Bordered pits in ray cells and axial parenchyma: the histology of conduction, storage, and strength in living wood cells

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INTRODUCTION

The occurrence of bordered pits between adjacent ray cells or in cross walls of axial parenchyma strands represents a phenomenon that has not been widely reported. Pit borders in secondary walls of wood cells are usually observed most frequently in face view by means of light microscopy. The wall thickness of parenchyma cells in wood, the presence of starch in ray cells, and the small diameter of bordered pits in ray cells make borders difficult to observe in this manner. Borders between ray cells are more readily observed by light microscopy in sectional view in radial sections of woods and have been reported and illustrated for a wide range of dicotyledon families (Carlquist, 1981, 1988a, b, 1989a, 1991, 1992a, 1996, 1997, 1999, 2000, 2001, 2002, 2005) as well as in Gnetales (Carlquist, 1989b, 1992b). Bordered pits on ray cells where a ray cell contacts a vessel were figured by Frost (1931) for Sassafras. Microcasting is a technique that offers an excellent potential for demonstrating borders on pits of parenchyma. Indeed, one can find borders among ray cells illustrated with this technique by Fujii (1993) for Fagus and Quercus and by Peter Kitin (pers. comm.) for Cercidiphyllum and Kalopanax. These authors also illustrated a curious allied phenomenon in ray cells: borders on blind pits that terminate in intercellular spaces. The interest in microcasting has thus far concentrated almost wholly on tracheary elements, and descriptions of ray cell features are few in such studies. Instances can be found in wood anatomical literature in which borders are illustrated but not noticed or even designated as simple pits, as in a clear transmission electron micrograph of Citrus ray cell walls (Fahn, 1990: 40). The...
definition rigorously followed in the present paper is that given by the IAWA Committee on Nomenclature (1964) for a pit border: 'the overarching part of the secondary cell wall'. This is a universally accepted definition.

In the present paper, scanning electron microscope (SEM) illustrations of bordered pits as seen on tangential walls of radial cells from tangential wood sections are presented. Both light microscope and SEM photographs have been offered here for Ephedra (Ephedraceae) and Buddleja (Buddlejaceae, Asteridae). These two genera are illustrated more thoroughly by way of showing a wide range of aspects preferably seen with both types of microscopy. Hopefully, these appearances may be used as a guide to locating bordered pits in ray cells more readily. In some species, phenolic compounds or other dark-staining materials may fill bordered pits and aid in seeing pit contours. Detailed drawings of ray cells by such authors as Braun (1970) and Greguss (1959) illustrate only simple pits and are probably not reliable: their drawings of pits in ray cells may reflect the conventional notion that pits among ray cells are nonbordered rather than pit-by-pit analysis. Core, Coté & Day (1979) offered a table that lists genera that show vessel-ray pitting ranging from 'simple' to 'bordered'. That table, however, does not indicate whether the 'bordered' instances represent pitting between vessels and rays that is composed of half-bordered pit pairs or fully bordered pit pairs.

Living ray cells that have bordered pits are not to be confused with ray tracheids. Ray tracheids have only been reported in conifers (Record, 1934). Ray tracheids are dead at maturity, and have bordered pits like those of coniferous tracheids (but smaller); they often occur at ray cell tips, but may occur in other configurations within rays as well (Pinus). Ray tracheids have been reported in Cupressaceae (Chamaecyparis nootkatensis Spach, Cupressus whiteyana Carr., Thuja plicata D. Don, Sequoia sempervirens (Lamb.) Endl. and in many Pinaceae (all species of Larix, Picea, Pinus, and Tsuga; Abies lasiocarpa Nutt., A. looviana A. Murr., and most species of Cedrus, and Pseudotsuga; Greguss, 1955; Core et al., 1979).

The phenomenon of perforated ray cells is excluded from consideration in the present paper. Perforated ray cells are derived from ray initials, but have the characteristics of vessel elements and represent pathways of vessels that traverse rays.

Vascular tissue embedded in ray tissue is likewise not included in the present paper. Boureau (1957) reported this phenomenon in Aeschnynome (vessels embedded in massive rays), Cytisus (fibre-tracheids with helical thickenings in rays), and Monopteryx (fibre strands in rays). These are all genera of Fabaceae. Radially orientated libriform fibres occur in rays of Cecropia of the Moraceae (Carlquist, 1988a). There are also numerous instances of wide rays, in various stages of fragmentation that contain vascular tissue that represents a remnant of vascular continuity between a stem and a lateral branch. In all instances cited in this paragraph, the vascular tissue in rays is dead at maturity, and thus can be differentiated from the living ray cells, which are the focus of this paper. By 'living' ray and axial parenchyma cell, I intend a contrast with cells dead at maturity: tracheary elements, ray tracheids, perforated ray cells, and allied phenomena mentioned above. The precise longevity of any given parenchyma cell is not implied here. The presence of starch and other photosynthates in ray and axial parenchyma cells suggests prolonged longevity, as in Acer, in which these cells function in the renewal of the conductive system at the end of winter (Sauter, Iten & Zimmermann, 1973).

The phenomenon of nucleated ray cells with bordered pits needs consideration in ways other than descriptive. On the basis of the observations made in preparation for the present paper, bordered pits are present in ray cells of numerous dicotyledons representing the major clades, as well as in Ephedra and Gnetum. This circumstance suggests that living ray cells with bordered pits should be examined in terms of physiology and mechanical strength. Living ray cells contain enormous quantities of photosynthates, the ingress and egress of which in the form of sugars should be considered in relation to pitting. Pit fields in ray cells with only primary walls represent broad thin areas that could accommodate photosynthesize transfer among ray cells. However, ray cells of many species have secondary walls that represent a significant deposition of wall material in the form of cellulose and other components. This investment in strength-producing wall structure must represent an enhancement of mechanical strength for the wood. Bordered pits offer an ideal compromise between optimal mechanical strength and optimal flow: retention of maximal pit membrane areas that favour conduction combined with minimal interruption of wall strength by virtue of the relative narrowness of pit apertures (Carlquist, 1988a). Greater pit density on tangential walls (as compared with radial walls) of ray cells, figured in many instances by Braun (1970), is one way of expanding the conductive surface, and the bordered nature of pits on these walls is another. The consideration of ray histology needs to take into account both mechanical strength and peak flow between cells, presumably when starch is hydrolysed into sugars that serve various functions. The mechanical strength of rays has been subsumed as a part of the strength features of wood, presumably because analysing the relative contributions of rays and of 'fibrous tissue' to mechanical strength is impractical where types of
strength testing are concerned. In the context of anatomical information, one finds a great deal of literature devoted to the distribution of ray cell types (upright vs. procumbent) and their phylogenetic significance (Carlquist, 1988a). The summary of Metcalfe & Chalk (1983) work on 'ray structure in relation to physiological function' is admirable, but by the small number of papers cited, it shows the rudimentary state of our knowledge.

Any consideration of ray structure and function invites concurrent consideration of axial parenchyma. Although the character states of the two parenchyma systems in wood are analysed separately by wood anatomists for purposes of description, the two systems are interrelated histologically and functionally. Braun & Wolkinger (1970) implicated axial parenchyma in water flow within wood. That is conceivable if one considers solutes that may be involved in that flow. Sinnott (1918) found that diffuse porous woods store fat in axial parenchyma in winter, whereas ring porous woods store starch in axial parenchyma in winter. The small number of observations on which these conclusions were base suggest the understanding of axial parenchyma phylogeny, like that of ray parenchyma physiology, is still in a rudimentary state.

Although bordered pits on ray cell walls proved common in my observations of many species of dicotyledons, bordered pits on axial parenchyma are much scarcer. One might have thought that the 'pseudotracheids' reported by Lemesle (1956) for Bruniaceae and by Lemesle & Duchaigne (1955a, b) were possibly axial parenchyma cells, but the existence of this cell type has not been confirmed (Carlquist, 1978, 1989c). Ray cells in both of these families do have bordered as well as nonbordered pits, and are like those of many woody dicotyledons (original data).

The nature of nucleated cells referable to the concept of axial parenchyma in Ephedra is explored in the present paper. New evidence is presented to clarify the nature of these cells.

Axially orientated cells termed strand tracheids have been reported in conifers, but not in angiosperms (Record, 1934). Strand tracheids recall axial parenchyma in shape, occurrence as strands, and distribution in conifer woods, but they are dead at maturity and have small coniferous bordered pits. Strand tracheids have been well illustrated by Butterfield & Meylan (1980) for Pinus radiata D. Don. Strand tracheids, like ray tracheids, are excluded from the present study.

Conclusions concerning the functions of bordered pits in living parenchyma cells of wood can only be inferential on the basis of the information presented here. Experimental work is needed for validation of concepts concerning physiological and biomechanical functions. However, understanding anatomical condi-

pits may be present on any given wall in addition to bordered pits. The ray and axial parenchyma cells described here do not differ from these cell types as observed in innumerable other woods, and should in no way be interpreted as showing features restricted to the species selected for illustration.

Sectional views of ray and axial parenchyma cell walls as seen with a light microscope have the potential disadvantage that pits are usually arranged randomly on a pit wall. One might therefore expect that median views of bordered pits would be difficult to obtain. In practice, median views of pits in axial and ray parenchyma are as readily obtained as they are in sectional views of conifer tracheids. The reader should keep in mind that face views of pits in parenchyma of woods are best rendered in face view with SEM, and in sectional view with light microscopy. Alternative modes of viewing these pits (in face view with light microscopy, in sectional view with SEM) are more difficult, but can be successful once one is accustomed to the appearances of these pits in various planes.

All longsections, whether rendered by light microscopy or SEM, have been orientated consistently in this paper (vertical axis orientated vertically on the page), except for Figure 15. The two transactions (Figs 4, 20) are represented with the radial axis horizontal on the page.

RESULTS

RAY CELLS

Ephedra

In a radial section of E. pedunculata wood (Fig. 1), the tangentially orientated walls of ray cells (vertical in the photograph) bear numerous bordered pits. Horizontal walls have fewer pits, but the pits are also bordered. In this species, the staining combination used tends to make the pit membranes and pit cavities look dark, in contrast to the light tone of the secondary walls. Ray cells of E. pedunculata, like those of other species of Ephedra, often have tangential walls that are orientated in diagonal rather than vertical directions in relation to the stem axis (Fig. 2). The number of bordered pits on diagonal walls is, by virtue of this angle, greater than the number of pits on more nearly vertical walls (Fig. 1). Ray cells of Ephedra are alive at maturity, as shown by nuclei (Fig. 3, cell at right; Fig. 4). In E. aspera, ray cell walls (Fig. 4) are notably thick and bear bordered pits. In all species of Ephedra studied, tracheid to ray pits and vessel to ray interfaces have bordered pit pairs.

SEM photographs of E. viridis wood (Figs 6–9) confirm the features described in terms of light microscopy. The tangential section in Figure 6 includes, at lower power, the cells shown in Figures 7–9; the cells enlarged are indicated with arrows in Figure 6. In Figure 6, some cells seem to protrude (bright tones), whereas socket-like pockets (dark) are evident. These appearances represent diagonally orientated ray cell walls that have been exposed rather than sectioned. Tangential walls of ray cells (Fig. 7) have numerous bordered pits. The pits are quite varied in diameter. Large bordered pits are seen near the tip of a diagonally orientated ray cell wall (Fig. 8). The pits on upright ray cells (Fig. 9, centre right) are small and sparse, but also bordered.

Buddleja

A light micrograph of a radial section of a B. bullata ray (Fig. 10) shows a tangential wall in sectional view. Bor~ed~ed ~pits ~are ~present ~on ~the ~wall. ~The ~same features may be seen for B. bullata rays using SEM (Fig. 11). The tangential walls of upright ray cells have bordered pits, as seen in sectional (right) and diagonal (left, above) view. The double crescents of the pits seen in diagonal view are indicative of the bordered condition. An enlarged portion of a wall (Fig. 12) reveals the characteristic appearance of several bordered pits as seen in sectional view. A tangential section of a pair of ray cells (Fig. 13) at relatively low magnification shows the lumen of the cell on the left, with two crystals. The cell on the right is very similar, but is viewed from the outside surface. This outside surface (Fig. 14) is randomly covered with pits, all of which are bordered. Two similar outside wall surfaces (Figs 15, 16) are presented to show the range of patterns to be expected. Pits can range from relatively large to minute (Fig. 15). The stripping away of pit membranes to reveal pit borders is only partial in Figure 16, but the contours of the borders can be seen vaguely, even for those pits covered by pit borders. Ray cell walls that face imperforate tracheal elements in Buddleja are thin and bear bordered pits.

Other angiosperm woods

Tasmannia purpurascens show markedly bordered pits on walls of ray cells (Fig. 17). Most ray cells in T. purpurascens are upright. The tangential walls (Fig. 17, upper three-quarters of photograph), the radial transverse (Fig. 17, bottom), and the radial vertical walls of the ray cells all bear dense coverings of bordered pits.

InDasypodylon spinescens (Fig. 18), ray cells are thick walled and bear bordered pits. The pits are densely placed not only on tangential walls, but also on transverse and radial vertical walls. Ray cells in the specimens of D. spinescens are square to upright.

Ray cells of Platanus racemosa are mostly markedly procumbent (Fig. 19). As seen in radial section, the 'tangential' walls are mostly markedly diagonal in orientation. There is a marked disparity in pit density.
Figures 1–5. Sections of Ephedra wood. Figs 1–3. *E. pedunculata*, views of ray cells from radial sections. Fig. 1. Bordered pits in tangential walls (vertical) are more numerous than in horizontal walls. Fig. 2. Ray cells have tangential walls orientated from near-vertical to diagonal. Fig. 3. Portions of two ray cells (seen at the bottom of Fig. 2) to show the nucleus to the right of the diagonal wall with prominently bordered pits. Fig. 4. *E. aspera*, wood transaction; ray cells are nucleate and have numerous bordered pits on the strongly oblique walls. Fig. 5. *E. pedunculata*, cross wall of an axial parenchyma strand in radial section; the cross wall contains bordered pits. Scale bars = 10 μm.
Figures 6-9. Scanning electron micrographs of rays from a tangential section of *Ephedra viridis* wood. Fig. 6. A low-power photograph showing rays; two tracheids on the left. Fig. 7. View of the ray cell surface corresponding to the uppermost arrow in Figure 6; pits are bordered and graded in size down to very small diameters. Fig. 8. Ray cell corresponding to the central arrow in Figure 6; bordered pits at the cell tip are relatively large. Fig. 9. Upright ray cell corresponding to the area near the lowest arrow in Figure 6; a single small bordered pit on the right. Scale bars = 5 μm.

Figures 10-16. Wood of Buddleja bullata. Fig. 10. Light micrograph of ray cells from a radial section; borders present on the pits of the wall to the left of the crystal. Figs 11, 12. Scanning electron micrographs of upright ray cells from a radial section. Fig. 11. Bordered pits in sectional view (right) and oblique view (left). Fig. 12. Enlarged portion of Figure 11 to show the bordered nature of pits on a tangential wall. Figs 13-16. Scanning electron micrographs of ray cells from a tangential section. Fig. 13. Two upright ray cells; the lumen of the cell on the left contains two crystals; on the right, the outer surface of the cell. Fig. 14. Portion of the cell on the right in Figure 14 to show the bordered nature of all the pits on the wall. Fig. 15. Another tangential wall surface, showing a wide range in size of the bordered pits. Fig. 16. Another tangential wall surface; the bordered nature of the pits is evident, even in those pits still covered by pit membranes. Figs 10, 11: scale bars = 10 μm; Figs 12-16: scale bars = 2 μm.

Figures 17-22. Light micrographs of radial (Figs 17-19, 21, 22) and transverse (Fig. 20) sections of angiosperm wood. Fig. 17. *Tasmannia purpurascens*. Portions of upright ray cells; bordered pits are dense on all walls. Fig. 18. *Dasyphyllum spinescens*, portions of ray cells showing bordered pits equally dense on horizontal and vertical walls (on the left, a portion of a vessel wall). Figs 19, 20. *Platanus racemosa*, portions of procumbent ray cells. Fig. 19. Tangential walls (which slant diagonally) are much more densely pitted than the horizontal walls. Fig. 20. Pits on tangential walls (vertical in photograph) are bordered, whereas pits on the radial walls (horizontal in photograph) are sparse, simple or minimally bordered. Figs 21, 22. *Trignostrum hypoleucum*, axial parenchyma cells. Fig. 21. Axial parenchyma cross walls bear simple pits: one large and some smaller pits in the cross wall on the left, one simple pit in the cross wall on the right (fibre-tracheids in the centre of the photograph). Fig. 22. Axial parenchyma cross walls bear bordered pits; pits are simple or minimally bordered on vertical walls. Scale bars = 10 μm.
between tangential and radial horizontal walls. The pits are dense and bordered on the tangential walls (Figs 19, 20). The pits on radial horizontal walls (Fig. 19, walls horizontal in photograph) and radial vertical walls (Fig. 20, walls horizontal in photograph) are sparse and either simple or minutely bordered.

*Trigoniastrum hypoleucum* ray cells (not shown) are relatively thick walled and have clearly bordered pits on tangential walls.

### AXIAL PARENCHYMA

A diagonal wall between two cells of an axial parenchyma strand is shown for *E. pedunculata* in Figure 5. The pits on this strand cross wall are bordered, although the borders are minimal, and simple pits can be seen on some strand cross walls in *E. pedunculata*. The pits on vertical walls of axial parenchyma in *E. pedunculata* are mostly inconspicuously bordered (Fig. 5). *Ephedra* presents a terminological problem because, as seen in *E. pedunculata*, one can call undivided fusiform living wood cells with small minutely bordered pits either fibre-tracheids or undivided axial parenchyma cells.

In *Buddleja, Tasmannia, Dasyphyllum*, and *Platanus*, vertical axial parenchyma walls are thin and bear sparse simple pits. Vertical axial parenchyma walls in *Trigoniastrum* (Fig. 21) are a little thicker than in the preceding genera but bear sparse, minutely bordered pits. The cross walls in axial parenchyma of these genera have relatively large pit areas, as seen in *Trigoniastrum hypoleucum* (Fig. 21). The pits may be simple or minutely bordered in *Buddleja, Dasyphyllum*, and *Trigoniastrum*, but appear simple in *Tasmannia*. The simple condition is featured in the cross walls of the two axial parenchyma strands in Figure 21, whereas the pits in the axial parenchyma strand in Figure 22 are minutely bordered.

### CONCLUSIONS

#### HISTOLOGICAL ASPECTS

The purpose of this study was to open vistas of structure and function in living wood cells for further examination, and to ask questions that have not been explicitly considered before. The patterns presented obviously form more of a framework than a completed picture. Without such a framework, interesting structure-function correlations cannot be addressed. Although numerous observations were made in preparation for this study, many more are clearly needed. In no way does the present paper differ in application of the term ‘bordered pit’ from those of other authors. The occurrence of these structures in ray and axial parenchyma of wood has been seriously underreported.

Bordered pits among living ray cells are clearly common in Gnetales and woody angiosperms. Bordered pits may be present exclusively, or intermixed with simple pits, or simple pits may be present exclusively on ray cell walls. When using light microscopy, the occurrence of pits among ray cells is best seen on radial wood sections, where views of ray cells in sectional view reveal pits more readily. When SEM can be used, viewing bordered pits in face view is desirable, and tangential sections are advantageous for revealing the dense pitting that often characterizes tangential walls of ray cells. Beginning with these methods, one can then readily locate bordered pits in ray cells using other ways of viewing ray cell walls.

Differential density and the degree of pit border representation are evident when one compares tangential walls of ray cells with radial walls. Tangentially orientated walls are more densely pitted and have more prominently bordered pits than radial walls (either horizontal or vertical) in the case of procumbent cells. Tangential walls of ray cells are often slanted or diagonal in orientation, and thus contain more numerous pits than vertically orientated tangential walls in a given ray cell. Square to upright ray cells tend to have pits that are approximately equally dense on tangential walls as compared with horizontal or radial vertical walls. Bordered pits in erect ray cells are common in many woody species.

There is a parallel between the direction of cell elongation, the density of bordered pits, and probable flow. Procumbent cells represent a design for radial flow efficiency where flow between living wood cells is concerned. The elongate nature of conductive tracheary elements, as well as sieve elements, by having fewer cross walls per unit length, has less impedance to vertical flow and represents, at a very simple histological level, a parallel to the radial flow design of procumbent ray cells. Square to upright cells, seen in this perspective, represent an intermediary flow design: a transition between the procumbent ray cells and the vertical nature of axial parenchyma.

Axial parenchyma cells that have secondary walls tend to have walls that are relatively thin compared with those of ray cell walls and imperforate tracheary elements in any given species. Indeed, the contrast in wall thickness is one of the features used to identify axial parenchyma in wood transactions. The lateral walls of axial parenchyma are more sparsely pitted than the cross walls. Cross walls may bear a single large pit. Borders are more commonly present on pits of the lateral walls than on the cross walls of axial parenchyma. These features represent the optimal design for flow within a vertical system of living cells in wood.

The living axial wood cells of *Ephedra* form a question of minor importance. They have bordered pits
much smaller than those of tracheids, and could either be termed fibre-tracheids (Esau, 1965) or axial parenchyma. Axial parenchyma cells need not be subdivided into strands, but can occur as nonsubdivided cells, as in Krameriaceae (Carlquist, 2005). However, as in E. pedunculata, the axially orientated living wood cells of Ephedra may have cross walls (not to be confused with septa) or may not be subdivided. Thus, these cells may be considered a type of axial parenchyma. Liquid-preserved materials, which were used extensively in the study of Ephedra woods (Carlquist, 1989b), demonstrate that these cells in Ephedra are always nucleate, which fibre-tracheids rarely are.

**Physiological and mechanical aspects**

The formation of secondary walls in secondary xylem represents a significant energy expenditure, which should be considered in an adaptive light. The function of secondary walls in resisting cavitation in tracheary elements has been stressed (Carlquist, 1975; Turner & Somerville, 1997; Niklas, 1992, 1997; Hacke et al., 2001; Franke et al., 2002). The strength of ray cell and axial parenchyma walls is probably not involved in that function, but these living cells may play secondary roles in promoting wood strength. Jacobsen et al. (2005) stated that the ‘mechanical properties of xylem fibers, as well as other cell types associated with vessels, including xylem parenchyma and, in some species, tracheids, are important to determining resistance to cavitation’.

The presence of secondary walls on tracheary elements is also cited as promoting mechanical support functions of the stem (Jagels & Visscher, 2006). The data of the present paper suggest that ray cells and, to a lesser extent, axial parenchyma cells also contribute to the mechanical strength of wood. The role of parenchyma cells in wood strength is difficult to measure, because isolating them from tracheary elements is impractical. There is no reason, however, to consider the secondary walls of living wood cells as playing no role in mechanical support.

Wall thicknesses of axial and ray parenchyma cells are generally less than those of the walls of tracheary elements with which they are associated, but often not markedly so. The measurement of wall thickness potentially offers a simple way of inferring the relative contributions of cell types in wood to the mechanical strength of wood (although microfibril orientation is a potential complicating factor). Axial parenchyma cells, because they are relatively thin walled, probably contribute a small amount to wood strength. Axial parenchyma cells in some woods can lack secondary walls altogether (Carlquist, 2005), so that secondary walls of axial parenchyma cells, where present, must represent some mechanical strength. The contribution of ray cells to mechanical strength is greater, judging by the wall thickness (and by microfibril orientation on the basis of polarized light observations). Burgert et al. (2001) offered an interesting insight into the role that rays play in the mechanical strength of wood. The function of axial and ray cell lumen volume as a space for the storage of starch and the housing of crystals, phenolic compounds, etc., sets a boundary above which an increase in wall thickness would not be adaptive.

Bordered pits represent a way of maximizing wall strength while providing a maximal conductive area between cells (Carlquist, 1988a: 108). If wall thickness is minimal, as it is between many parenchyma cells in plants, there is little selective value for bordered pits. Selection for border presence increases with secondary wall thickness. Bordered pit presence is by no means always correlated with the wall thickness of axial and ray parenchyma cells. Because the function of bordered pits in nonliving cells of wood has so frequently been stressed, one must enquire into how the trade-off between mechanical strength and conduction represented by bordered pits functions in parenchyma of woods.

The function of axial parenchyma and ray cells in woods in the storage of starches and oils has occasionally been studied (e.g. Sinnott, 1918). Sauter et al. (1973) implicated living parenchyma cells in the transfer of sugars into vessels of Acer, an action that renews conduction in vessels by increasing their osmotic pressure. Starches and oils are rarely reported in studies of wood anatomy. In part, this is a methodological matter. Oil and starch can disappear during the drying of wood specimens, and dried wood samples are used much more often than liquid-preserved samples in wood anatomy. The presence of starch or oil is not considered a diagnostic feature, and thus those interested in wood identification have little reason to consider them.

In fact, sections of living or liquid-preserved woods often reveal the storage of large quantities of starch or other photosynthates. The accretion of starch is probably a gradual process, taking place over a period of months. The reverse process, the mobilization of starch into sugars, may be much more rapid. Translocation rates of sugars to utilization sites have been little studied in xylem. Sudden flushes of growth, rapid flowering events, or the input of photosynthates to fruit and seed formation may be involved with high flow rates of sugars, not merely in phloem, but in parenchyma cells of the wood. If bordered pits represent a compromise between conductive efficiency and wall strength, then the dense placement of bordered pits on tangential walls of ray cells and on cross walls of axial parenchyma strands becomes understandable. Axial parenchyma represents a conduit for the vertical conduction of photosynthates within the wood.
whereas procumbent ray cells presumably serve for radial conduction within the wood and into phloem and bark. Upright ray cells can serve for photosynthetic conduction between axial parenchyma and procumbent ray cells. The strong distinction between ‘contact cells’ (radially elongate ray cells related to radial conduction processes) and ‘isolation’ cells (axially elongate parenchyma cells) promoted by Braun (1970) is not confirmed here, although distinctions between cells representing extremes can be made. Bordered pits can occur on both tangential and horizontal walls of upright ray cells in approximately equal numbers (Buddleja, Tasmannia), indicating that radial conduction occurs in upright cells. Bordered pits may occur on horizontal walls as well as tangential walls of procumbent ray cells (Ephedra), indicating that axial conduction between procumbent ray cells can occur.

The phenomena described above are widely represented in woods, but the citation of them to date has been relatively small. From information at hand, there is no evident correlation between the phylodetic position and presence of bordered pits in axial or ray parenchyma cells. The introduction of Ephedra into this study should not be taken as an indication that bordered pits represent a symplesiomorphic feature. Bordered pits in axial and ray parenchyma cells, on the basis of present knowledge, occur widely in angiosperm clades and show no clear systematic pattern. Species with greater parenchyma cell wall thickness may be more likely to have bordered pits in axial and ray parenchyma.

Bordered pits are not conspicuous on most axial and ray parenchyma cells. This lack of conspicuousness must not be equated with absence, or a lack of inherent histological interest. Fibre-tracheids often have minute bordered pits, the pit cavities of which are often much more difficult to see than those of ray cells, but those have often been noted. The methods used in the present study are easily performed and can be included in routine studies of wood anatomy. Studies of wood strength in axial and ray parenchyma can be made, at least at an inferential level, by the calculation of the volume of secondary wall material. Examination of the photosynthetic flow within woods may seem daunting, but the methods of Sauter et al. (1973) offer a promising template. Thus, a wider appreciation of the function and structure of axial and ray parenchyma cells can be accomplished by methods already at hand.

REFERENCES


