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DISTRIBUTION OF VESSEL DIAMETER IN RING-POROUS TREES

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ABSTRACT

The wood anatomy of ring-porous trees presents difficulties of description and measurement. Information regarding the distribution of vessel diameters within the yearly growth increment may be of use of interpreting wood anatomy and function. Two distributional patterns can be recognized in the trunk xylem of the five ring-porous species investigated. The following terms are proposed: *graduated-unimodal,* to refer to ring-porous woods with one population of vessels, and *graduated-bimodal,* to refer to woods with two distinct peaks in vessel frequency.

Key words: wood anatomy, ring-porous woods, vessel diameter distribution, graduated-unimodal distribution, graduated-bimodal distribution.

INTRODUCTION

The anatomical terms ring porous and semi-ring porous have been used variously in the botanical literature. The initial use of these terms undoubtedly derives from the presence, in trees with ring-porous wood, of large vessels at the beginning of the growth increment and the ring, generally visible to the naked eye, that these vessels form. The term is used in this sense by Jane (1970) among others. Semi-ring porous is then used to refer to cases in which the vessels in the earlywood increment are not immediately adjacent and the ring is less well defined. A different usage is followed by other authors (Brown and Panshin 1934; Metcalfe and Chalk 1950; Carlquist 1980). These anatomists use the term ring porous to refer to woods in which there is a sharp difference in vessel size across the width of the ring. Semi-ring-porous woods are then differentiated from ring porous in showing a gradual change in vessel size across a ring. For some species, both these criteria are met, i.e., a distinct pore ring is present with the vessels exhibiting an abrupt change in size at the transition zone. In other cases, however, this is not true and the designations differ correspondingly. An example is *Tilia americana* L. (American basswood), which has a distinct pore ring but a gradual transition in vessel size across a ring and would be described as ring porous by Jane and semi-ring porous by Metcalfe and Chalk. Usage of these terms in the International Glossary of Terms Used in Wood Anatomy (Committee on Nomenclature, International Association of Wood Anatomists 1964) is again somewhat different.

These distinctions became important to me in the course of a study of the climate sensitivity of the anatomical characteristics of the wood of several species of ring-porous deciduous trees (Woodcock 1987). For this project, it was necessary to obtain measurements from successive yearly increments over a fairly long interval (50 years). Measurements such as vessel diameter and density were obtained from both the early- and latewood increments. Being able to delineate early- from latewood was important, especially for some of the variables measured. Here I fell back on both criteria that have been used to define ring porosity.

However, in the principal species I worked with, *Quercus macrocarpa* Michx., which is consistently described in the literature as ring porous, occasional years have wood in which the earlywood vessels do not form a complete ring and the transition in vessel size across the ring is gradual rather than abrupt. In other words, the early- and latewood cannot be unambiguously determined in all cases. (My experience has been that other species described as ring porous, i.e., exhibiting an abrupt transition in vessel size across the ring, actually show a gradual transition in some years.) Three species native to southeastern Nebraska were included in the study. Of these, *Quercus rubra* L. has wood in which the distinction between early- and latewood is difficult and must be made by reference to the continuity of the ring; *Q. macrocarpa* has wood in which the distinction can be made in most years by one or the other of the criteria mentioned; and *Fraxinus americana* L. consistently exhibits an abrupt change in vessel size that serves to delineate the two parts of the growth ring.

The anatomical characteristics of the wood of deciduous trees are noted for their complexity. The measurement difficulties met with are one indication of the inadequacy of existing descriptions. Carlquist (1980, 1988) has attempted to deal with some of these problems in a classification scheme that includes changes in diameter of the conductive elements and in the composition of cell types across the ring; 15 types are recognized, most of which exhibit some degree of gradation in vessel size across the ring.

One practical consequence of the problems of differentiating early- and latewood is that it is in many cases difficult or impossible to obtain consistent measurements of anatomical variables in ring-porous trees. Vessel diameter can generally be sampled randomly, but any variable which must be determined with respect to an area—as for example, vessel density, total conductive area, or conductivity (sum of the diameters to the fourth power)—is problematic. The uncertainty introduced with measurements of this type is particularly undesirable in studies of yearly variations within the wood.

The above-mentioned problems in measurement, and, to some degree, terminology, led me to wonder whether the spatial pattern exhibited by vessels is the most significant characteristic of the wood. Anatomical descriptions have tended to emphasize temporal shifts in vessel size (and the resultant spatial pattern), whether with respect to presence of an observable growth ring or changes visible across the ring itself. Studies of wood ecology have had this same focus. However, the conductive capacity of wood should in general be determined, not by the arrangement of vessels, but by the number of vessels and their size.

If the conductive elements are idealized as a series of pipes in parallel, then volumetric flow (conductivity) is proportional to the sum of the diameters to the fourth power. Wood deviates from this ideal in at least several respects, however (vessels anastomose and are not of infinite length), and measurements of flow rate yield values both considerably less than and approximating calculated values of conductivity (Zimmermann 1983; Ellmore and Ewers 1985). The exact relationship between anatomical characteristics and conduction is thus not clear. Flow rates should, however, be a function, although perhaps a complex function, of diameter, and distribution of vessels within the ring should be of functional significance. The diameter distributions of vessels in the trunk xylem of six species of deciduous trees are presented here.

MATERIALS AND METHODS

Two types of material were used in the study. Thin sections of tree cores from native tree populations growing in southeastern Nebraska were the source of data for *Fraxinus americana* (green ash), *Quercus rubra* (red oak), and *Q. macrocarpa* (bur oak). The Hough collection wood slides was utilized to obtain measurements for the remaining species (*Acer pennsylvanicum* L., striped maple; *Juglans cinerea* L., butternut; and *Carya tomentosa* [Poir.] Nutt., mockernut). Choice of species was influenced by the requirement that 20 yr be available for measurement. An attempt was made to include a variety of different wood types. The large number of measurements obtained for each species placed a limit on the number of taxa included.

Wood characters are known to vary within an individual tree. The measurements are for trunk xylem; it is quite possible that twigs or roots may have different distributional patterns. Characters are also known to change with age of the tree; in all cases, the measurements are for the outer wood rather than the early growth.

All the vessels were measured within an area approximately 5 mm in width extending across 20 yr of growth. The long and short axes were averaged in the case of vessels that were noncircular in cross section. Observations were made with a light microscope, and data were recorded by hand.

Because of the limitations imposed by the techniques used to collect and record data, the treatment presented here focuses on the number of populations present, which can be evaluated subjectively by reference to the histograms. Statistical analyses of various sorts could be applied to measurements collected with digitizing or image-processing techniques and transmitted directly to a computer; this type of approach is recommended for future studies.

RESULTS AND DISCUSSION

The frequency distributions are presented in Figure 1. Diagrams showing the arrangement of vessels across a ring in these species are provided for comparison in Figure 2. One diffuse-porous species, *Acer pennsylvanicum*, is included in the analysis. The vessels in this species have a symmetrical distribution with a small range (Fig. 1a). All the other species are ring porous (this term used here to indicate a significant gradation in vessel size across the ring). In these five species, the range in vessel diameter is one order of magnitude or greater (corresponding to a range in conductivity of the individual vessels of 10^4). The widest range is seen in the wood of *Quercus macrocarpa*, which has vessels as large as 0.4 mm in diameter (Fig. 1f).

Two distinct types of distribution are recognized among the ring-porous species. One species, *Juglans cinerea*, exhibits a unimodal distribution of vessel diameter (Fig. 1b). Four of the ring-porous species (*Fraxinus americana, Carya tomentosa, Q. rubra*, and *Q. macrocarpa*) have distributions that are bimodal. The species investigated here have a greater number of earlywood vessels; however, this is not the case in all ring-porous species (Carlquist 1980) or in all years in a taxon like *Q. macrocarpa*, and there is a trend toward a smaller number of latewood vessels (and a narrower ring) as a tree ages.

The terms "graduated-unimodal" and "graduated-bimodal" are proposed to refer to the two distribution types. Woods that are quite different in structure

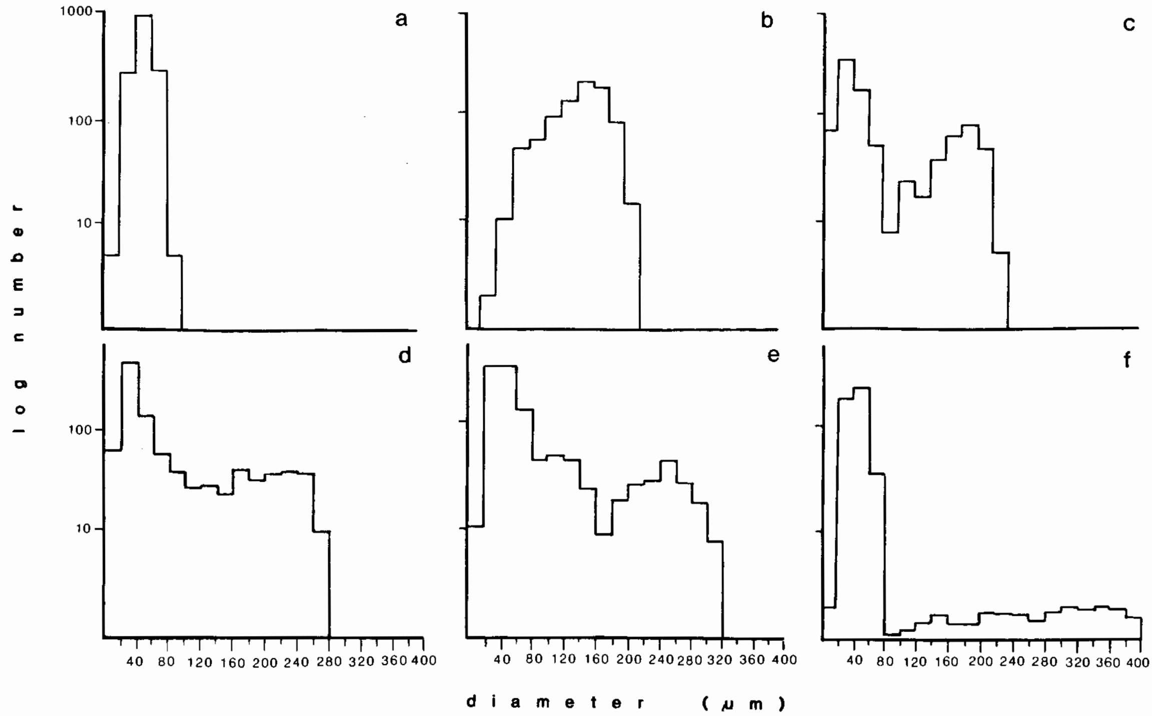

Fig. 1. Distribution of vessels by diameter in six species of deciduous trees: a) *Acer pennsylvanicum*; b) *Juglans cinerea*; c) *Fraxinus americana*; d) *Carya tomentosa*; e) *Quercus rubra*; and f) *Q. macrocarpa.*

have a bimodal distribution of vessels. Consider, for example, *F. americana* and *Q. rubra* (Fig. 1c and e). These species would be described as ring porous and semi-ring porous, respectively, according to the terminology of Metcalfe and Chalk (1950). If measurements for the early- and latewood increment are plotted separately (Fig. 3), there is a different degree of overlap in vessel size between the two parts of the ring owing to the following characteristics of the woods. (Here the continuity of vessels in the earlywood increment is used to distinguish early- from latewood.) In *F. americana* there is little overlap in vessel size between the two parts of the ring (although some smaller cells are present within the earlywood increment). In *Q. macrocarpa,* in contrast, large vessels are produced in the early part of the latewood (the gradual shift in vessel size referred to by the term semi-ring porous *sensu* Metcalfe and Chalk) and smaller cells are present within the earlywood as well. As noted, however, these woods are quite similar with respect to total distribution of vessels.

The patterns seen here can be compared to the classification categories proposed by Carlquist (1980, 1988). The unimodal distribution of *Juglans cinerea* is consistent with the description given by Carlquist for Type 3 woods. These woods are described as having vessels that vary little in number across the ring but are larger in size in the earlywood. The example he cites is *Juglans nigra* L. In order for a unimodal distributional pattern to exist when vessels change size across the ring, the spatial distribution of vessels must be constant and the total range in size must be within certain limits (this pattern could not exist in ring-porous oaks

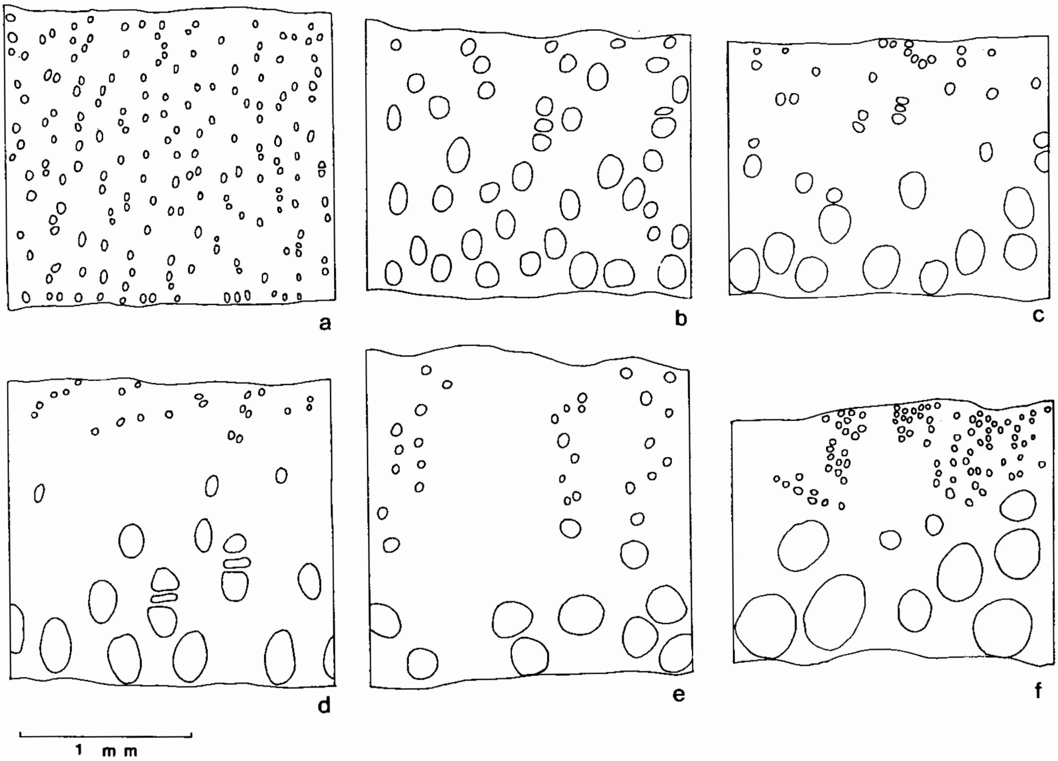

Fig. 2. Arrangement of vessels across a representative portion of the ring for the same species as in Fig. 1. Taxa are as follows: a) *A. pennsylvanicum*; b) *J. cinerea*; c) *F. americana*; d) *C. tomentosa*; e) *Q. rubra*; and f) *Q. macrocarpa*.

such as *Q. macrocarpa* owing to the very large size of the earlywood vessels and constraints relating to packing). The remaining species of ring-porous trees fall under various of Carlquist's categories. To give an example for the two oak species, *Q. macrocarpa* has Type 4 wood, described as having latewood vessels showing little gradation in size within the latewood increment, and *Q. rubra* has wood of Type 8, having latewood vessels more numerous than earlywood but thicker-walled. (Diagnostic characteristics relating to types of subsidiary cells present not taken into consideration here.)

Ring porosity in trees and the differentiation of two types of wood has long been interpreted as an adaptation permitting increased flow of water early in the growing season. More recently, it has been recognized that ring-porous trees (at least the strongly ring-porous types) leaf out later in the year than diffuse-porous species while initiating cambial activity earlier in the year (Lechowiez 1984). These trees appear to be dependent on high flow rates during the relatively short time when the leaves flush in the spring. Likewise, the small, numerous vessels of some woods have been described as adaptations that decrease the vulnerability of the plants to water stress since smaller vessels are less susceptible to embolism and a greater number of vessels provides insurance against the loss of some conductive elements under conditions of water stress (Carlquist 1975). Wood with small, numerous vessels is typical of woody plants in xerophytic environments and also

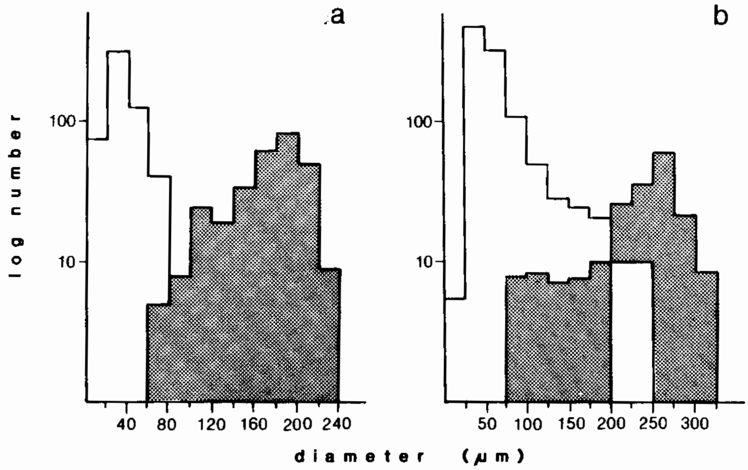

Fig. 3. Distribution of vessels in (unshaded) earlywood and (shaded) latewood of a) *F. americana* and b) *Q. rubra.*

of the late growth of ring-porous trees. The large springwood vessels of ring-porous taxa supply most of the transpirational needs of the tree while they are functional (Ellmore and Ewers 1985); the latewood may be more important later in the year as water stress increases and the larger vessels are more subject to embolism. The distributional analysis showing that most ring-porous trees clearly have two different populations of cells is consistent with the idea that two adaptive strategies are in play.

Chalk (1937) considers the latewood of ring-porous species to be comparable to the entire growth increment of diffuse-porous species. In support of this idea he cites the similarity in structure, in groups such as the oaks, between the latewood of ring-porous species and the diffuse-porous wood of related taxa. The transition from a diffuse-porous to a ring-porous condition appears to have been arrived at in different ways. The wood of taxa such as *Juglans* spp. may represent one end of the spectrum, with a smooth gradient in vessel size developing over the ring. In other species, two distinct populations of cells became differentiated. This type of distributional pattern could be produced by differential expansion of cells produced at the same time, a gradual or abrupt transition in size of the vessels produced within the ring, or differences in the numbers of vessels or their arrangement within the ring. The variety of patterns evident among ring-porous woods suggests that ring-porous woods developed in all these ways and is consistent with the idea that ring-porosity evolved many times in separate lineages.

In conclusion, it appears that two types of vessel distributions can be recognized within ring-porous woods, with a variety of wood types having distributions that are graduated-bimodal. Distributional data of this type give information of functional significance that may be helpful in dealing with the complexity of wood types seen among deciduous trees.

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FOOTNOTE

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