AN OUTLOOK FOR BASIC WOOD ANATOMY RESEARCH[1]

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ABSTRACT

Consideration is given to the applications of scanning electron microscopy, X-ray densitometry, and ultraviolet microspectrophotometry to certain problems in wood anatomy. Several other problem areas are mentioned briefly, and specific studies of ray cells and reaction wood formation are highlighted.

Attempts to forecast trends in research should be viewed with much the same skepticism as most of us treat other predictions of future events. Because different individuals may anticipate quite contrary events, I have attempted to hedge my outlook by consulting certain colleagues. Since we all feel somewhat reluctant to predict our own personal courses of action, their replies were understandably vague or reticent. A review of wood anatomy research presently in progress, conducted through the services of the Smithsonian Institution Science Information Exchange and the current Research Information System of the U.S. Department of Agriculture, provided some broad indications of trends in research, but did not permit a logical synthesis of future expectations. This review therefore emerges as an outlook strongly colored by my own bias. What follows is largely an account of certain topics of personal interest, some of which are supplemented by fragmentary observation for illustrative purposes.

INSTRUMENTATION

One clue to anticipated progress can be secured from a consideration of new tools recently made available to the wood anatomist. Perhaps the most obvious of these is the scanning electron microscope. Its outstanding depth of field permits graphic comprehension of structural details in wood (Figs. 1–3) that previously had to be determined by painstaking accumulation of sections oriented in various planes. The microscope may not contribute significantly to our knowledge of intrinsic cell structure, but it may indirectly enhance our understanding through its unique pictorial ability. It is more likely that scanning electron microscopy will be employed for rapid and direct examination of wood surfaces, to indicate areas that should be studied more thoroughly by transmission electron microscopy. Applications of the scanning electron microscope will probably include studies of the surface morphology of wood fractures, the effectiveness and nature of wood coatings, the cell-wall penetration of chemicals and the extent of adhesive cell-wall bonding.

A second major instrumentation development is the X-ray densitometer, pioneered in France by Polge. This permits automated measurement of annual ring width, early- and latewood per cent and wood density directly on increment cores or other small wood samples. The technique normally requires X-ray exposure of wood, followed by development of a radiograph and densitometric evaluation of a negative. Methods are presently being developed to allow a direct reading of density, thereby eliminating the radiograph stage.

The X-ray technique has already found wide application in dendrochronological studies, where it has been found that maximum annual latewood density is particularly sensitive for cross dating. An example of an X-ray scan is given in Fig. 4, in which the 1960 to 1967 annual rings at breast height from two very different Douglas-fir

[1] The scanning electron micrographs were taken by Dr. R. W. Meyer, and the X-ray scans were prepared by Mr. M. L. Parker.

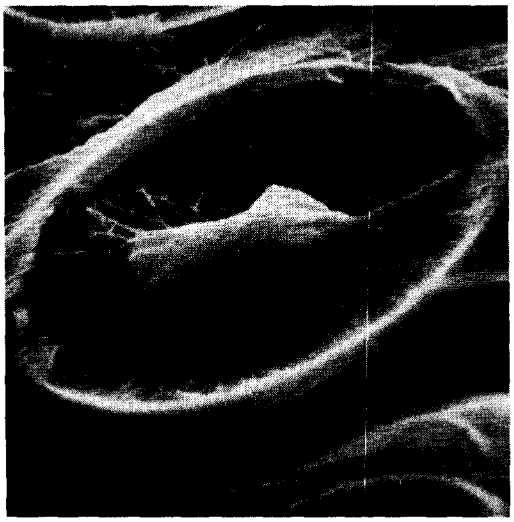

FIG. 1. Scannning electron micrograph of a bordered pit in Douglas-fir, showing the torus suspended by margo microfibrils.

[*Pseudotsuga menziesii* (Mirb.) Franco] trees are compared. The trees were grown within a few miles of one another in a typical coastal forest environment. However, the faster grown tree was taken from an open-grown, 30-year-old stand, while the slow-grown tree was nearly 500 years old. Nevertheless, the trees were comparable in terms of maximum annual

FIG. 2. Scanning electron micrograph of a radial surface of Douglas-fir, showing ray cells between two layers of vertical tracheids.

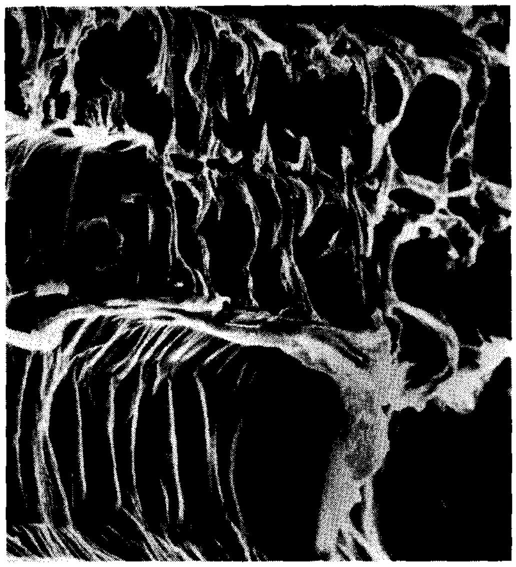

FIG. 3. Scanning electron micrograph showing two rows of ray tracheids in ponderosa pine (*Pinus ponderosa* Laws.) with dentate thickenings.

density, which was highest in 1967 and lowest in 1964.

The X-ray density scans of seven 30-year-old Douglas-fir trees (including that of Fig. 4A) were examined over the years 1960 through 1967 and the annual increments ranked in order of descending maximum latewood density (Table 1). The greatest latewood density occurred in 1967, corresponding to the lowest summer rainfall and highest summer temperatures among the eight years examined, while lowest latewood density was found in 1964, the year of greatest summer rainfall and coolest temperatures. Latewood percentages and ring widths were almost constant from year to year and therefore unrelated to climatic variation. The correlation observed between maximum latewood density and climatic data promises to be a useful tool in assessing past climate through dendrochronological studies.

X-ray analysis of wood should also be applicable in scanning candidate trees for breeding purposes, when the objective of the program is to achieve intra-increment uniformity in density. Effects of fertilization and thinning trials could also be

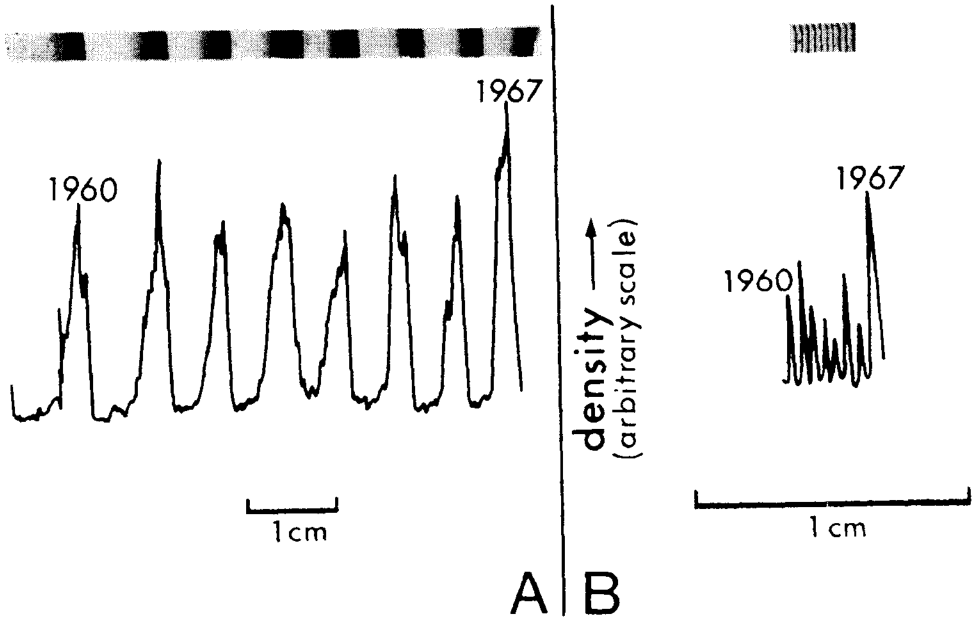

FIG. 4. X-ray density scans of two samples of Douglas-fir representing the 1960 to 1967 annual increments. A. 30-year-old, open-grown tree; B. 500-year-old, overmature tree.

rapidly studied in terms additional to the usual growth rate responses. It might even be feasible to relate differences in ring structure to atmospheric changes created by industrial pollution, although this would require careful understanding of the variation due to normal climatic conditions alone.

A third piece of apparatus with potential for anatomical research is the ultraviolet microspectrophotometer. Instruments have been developed to scan a spot as small as 1 μm. Lignin and polyphenol concentrations across the cell wall have been determined in Australia by this technique. Because of its ability to record absorption spectra, the microspectrophotometer can prove valuable in qualitative determination of extractives in specific cell-wall or lumen regions.

RAY ANATOMY AND FUNCTION

The ray cells constitute a relatively fertile field for basic research in wood anatomy. The chemical nature of extractives in rays, as opposed to those in vertical parenchyma or cell walls, can now be specifically determined through the use of gas-liquid chromatography and microspectrophotometry. Better techniques should be developed to remove all extractives from ray and vertical parenchyma cells. Laboratory studies with radial microtome sections of western red cedar (*Thuja plicata* Donn.) and Douglas-fir have shown that extractive deposits in lumens resist soxhlet extraction with a graded series beginning with water and proceeding through alcohol-water, alcohol, alcohol-benzene, and back to water in reverse order.

Ray condition may be linked closely to permeability. The ease of penetration of hard pines with preservatives may be linked with the delayed maturation of ray parenchyma cells in the sapwood of this group of species. Observations on consecutive sections from cambium to heartwood boundary in conifers indicate that death of the ray parenchyma cells begins in the sapwood and generally occurs first in the

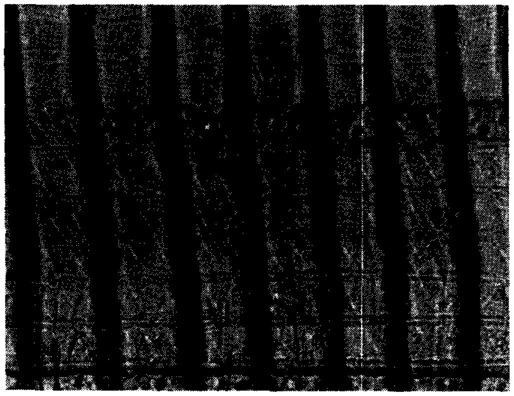

FIG. 5 Pattern of ray parenchyma cell death in young sapwood of Engelmann spruce (*Picea engelmannii* Parry) sectioned without prior aspiration. Marginal ray parenchyma cells contain air voids, have lost their nuclei, and have extraneous materials appressed to their walls.

marginal cells, which often appear infiltrated with air (Fig. 5). The effect that this death may have on radial permeability of sapwood is not known. An accelerated rate of death occurs during the transition from sapwood to heartwood. Recent work in Australia indicates that an increase in respiration occurs at this period in rays of the eucalypts.

The nature of rays in reaction wood may be a subject for further investigation. Limited data comparing compression wood of two second-growth Douglas-fir trees with the contemporaneously formed normal wood opposite to it is shown in Table 2. The compression wood had a much greater proportion of narrow rays, in part biseriate (Fig. 6), and a greater ray volume as well.

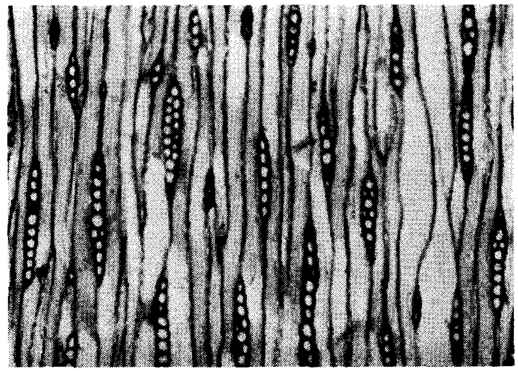

FIG. 6. Biseriate rays, common in compression wood of Douglas-fir.

Whether these differences extend to other trees of this or different species, or whether there are ultrastructural variations in reaction wood rays has apparently not been studied. However, biseriate rays and increased ray volume have been found in the apparent compression wood of *Abies* species that have been attacked by the balsam woolly aphid.

PHYSIOLOGY OF WOOD FORMATION

The possibility exists that tree rotations might eventually be shortened to as little as two or three years because of increasing pressure for land to produce maximum fiber returns. This should stimulate research aimed at increasing the efficiency of trees. For example, the mechanism of the cessation of cambial activity is not understood, but it may involve accumlation of inhibitors that stop further wood formation before auxin availability or environ-

TABLE 1. *Ranking of climatic data and maximum latewood density for years 1960 to 1967 in seven 30-year-old Douglas-fir trees*

Maximum latewood density (average of 7 trees)	June 1–Aug. 31 rainfall (inches)	June 1–Aug. 31 mean temp. (°F)
1967 (highest)	1967 (3.05)	1967 (67°)
1961	1965	1961
1965	1961	1965
1960	1960	1960
1963	1966	1963
1966	1963	1966
1962	1962	1962
1964 (lowest)	1964 (18.40)	1964 (59°)

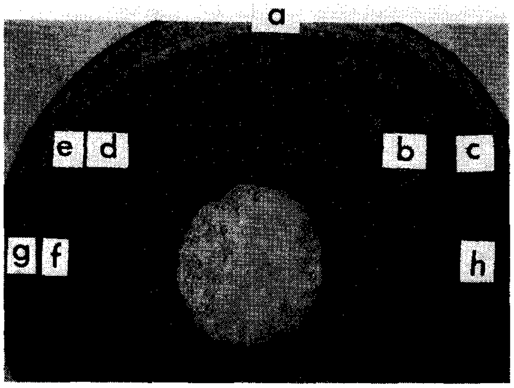

FIG. 7. Tension wood (b,c) and contemporaneously formed opposite wood (d,e) in box elder (*Acer negundo* L.). Full explanation in text.

mental factors become limiting. Trees also may vary in their ability to convert solar energy into photosynthate and ultimately into cell-wall material. For maximum quality and productivity, trees should be capable of efficient photosynthesis over an extended growing period, and wood produced should exhibit minimal juvenile characteristics. As rotations are shortened, the physiologist, geneticist, and fiber user may be expected to converge on some of these problems.

Because of its unique properties and cell-wall structure, reaction wood will continue to offer a challenge for study, particularly in aspects of biosynthesis. An example of problems in formation of tension wood is shown in Fig. 7, a transverse section of a 110-day-old seedling of box elder (*Acer negundo* L.) that had been tilted at approximately 60° from vertical and supported to prevent bending. The seedling was tilted on two separate occasions for 14 days, separated by a 14-day period in the upright position. Prior to harvesting, it was grown vertically for a final two-week period. It is evident that the only completely normal wood was produced on the lateral sides of the seedling (Fig. 7a). Two separate arcs of tension wood (b,c) were differentiated on the upper side of the stem during the tilting period. If we accept the available evidence that tension wood formation is stimulated by a decrease in auxin availability to the cambium, the increased radial growth on the upper side of a leaning stem is difficult to reconcile.

Figure 7 also shows that wood formed on the underside, contemporaneously with tension wood of the upper side, is abnormal in that thick-walled, highly lignified fibers similar to those in the terminal portion of a growth ring are produced (d,e). The mechanism by which this abnormal "opposite wood" is formed is unknown. When the tree was returned to the vertical position, normal cambial activity appeared to be limited to the former underside location (f,g), while "opposite wood" was produced on the former tension-wood side (h). This growth pattern resulted in the maintenance of a circular cross section, but the nature of the stimulus to the cambium is not understood.

There is also interest in the effect of mechanical stresses alone on developing xylem, independent of the effect of gravitational forces that appear to be so critical to reaction wood formation. The fact that wood, in common with other crystalline materials, displays a piezoelectric potential under stress, has generated interest in the role of bioelectric phenomena in xylem de-

TABLE 2. *Comparison of rays in normal and compression wood of Douglas-fir*

Tree No.	Age of wood from pith (years)	Type of wood	Narrow rays[1] in part biseriate (per cent)	Ray volume (per cent)
1	28	Normal	1.0	5.5
		Compression	37.3	9.1
2	65	Normal	1.4	3.5
		Compression	17.8	6.8

[1] Rays 3 or more cells high.

velopment. The difference in stem form that has been observed with changing mechanical stress patterns may be due to altered carbohydrate translocation or hormone distribution, stimulated by potentials developed piezoelectrically. The elaboration of this hypothesis awaits the development of a technique for measuring bioelectric potentials in trees under stress.

In general, we need to synthesize our somewhat fragmented research on the phenomena involved in wood formation and relate them to growth and development of whole trees, so that we can better understand the forces acting to regulate wood formation. Unifying studies of the functional relationships between the secondary xylem of leaf, stem, and roots represent an approach to this problem.

CONCLUSION

There are a multitude of other important problem areas. Continued study of bark anatomy is basic to our better utilization of bark as a raw material, a subject that currently generates particular interest because of the criticism of the polluting effects of bark disposal systems. Taxonomic studies of wood, which have been under low pressure for some years, may become increasingly important as tropical hardwoods gain greater attention in timber-poor countries such as Great Britain.

A clearer understanding of the behavior of various wood elements in paper is being developed. It may shortly be possible to compare the economic gains that can be achieved through tree improvement and silvicultural techniques with the potential for enhanced paper properties that can be attained through technological manipulations.

The mechanism of heartwood formation will receive continued emphasis with the aid of ultrastructural cytology, in an effort to elucidate the nature of heartwood extractives that have such a profound effect on wood properties and utilization. Basic studies that can be linked to practical problems may enjoy greater support because of the climate presently favoring research with potential for application.

Wood and Fiber publishes abstracts of articles from appropriate foreign journals. These abstracts are not printed in a separate section, as are Thesis Abstracts, but are spaced throughout the journal. Francis C. Beall, of Pennsylvania State University, is chairman of the committee responsible for these abstracts. Other members of the committee are: R. M. Kellogg, R. T. Lin, R. L. Ethington, Ali Moslemi, J. D. Wellons, E. G. King, D. D. Nicholas, J. D. Snodgrass, and Joe Yao.

SCHEFFER, T. C. 1969. Protecting stored logs and pulpwood in North America. *Material und Organismen* 4(3):167–199 (E.g,fr,sp). Storage of logs in water can give maximum protection, but a number of disadvantages discourage use of this method. Water spraying and sprinkling are more and more preferred. Chemical spraying can give effective protection for many months. Biological protection by infecting the logs with a fungus such as *Trichoderma* seems to be promising. Microbiological damage to rough pine pulpwood can be lessened by measures that retard drying; the reverse is true for peeled wood. Spraying roundwood with a fungicide has not proved worth while, but treatment of unbarked wood with an insecticide can be helpful if there is risk of beetle infestation. Measures considered to protect chip piles include piling on paved ground, compacting, water sprinkling, treating the chips with a fungicide, turning over the pile, and limiting the amount and concentration of fines. (H.K.)