fig. 7). The latter instance shows extremely wide pits with very narrow borders. An extreme expression of this trend is found in the vascular tracheids (imperforate vessel elements) of *Sedum praetum* (Fig. 12). In this species, vascular tracheids of the secondary xylem appear to have annular or helical wall patterns. Actually, the pattern is near-scalariform, because fine vertical connections between the horizontal bands are present. Borders are entirely lacking. Reduction of borders is characteristic of some herbs. Border reduction was proposed by Frost (1931) as a trend in advancement, and by itself this feature should not be construed as an invariable indication of paedomorphosis. Wideness of pits, however, is characteristic of woods in the present study, as Table 1 indicates.

Scalariform-transitional pitting is present in transfusion cells of *Brighamia* (Fig. 10). These cells are adjacent to vessels, and are probably parenchyma cells with lignified walls. Pit fields in other parenchyma cells in *Brighamia* do not take this form, however.

Wide, long pits do decrease the mechanical strength of vessel elements. However, the growth form of many of the species studied here (e.g. stem succulents) minimizes the value of mechanical strength.

Other Axial Xylem Elements — All of the annual Compositae listed above under “vessel-element length” have wide, thin-walled fibers in secondary xylem. This condition also occurs in the primary xylem of these species and of many of those listed in Table 1. Wide, thin-walled fibers are frequent in the woods of Umbelliferae studied by Rodriguez (1957). Thin-walled fibers of this sort are illustrated in the present study by *Lobelia gibbosa* (Figs. 23, 24). Presence of thin-walled fibers could be governed by the modest mechanical support in woods of rosette-trees, etc. However, secondary xylem characterized by thin-walled, wide fibers, may be considered a continuation of the parenchyma-like aspect of primary xylem fibers. In ontogenetic terms, this certainly is the most immediate cause.

Another mode of parenchymatization is illustrated by species in which axial parenchyma is more abundant than is typical for a given family or genus. This could be interpreted as a specialized condition, in agreement with the general conclusion of Kribs (1937) that abundant parenchyma, both paratracheal and apotracheal, is more specialized than scanty conditions. Delineating precise phylogenies of axial parenchyma types is difficult, however. In the present study, *Scaevola kauaiensis* (Figs. 17, 18) and its close relative *S. glabra* are characterized by much more abundant axial parenchyma than the other species of *Scaevola*, in which axial parenchyma is of a very scanty, diffuse type, or is absent. *Wunderlichia mirabilis* shows more abundant axial parenchyma than most Compositae (Fig. 20, lower right); its libiform fibers are not at all parenchyma-like.

A third mode of parenchymatization, which is almost certainly an indication of paedomorphosis, is represented by species in which parenchyma cells are the only axial components of xylem other than vessel elements. Examples here include *Talinum guadalupense* (Figs. 13, 14), *Brighamia insignis* (Figs. 21, 22) and *Carica candamarcensis* (Fig. 19). That the exclusion of mechanical elements by parenchyma is related to the growth form of these plants seems reasonable. However, primary xylem in these species lacks mechanical elements, and in formal ontogenetic terms, this ultimate degree of parenchymatization is clearly a continuation of primary xylem structure. Attention is called to the fact that many
Figs. 17-20 — Figs. 17, 18. *Scaevola kauaiensis*, sections of secondary xylem. Fig. 17. Transection, most recently formed elements above, showing wide rays, abundance of axial parenchyma. Fig. 18. Tangential section, showing wide, high rays. Fig. 19. *Caricaria candamarcescens*. Transection, most recently formed elements at right. Small dark-appearing cells, center, are laticifers. Five vessel elements are seen in transection; the remainder of the xylem is parenchyma. Fig. 20. *Wunderlichia mtrabilis*. Transection of secondary xylem, showing prominent zones of libriform fibers, angular vessels. Most recently formed elements above. Figs. 17, 18, × 65. Fig. 19, × 65. Fig. 20, × 109.
woody species can be observed to have a primary xylem rich in parenchyma, but a secondary xylem incorporating chiefly fibers or tracheids.  

RAYS — Jeffrey & Torrey (1921) contend that specialization in herbs is accompanied by increase in vertical height of rays, and failure of cambial initials to break up these large rays into smaller ones. This observation seems acceptable as a generality, for wide, high rays characterize woods of many herbaceous or herb-like dicots. Size of rays in such species is predetermained by size of pith rays. Active breakup of large rays may be observed in secondary xylem of woody dicots (Barghoorn, 1941a). Failure of ray breakup characterizes most woods of the present study. Comparison of wood of twigs with wood of older stems in certain species (Scaevola kauaiensis, Trematolobelia macrostachys, Carica candamarcesis) showed this to be the case. Observation of transects of other species afforded confirmation, for breakup of rays originating at the pith could rarely been seen. A good example of a species in which little alteration of rays takes place is Scaevola kauaiensis (Figs. 17, 18). Rays in this species are exceptionally wide and high in comparison with wood of other Scaevolas.  

The tendency of ray cells to be exclusively, or almost exclusively, square to erect as seen in radial section is notable in the woods studied here. In some, a few rows of procumbent cells may be present in the central portions of larger rays. Erectness of ray cells is illustrated here for Scaevola kauaiensis (Fig. 18) and Lobelia gibbera (Fig. 24). In some of the species studied, rays are ill-defined, because markedly erect rays closely simulate adjacent libriform fibers. Loss of heterogeneity of rays by absence of procumbent cells does not characterize many woody species. It was, in fact, not taken into account in Kribs' (1935) classification of ray types, a fact pointed out by Barghoorn (1941a). Examples can be found in which pith rays have few procumbent cells, although such cells are produced abundantly as secondary growth progresses (e.g. Phoenix soseras regia). Barghoorn (1941a) illustrates such an example in the case of Bursera simaruba.  

Survey of radial sections of the woods listed in Table 1 and of other woods shows that pith-ray cells are prominently erect in woods with juvenile tendencies. During production of secondary xylem, this pattern changes very little. Thus, this characteristic seems justifiably called a juvenile one for woods such as those of Table 1.  

RAYLESSNESS — Barghoorn (1941b) has stated clearly that raylessness in dicot woods is the result of phylogenetic increase in erectness of ray initials, to the point where ray-cell length equals that of libriform fibers, and the two are identical histologically (Fig. 16).  

Two factors concerning raylessness do not seem to have been appreciated. First, rayless woods initiate the rayless condition almost simultaneously with commencement of secondary growth. Some rayless woods finally initiate rays later in ontogeny, however. Second, rayless woods begin with prominently erect pith ray cells. This is shown for Plantago princeps in Fig. 15.  

Thus, raylessness seems partly a matter of a species having erect pith ray cells prior to secondary growth, partly a matter of elongation of ray initials, and partly a matter of failure of ray initials to subdivide horizontally.  

Why do pith rays of rayless woods have a predominance of erect ray cells? A possible explanation seems to be that the cells in future pith ray areas of a meristematic stem share the elongation which procambium in such a stem experiences. If true, this may be regarded as a specialization. Barghoorn's proposition that elongation of ray initials is a specialization seems wholly plausible. However, one must still explain why some rayless woods ultimately form rays.  

The explanation which appeals to me as most logical and in accord with observed facts is that an essentially juvenile phenomenon is, in part, involved. Elongation of ray initials may be a specialization, but protraction of a juvenile condition is needed to maintain this. Subdivision of ray initials is needed for production of rays in a rayless wood, and onset of such subdivision should logically be interpreted as criterion of maturation,
Figs. 21-24 — Figs. 21, 22. Brighamia insignis, sections of secondary xylem. Fig. 21. Transection, most recently formed elements at right. Pointers indicate three fascicular bands, which contain only a few vessel elements each. Fig. 22. Tangential section. Fascicular areas run from left to right. Figs. 23, 24. Lobelia gibbera, sections of secondary xylem. Fig. 23. Transection. Most recently formed elements above, note thin-walled fibers. Fig. 24. Tangential section, illustrating erectness of ray cells. Figs. 21, 22, × 33. Figs. 23, 24, × 60.
or elimination of the juvenile condition. Corroborative evidence for the role of paedomorphosis in raylessness is provided by the tendency for rayless woods to occur in herbaceous or herb-like plants, a tendency noted by Barghoorn (1941b). Species with rayless woods listed by Barghoorn and by Bourreau (1957) are of this nature. Additional examples can be added, such as the Hawaiian species of Plantago, Jacobinia carneae, Sedum praetatum, certain Heleneae (Carlquist, 1959) and Leptodactylon californicum. All of these can be termed herbs. Bourreau notes that a number of woods with anomalous secondary thickening are rayless. A detailed discussion of the significance of anomalous woods cannot be undertaken here. One may hypothesize, however, that at least some woods with successive cambia represent herbs which have lost true cambial activity, and in which the products of each successive cambium are essentially juvenile wood, at least in some ways.

Discussion

The features described above cannot be analyzed by statistical means, because the tendency toward paedomorphosis would represent a series of interpolations within phyllads, independent of the major trends of wood evolution. Comparisons of the sort offered in Table 1 show that features proposed here as juvenile in whole or in part tend to show a strong degree of correlation with each other, however.

The features involved in paedomorphosis can be expressed independently of each other. The significance of this seems to be considerable, because herbs and herb-like plants can show juvenile wood very clearly, whereas many species possess these features to a limited degree. In other words, one or two juvenile features may occur in a wood which otherwise shows a mature pattern. This, if true, would support the warning of Bailey (1957) against use of vessel-element length of a given species as a precise indicator of the phyletic advancement of that species. Differential rates of evolution in vessel-element length would provide another reason for this warning, of course. This latter reason, however, does not seem to apply to all cases investigated by the writer. On account of this and other anomalies in patterns of wood anatomy in the woods studied and mentioned here, the concept of paedomorphosis has been evoked in order to explain how woods of this nature could exist within the framework of irreversible trends of xylem evolution. The data presented above seem to support the idea that paedomorphosis does exist in dicot woods, although, as in all lines of scientific investigation, additional data will be of value in shaping the applicability of this theory.

The writer had hoped for some criteria in woods showing paedomorphosis which would enable a decision as to whether or not the ancestry of a species (or genus) was woody or herbaceous. This does not seem possible in terms of the present data, and such decisions must be based on other lines of evidence or inference. Paedomorphosis could characterize not only species which appear to have had an herbaceous ancestry (Sedum praetatum, Talinum guadalupense) but also those which seem derived from woody origins (most Compositae). A priori reasoning would suggest that some herbaceous dicots can evolve into woodier forms (independent of the probability that most herbaceous groups appear, ultimately, to be derived from woody stocks) and that, on the other hand, some woody dicots can evolve into a greater degree of herbaceousness. These propositions appear to be probable in certain groups which have been studied carefully. If they are true, one would expect juvenile characters in secondary xylem of plants undergoing either type of phylesis.

Our concepts of juvenile and adult wood are unsatisfactory, as pointed out by Rendle (1958). The above data could be an aid to discovery of, and delimitation of, juvenile features. The use of graphs of element length (Fig. 1) seems to offer the greatest promise as a determinant of beginnings of adulthood in woods.

Summary

Well-established trends of wood evolution, such as those propounded by Bailey, Frost, and Kribs, seem clearly valid.
These trends, however, have been derived from, and must therefore apply to, secondary xylem with mature patterns of construction. Plant anatomists have long been aware that primary xylem differs from secondary xylem in a number of ways. For example, length of elements in primary xylem is often greater than length of elements at the beginning of secondary growth. This involves a change in length of cambial initials. If such a change does not take place, and elements similar in length to those of metaxylem are formed in secondary xylem, a juvenile characteristic may be said to result. A graph of vessel-element length during the growth of a stem (viz. Fig. 1) would serve as one indicator of how soon a wood changes to a mature pattern, or whether it stays in a permanently juvenile condition. In truly woody plants, length of fusiform cambial initials tends to increase rapidly at first, then very slowly during the course of secondary growth. Some of the woods studied here, however, showed a continual decrease in length of elements, or a nearly flat curve. These curves are interpreted as a protraction of the sharp decrease in element length which occurs during the sequence from metaxylem to the beginning of secondary xylem production. Woods with such a hollow or nearly flat curve could be said to be permanently juvenile. Other lines of evidence, however, are required. Presence of scalariform and scalariform-transitional pitting on lateral walls of vessels in species with highly advanced wood structure is cited as another criterion of paedomorphosis, provided it is carefully analyzed. Other features, which are listed in Table 1, are found to bear a strong correlation with the two above characters and with each other in woods of species with herbaceous or herb-like habits (stem succulents, rosette trees, rosette shrubs, etc.).

If paedomorphosis takes place in a wood, appearance of more primitive characters in secondary xylem may result, because primary xylem tends to be a "refugium" for certain primitive characters, and transference of these characters to secondary xylem would result in an admixture of primitive with specialized characters. Examples are given where this appears to be the case. If woods show paedomorphosis, they are not really comparable, phylogenetically, to truly adult woods, and comparative work must take this into account. Phyletis both toward or away from herbaceousness would involve juvenile expressions, so these could not be used as criteria of one ancestry or the other.

Paedomorphosis has probably been interpolated into various groups of dicots, and is not a continuous trend throughout dicots as a whole. Therefore, methods of statistical correlation such as used by Frost, Kribs, and others, cannot be used to establish presence of this phenomenon. Methods used in this paper for determination of juvenile characters included survey of primary xylem characteristics; study of woody plants with herb-like habits; study of the ontogenetic changes within wood of these species, chiefly by means of radial sections; and comparison of wood of these species to wood of annual herbs with sufficient secondary xylem accumulation for comparison.

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