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Lateral Flow in Beech and Birch as Revealed by the Electron Microscope*

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Summary. Sapwood of beech and birch was impregnated with aqueous salt solutions and suspensions of carbon particles and india ink under a low initial pressure; the pathways marked by the impregnating substances were examined by the electron microscope. The micrographs revealed dark deposits in cell lumina, pit membranes, and other parts of the cell wall. The size of voids occupied by dark deposits ranged from infinitely small to 700 A in vessels and rays, and from infinitely small to 1,300 A in fibers. It was concluded that the penetration path of impregnating substances from one cell to the next was through the minute intermicrofibrillar openings in the communicating pit membranes and in the rest of the cell walls. Carbon particles, suspended in plastic monomer, were not observed either in pit membranes or in the rest of the cell wall; they probably represent a nonpolar substance.

Introduction

Permeability of wood greatly affects preservation, drying, and pulping. Tesoro and Choong [1976] studied the relationship between permeability and treatability of nine hardwood and three softwood species and showed that, in general, treatability is a function of permeability.

Wood is anisotropic in permeability (as in other properties) and a large difference exists between the longitudinal and the lateral flow in any one species. Flow in wood is predominantly in the longitudinal direction. The ratio of longitudinal to lateral flow is about 30 to 1 [Stamm 1973]. However, lateral movement of fluid is of great significance when preservative treating wood. Without lateral fluid movement, timbers could not be adequately treated because of low retention and poor distribution of preservatives in the wood.

Lateral flow has been demonstrated in several hardwood species [Wardrop, Davies 1961; Tesoro, Choong, Skaar 1966; Kininmonth 1971, 1972]. The rays provide a path for lateral flow, and the pits provide channels between adjacent cells. Inter-

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cellular spaces supposedly contribute to the overall movement of fluid also [Back 1969]. However, the submicroscopical path of fluids between the cells in hardwoods was demonstrated with the electron microscope [Rudman 1966; and others].

The purpose of the present study was to explore the lateral penetration path in two commercial North American hardwoods, beech and birch, by the electron microscope. It was felt that this type of knowledge would add to a full understanding of the penetration of wood by fluids and, consequently, by wood preservatives.

Materials and Methods

Sapwood from next to the cambium of beech (*Fagus sylvatica* L.) and of birch (*Betula papyrifera* Marsh) was prepared as circular test wafers from billets as described by Chudnoff [1970]. The wafers were 25 mm in diameter and 6mm thick. End grain of wafers was sealed (edge-coated) with two coats of brushable epoxy resin to insure transverse flow. In a preliminary examination of the wafers, vacuum-pressure treatment for 10 minutes at a 1 x 10^{-3} Torr vacuum, followed by 10 minute of atmospheric pressure, resulted in complete penetration with either tap water or No. 2 fuel oil. Water absorptions and oil absorptions of both beech and birch were similar (ca. 35 lb/ft^3 and 22 lb/ft^3, respectively). This indicates an excellent across-the-grain flow of polar and nonpolar liquids.

For these flow-path studies, we used aqueous salt solutions containing heavy metal ions, a carbon particle suspension, and an india ink suspension (a suspension of finely divided carbon particles). The basic size of carbon particles was almost undeterminable because they easily coalesce. However, a group of small, repeating particles measuring about 350 ¡ in diameter could be distinguished. The basic size of india ink particles also measures about 350¡ in diameter.

The heavy metal salt solutions were: 2% aqueous copper sulfate (followed by a precipitation reagent, dithiooxamide) and 5% aqueous silver nitrate (with previous treatment of wood using chlorine water and monoethanolamine [Wardrop, Davies 1961]. India ink was suspended in water and carbon particles were suspended in a monomer of butyl methacrylate or epoxy resin. Wood samples were immersed in the solutions, subjected to vacuum-pressure treatment as described, and then air dried After brief dehydration, both impregnated and untreated samples were embedded in epoxy casting resin A (Araldite 6005)—Epon resin 812 (Shell Chemical Co.)—dodecenyl succinic anhydride mixture (1 :1 :3). After the embedding material polymerized, the samples were sectioned and examined in the transmission electron microscope.

Results and Discussion

Submicroscopic deposits from metallic salt solutions (due to precipitating reagents) were observed in pit membranes and in the rest of the cell wall in both beech and

birch. These results agree with results of an earlier electron microscopy study by Rudman [1966] on Eucalyptus species.

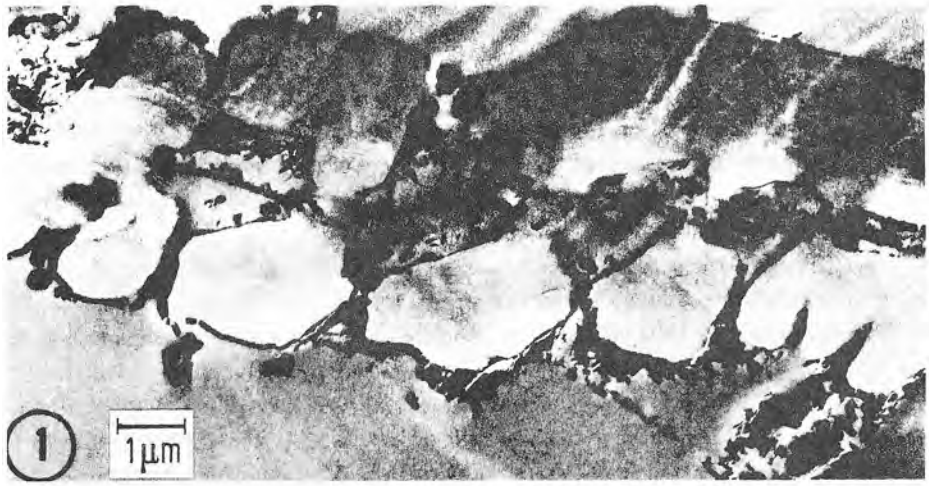
The copper sulfate/dithiooxamide combination appears as a dark, needle-like precipitate which was observed in lumina of vessels and fibers, and also in vessel-vessel and vessel-fiber pit chambers and their pit membranes (Fig. 1). These deposits were not observed in the rest of the cell wall. (Because beech and birch gave similar results, figures will not always show both.)

Silver nitrate/ethanol amine gives black, isodiametric deposits of silver. These silver deposits were encountered in cell lumina, pit chambers, pit membranes, and embedded in cell walls of all cell types (Fig. 2). In several instances, when observing two adjacent cells, one cell had precipitate in its wall while the other had none (Figs. 3 and 4). In Fig. 3, the vessel wall shows silver deposits, but the walls of two fibers do not. Similarly, in Fig. 4, the wall of one vessel is penetrated starting from the lumen while the wall of the other vessel is not. Unequal distribution of impregnating substances has been observed by other workers [Wardrop, Davies 1961; Rudman 1966; and others]. It is believed to be caused by the presence of tyloses, air bubbles, gums, or cytoplasmic debris in cells which were not penetrated. In Fig. 4, silver deposits are visible within intervascular pit membranes and as heavy aggregations in pit chambers. The openings in the vessel pit membranes range up to 700 ¡ in diameter and are of the same size as openings elsewhere in the cell wall.

Silver deposits in vessel-ray pit membranes and cell lumina are shown in Fig. 5. The openings here are of the same size as those in the vessel-vessel pit membranes. These micrographs suggest that direction of flow is from rays via vessel-ray pits to the vessels. Fig. 6 shows two ray cells in which the penetration path of silver deposits follows from ray to ray through plasmodesmata in the pit membranes. Very often the walls of ray cells are not penetrated, but when they are (Fig. 2) the openings are small and similar in size to those in the vessel walls.

Fig. 7, a radial section, shows orientation of openings in different cell wall layers in fiber and also shows the different sizes of openings, the maximum being 1,300 A in diameter. In the middle lamella, primary wall, and S_1 layer of the secondary wall, the openings are smaller than in the S_2 layer, but seem to be present in larger numbers. Rudman [1966] showed a similar penetration pattern of silver salt solution in Eucalyptus species: Liquid passed through the various lamellae of the cell wall and also penetrated and crossed the middle lamella. He found that the size of openings in the middle lamella was small, as has been also pointed out by Wardrop and Davies [1961]. However, Wardrop and Davies showed that, while heavy metal salt solutions moved from the cell lumen into the wall, they did not penetrate the middle lamella.

Fengel and Wolfsgruber [1971], using heavy metal salt solutions (which are used as stains in electron microscopy), showed by the electron microscope and electron probe microanalyzer an increase of staining material in the compound middle lamella region and in the bordered pits in pine sapwood. These authors found that, in general, the secondary walls were less stained than the middle lamella region. Klein and Bauch [1977] showed localization of ions (from aqueous 1% KMnO4



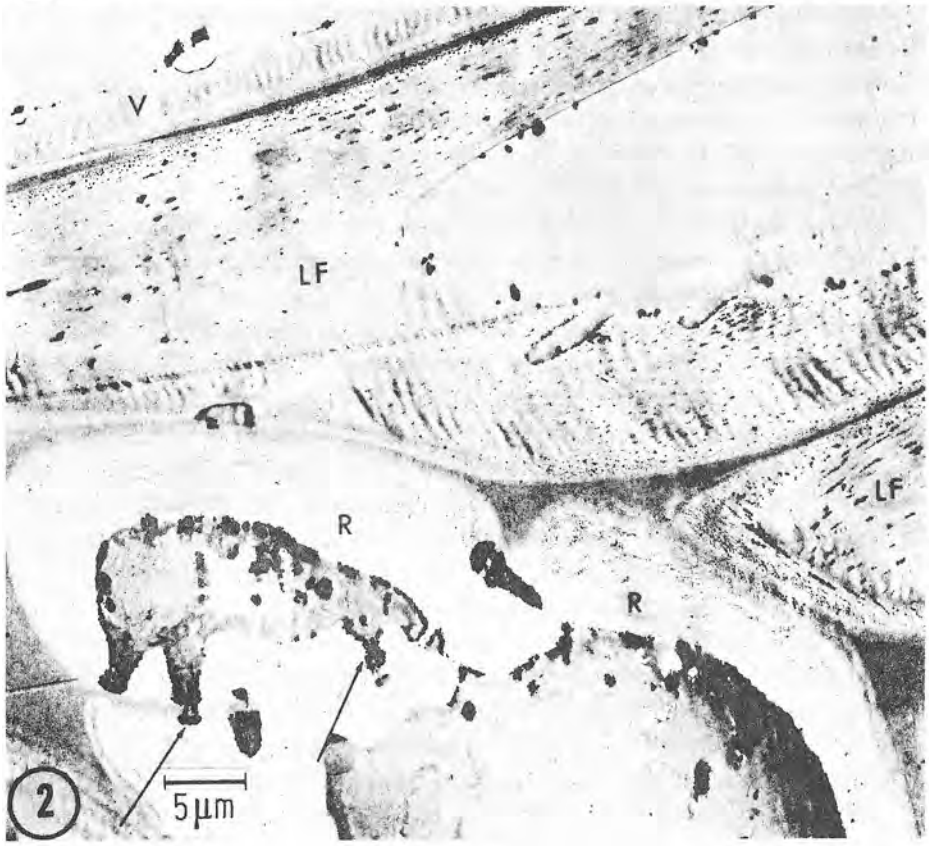
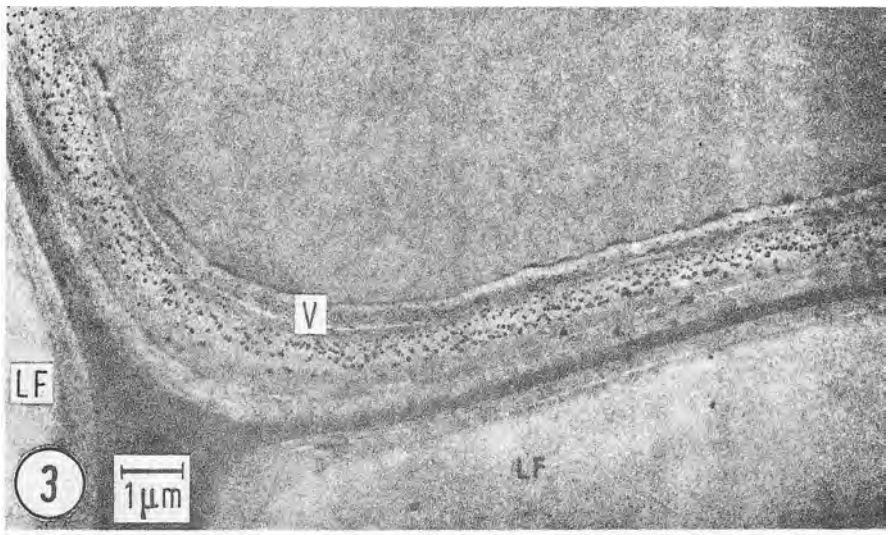


Fig. 1. Vessel pits in birch. Copper sulfate/dithiooxamide deposits are in lumina, pit chambers, and pit membranes. X 7380

Fig. 2. Different cell types in birch—rays (R), vessel (V), libriform fibers (LF)—with silver deposits in cell lumina and ray-ray pits (arrows). X 2100



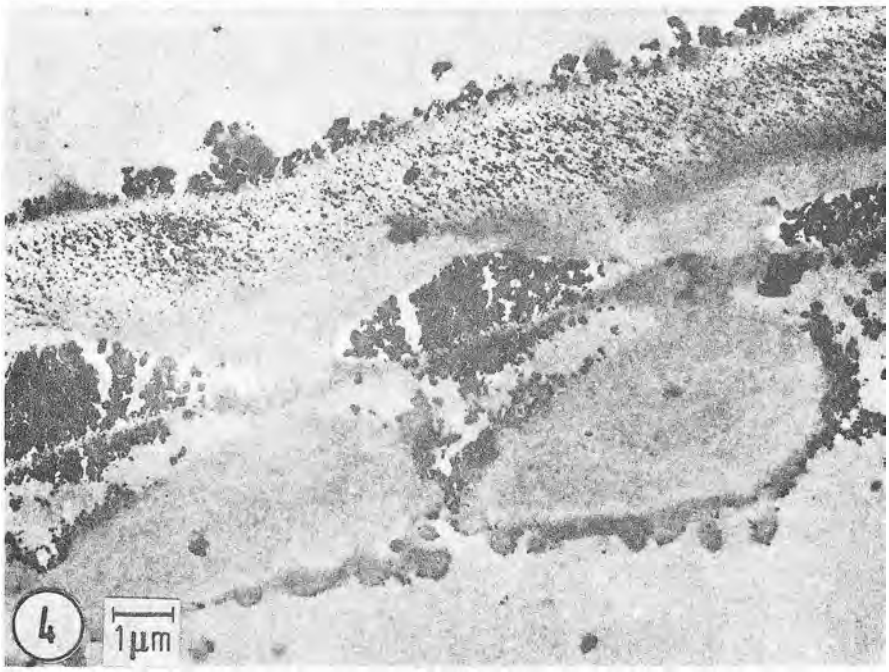
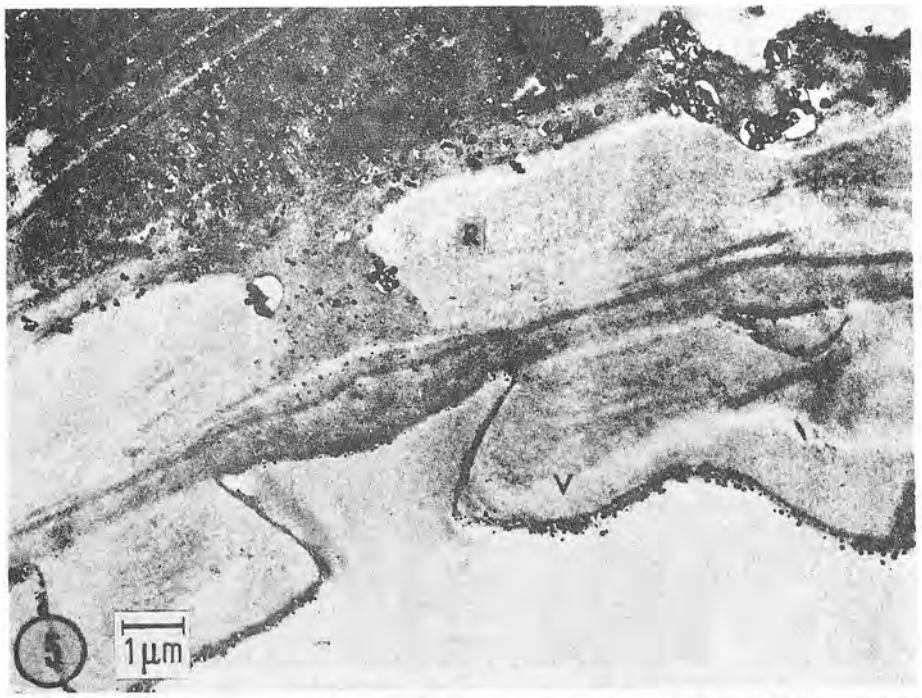


Fig. 3. Vessel (V) and libriform fibers (LF) in birch. Silver deposits are in the wall of the vessel, but not in the walls of the fibers. X 6970

Fig. 4. Vessel pits in beech. Silver deposits are in pit membranes, pit chambers, and the wall of one vessel. X 7480



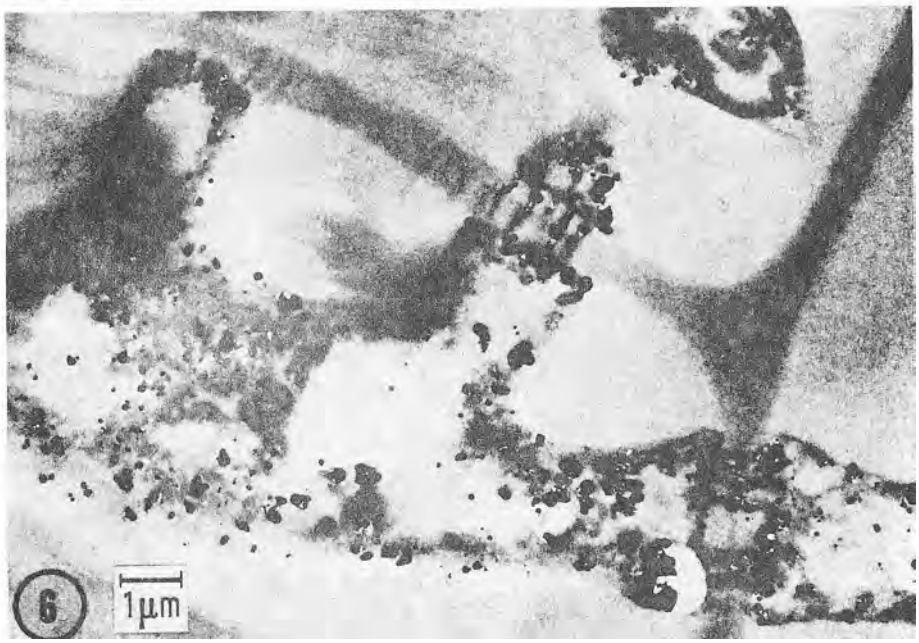


Fig. 5. Vessel-ray pits in beech. Silver deposits are in cell lumina, pit chambers, and pit membranes. X 11,480

Fig. 6. Ray-ray pits with silver deposits in lumina and pit membranes. Deposits pass through plasmodesmata. X 6120

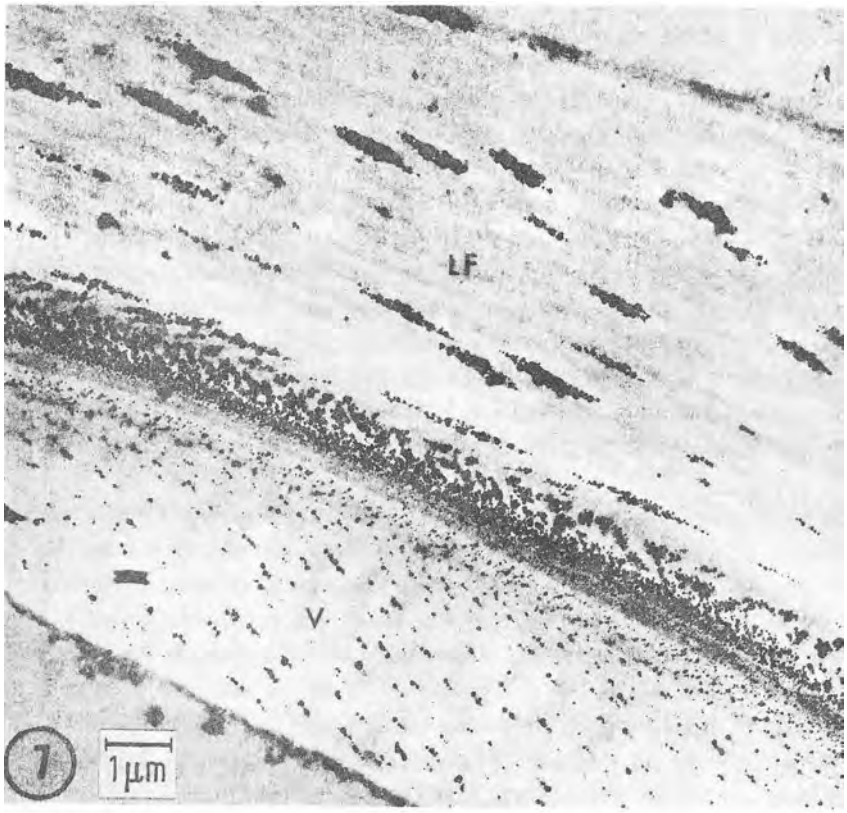


Fig. 7. Radial section, showing orientation of silver deposits and different sizes of capillaries in different cell wall layers of libriform fiber (top). Vessel is at bottom. X 15,000

Fig. 8: Intervascular pit in beech. India ink particles are in lumina and pit chambers, and apparently attached to the pit membrane. X 13,800

solution) by microspectral photometry within a single cell. By contrast, their results indicated that in *Pinus sylvestris* L. and *Picea abies* Karst. the secondary wall had a larger amount of ions than had the middle lamella and the primary wall.

These examples clearly demonstrate the present lack of agreement about the distribution of impregnating substances within the cell wall layers.

India ink particles, suspended in water, were mainly seen in cell lumina, in pit chambers of vessels and fibers, and apparently attached to the pit membranes (Fig. 8), but not in the other parts of the cell wall. Carbon particles, suspended in methacrylate and epoxy resin monomers, were observed in lumina of vessels and fibers and in their pit chambers. Carbon particles and india ink were not seen in the pit membranes or in the rest of the cell wall; they apparently represent a nonpolar substance; like oil-borne preservatives in water-immiscible solvents, the carbon particles move from one cell to the next only through lumina and pits [Walters, Cote 1960].

Results of the present study, in accord with results of Rudman [1966], Kininmonth [1971, 1972], and others, suggest that polar liquids may flow from cell to cell by two routes: The pit system and the cell wall capillary system. However, it is generally believed that most of an aqueous solution passes through the pit system. There is some evidence that the pit membrane is not as lignified as the middle lamella/primary wall in general [Bamber 1961]: Therefore, there could be sufficient interconnecting voids between the cellulose microfibrils to enable the flow to proceed through the pit membrane in the absence of larger openings. As Rudman [1966] pointed out, even if pit membrane pores may have existed at one time in eucalypt sapwood, such pores are partially or completely blocked in dried sapwood. It should also be mentioned that the pit membrane is much thinner than the rest of the cell wall: The flow, because it is an inverse function of length, should move preferably through the pit membrane. The rest of the cell walls are later penetrated from the cell lumina.

It is believed that findings of the present study using heavy metal salt solutions as impregnating substances bear a relation to the distribution of wood preservatives in pressure-impregnated timbers.

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