The penetration and growth of blue-stain fungi in the sapwood of lodgepole pine attacked by mountain pine beetle

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The growth of blue-stain fungi was investigated in naturally blue-stained lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) sapwood. Events occurring at the leading edge of hyphal penetration were studied. Fungi are initially confined to the sapwood rays. Hyphae readily penetrate the primary cell walls of ray parenchyma cells and proliferate within. Hyphae also grow freely in the region of the middle lamella of the rays. Host cell walls are breeched mechanically by a penetration peg originating from an appressoriumlike structure. Eventually, hyphae enter tracheids by penetrating the primary cell walls of pinoid, half-bordered pit pairs. Within the tracheid, fungal hyphae grow in a longitudinal fashion, branching infrequently. Hyphae may pass from tracheid to tracheid via bordered pit pairs. Ensuing water stress and eventual tree death is discussed in light of histological evidence presented.

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Les auteurs ont étudié la croissance des champignons de la coloration bleue dans l'aubier de *Pinus contorta* var. *latifolia* Engelm., naturellement colonisés par ces champignons. Ils ont observé les événements qui se déroulent au point d'avance de la pénétration par les hyphes fongiques. Au départ les champignons sont confinés aux rayons de l'aubier. Les hyphes pénètrent les parois cellulaires primaires des cellules de parenchyme des rayons et se développent à l'intérieur. Les hyphes se développent aussi avec facilité dans la lamelle moyenne des rayons. Les parois des cellules hôtes sont traversées mécaniquement par un hyphe de pénétration provenant d'une structure ressemblant à un appressorium. Eventuellement, les hyphes pénètrent les trachéïdes en traversant les parois cellulaires primaries des paires de ponctuation pinoïdes demi aréolées. À l'intérieur de la trachéïde, les hyphes fongiques croissent de façon longitudinale en se ramifiant fréquemment. Les hyphes peuvent passer de trachéïde en trachéïde via les paires de ponctuations aréolées. Les auteurs discutent le stress hydrique et l'éventuelle mort de l'arbre qui suivent l'infection à la lumière des données histologiques présentées.

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Introduction

Mountain pine beetles (*Dendroctonus ponderosae* Hopk.), in their mass attack on lodgepole pines (*Pinus contorta* Dougl. var. *latifolia* Engelm.), inoculate blue-stain fungi into the tree resulting in eventual tree death.

While tunnelling in the inner bark region, the beetles apparently inoculate a "fungus complex" into the host. Propagules of the fungus complex germinate and grow in the beetle frass and feces within the beetle galleries (Whitney 1971). Hyphae grow into the radial parenchyma tissue system (Rumbold 1941; Ballard *et al.* 1982). The fungal complex is reported to consist of several species of *Ceratocystis* and *Europhium* as well as other mycelial fungi and yeasts (Robinson 1962; Robinson-Jeffrey and Grinchenko 1964; Robinson-Jeffrey and Davidson 1968; Whitney 1971). It is well-known that fungal pathogens follow a pattern of succession in blue-stained trees.

Early histological studies of blue-stained wood of southern pines showed fungal hyphae to be essentially confined to medullary rays (Nelson 1934). Rumbold (1941) reported a similar finding in blue-stained lodgepole pine sapwood. Liese and Schmid (1961), studying *Ophiostoma* (Munch) Syd. spp. growing in blue-stained European pines and spruce, demonstrated the presence of hyphae within ray cells. Ballard *et al.* (1982) showed complete destruction of ray parenchyma cells and resin duct epithelium in the late stage of the disease cycle and extensive colonization of axial tracheids.

In this study we report on the process of cell penetration and growth of fungal hyphae in the rays at the leading edge of the inward-developing blue stain in the sapwood, and on the early penetration of tracheids by fungal hyphae. These events occurred in the 8- to 10-week period of time following mountain pine beetle attack in August.

Materials and methods

Study sites were located near the head of Logan Canyon in Cache County, UT (Ballard *et al.* 1982). Sampling began in August 1980 when pitch tubes (resin exuding from beetle galleries onto bark surfaces) became apparent on trunks of beetle-attacked lodgepole pines in the study area. Eight trees were utilized in the study. Tissue collections were made using an increment borer in the sapwood region adjacent to beetle galleries. Blue-stained tissues were determined visually. Sapwood chosen for study was taken from near the inner margin of the inward-developing blue stain. Sampling was conducted biweekly for the remainder of the summer.

Tissue was processed for light and electron microscopy in a sodium cacodylate buffered, full-strength Karnovsky's (Karnovsky 1965) fixative and postfixed for 2 h in 1% (aqueous) osmium tetroxide. Samples were dehydrated in ethyl alcohol and infiltrated in Spurr's low-viscosity medium (Spurr 1969). For light microscope observations, sections 1–2 μm thick were taken with glass knives on a Sorvall

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MT-2 Porter-Blum ultramicrotome, stained with toluidine blue 0, and viewed and photographed with a Zeiss WL research microscope. For transmission electron microscopy, thin sections were taken with a diamond knife on a Sorvall MT-2 ultramicrotome. Sections were stained with uranyl acetate and lead citrate; observations were made with a Zeiss EM-9 electron microscope. Tissue for scanning electron microscope observation was obtained in much the same way as for light and transmission electron microscope work. Tissue was sliced into blocks measuring 1 cm on a side by 5 mm deep with a sharp razor blade, then fixed with Karnovsky's fixative. Tissue was dehydrated in ethanolic series, transferred to Freon, and critical-point dried on a Bomar critical-point machine. Samples were mounted on aluminum stubs and coated with gold–palladium on a Denton sputter coater. Samples were observed and micrographed on an AMR 1000 scanning electron microscope.

Results

The uniseriate rays typical of diploxylon pines were composed of thin-walled parenchyma cells (RP) and thick-walled ray tracheids (RT) with dentate projections into the cell lumen (Fig. 1). Ray tracheids were located either at the top or bottom margins of the uniseriate rays or interspersed with the parenchyma cells within the ray (Fig. 1). The ray parenchyma extends inward into the sapwood and outward into the inner bark (phloem). The ray parenchyma cells were rich in cytoplasmic content (Fig. 2). In Fig. 2, note the progressive development of the vacuolar system as cells mature (youngest cell at right margin of the micrograph). The storage product of sapwood ray parenchyma appeared to be primarily lipid (L) in nature at the time of beetle attack (Fig. 3). The tangential primary walls of ray parenchyma cells were uniform in thickness and possessed numerous plasmodesmata (Fig. 3, arrows). The radial walls, in contrast, possessed comparatively few plasmodesmata.

The fungal spores (or propagules) carried into the host tree apparently germinated in the frass and feces within the egg galleries (Whitney 1971). Consequently, the fungi must live saprophytically for a short time. With feeding activity by the larvae, new routes for lateral fungal growth are opened to the fungi in the bark region. Presumably, fungal hyphae grow to the exposed outer portions of the numerous uniseriate rays of the sapwood and inner bark. Thus, many infection courts are made available to invading fungal hyphae.

As the fungal hyphae penetrated the rays, they grew radially toward the center of the tree. The hyphae penetrated ray parenchyma cells and grew within the lumen of the cells. Hyphal proliferation within ray parenchyma cells was extensive (Fig. 4). Fungal hyphae, upon reaching tangential cell walls of colonized cells, proliferated greatly or formed an appressoriumlike structure (Fig. 4, arrows), and then passed through to the next cell.

The mechanism of host cell wall penetration by fungal hyphae is still in question, but evidence presented here suggests that primarily a mechanical process is involved. The fungal hyphae appeared to utilize penetration pegs (Fig. 5) that originated from an appressoriumlike structure (Ap). The deformation of cell wall layers where cell wall lamellae bow inward (Fig. 5, arrow) suggests a mechanical penetration process. Figure 6 shows passage of fungal hyphae from cell to cell. Note the appressoriumlike structure (Ap) on the left side of the tangential cell wall. At the cell wall passage point, the fungal hypha remains constricted, however the uneven nature (Fig. 6, arrow) of the host cell wall suggests that a secondary enzymatic process was at work. Much of the host cell lumen is occupied by fungal hyphae. Fungal hyphae grew extensively in the intercellular regions of the rays (Fig. 7) in the middle lamella, between parenchyma cells. Fungal hyphae appear to pass fairly readily through host cell walls to either exit (Fig. 7, large arrow) or enter cells (at appressoriumlike structure; Fig. 7, small arrow).

Hyphae appeared to be of two morphological types (Fig. 8). There was a large, darkly pigmented type (approx. 9 μm diam) and a smaller hyaline type (approx. 3 μm diam).

Though fungal hyphae appeared initially confined to the rays, there appeared to be a significant number penetrating into neighboring tracheids (Figs. 9 and 10). Hyphae must penetrate through the loosely arranged cellulose microfibrils of the primary cell wall of the pinoid, half-bordered pit to gain entrance into the tracheids. Counts of occupied tracheids at the inner margin of blue stain showed rougly 5–18% to contain hyphae. Later disease stages have considerably more colonized tracheids (Ballard 1982).

An occasional hyphal branch reached a bordered pit pair and passed through (Fig. 11). The hyphal tip did not differentiate between torus or margo of the bordered pit "membrane" and passed through via the torus which was lodged against the bordered pit aperture. The margins of the destroyed pit membrane (Fig. 11, arrow) are turned back, suggesting mechanical pressure for hyphal passage through it. The hyphae, after entering the tracheids, grew in a longitudinal fashion through the tracheid lumen (Fig. 12). Hyphal branching occurred infrequently in colonized tracheids (Fig. 12, arrows). An occasional branch would reach a bordered pit and pass through it.

Discussion

From initial observations (Ballard *et al.* 1982) it was apparent that fungal hyphae were fairly widespread in sapwood tracheids in late stages of the blue-stain disease cycle. However, this study has shown that, in the initial stages of blue staining, fungal hyphae are confined to the symplastic system of the sapwood, the rays. Hyphal growth therein is directed along the path of least resistance in the sapwood. Lodgepole pine, being a diploxylon pine (or hard pine), does not, in contrast to haploxylon pines, develop lignified secondary cell walls in ray parenchyma cells (Balatinecz and Kennedy 1967). As a consequence, cell walls provide little resistance to fungal penetration and hyphae readily reach untapped food sources. Also, hyphae grow readily in the middle lamella region of the rays. One result of this is that mycelia proliferate extensively within this tissue before much penetration has occurred into thick-walled tracheids.

Late in the disease cycle, ray parenchyma cells collapse, with fungal hyphae filling the space left by the collapsed ray parenchyma cells (Ballard *et al.* 1982).

Growth of blue-stain fungi in sapwood appears mainly to affect the moisture content of host trees (Nelson and Beal 1929; Nelson 1934; Caird 1935; Bramble and Holst 1940; Reid 1961; Mathre 1964; Amman 1972). Several researchers have reported that, with development of blue stain in the sapwood, the transpiration stream of bark beetle infested trees became restricted to the inner portions of sapwood and eventually stopped altogether (Nelson 1934; Caird 1935; Bramble and Holst 1940; Reid 1961; Mathre 1964; Basham 1970). Dye-conduction studies have indicated that disruption of the transpiration stream occurs immediately in front of the leading edge of the inward developing blue stain (Mathre 1964).

Nelson (1934) and Basham (1970) looked at sapwood tra-

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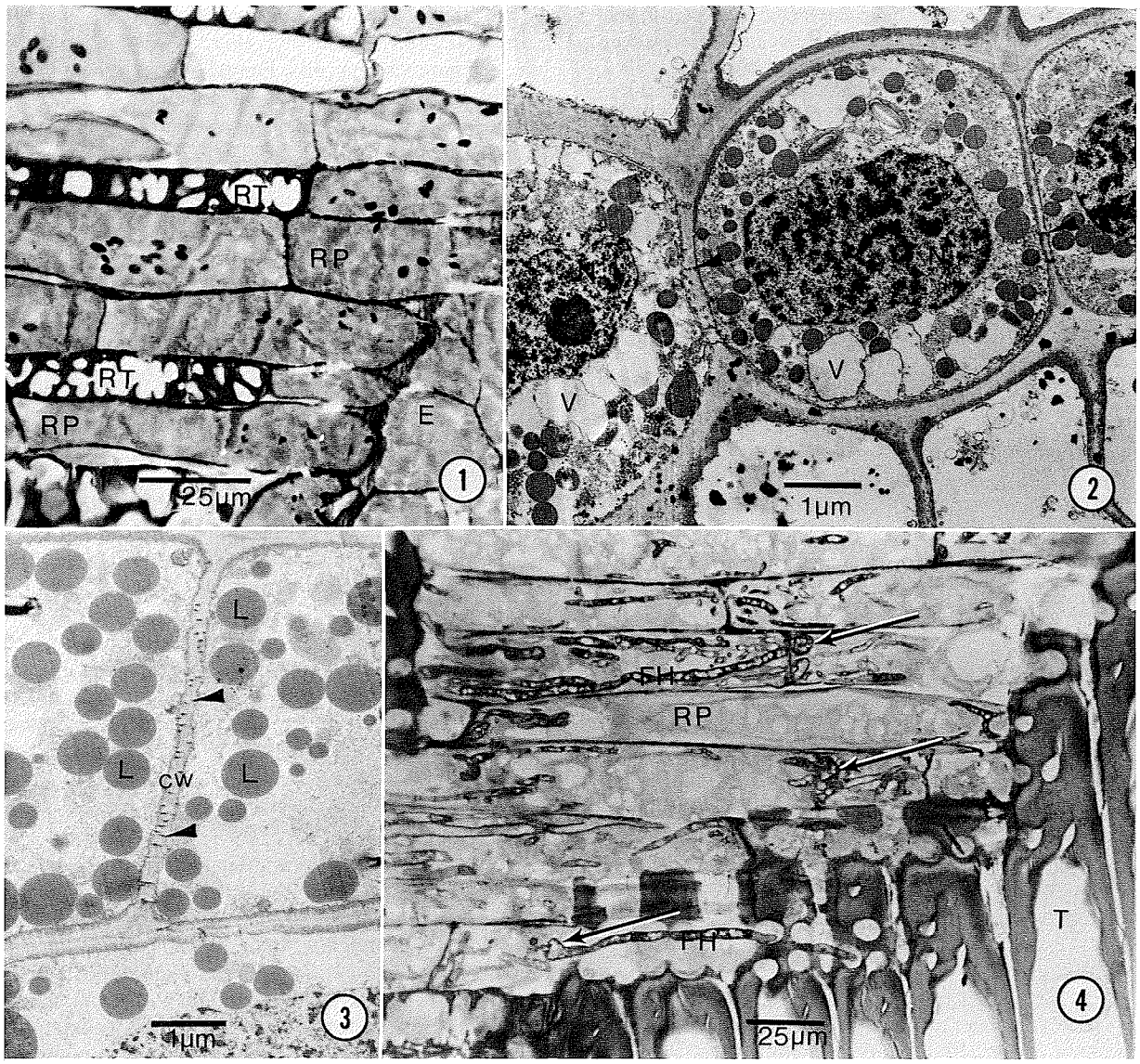

FIGS. 1–4. Fig. 1. Light micrograph of radial section of *P. contorta* sapwood showing arrangement of ray parenchyma (RP) and ray tracheids (RT). Note the procumbant cellular arrangement and storage product in plastids scattered throughout the parenchyma cells. E, epithelial cells of vertical resin duct. Fig. 2. Transmission electron micrograph of transverse section of *P. contorta* showing phloem rays near vascular cambium. Storage product within cells appears to be composed primarily of lipid. Arrows indicate plasmodesmata connections in the primary cell wall. Note developing vacuoles (V) in cells. Sample was taken 21 August 1978 from a healthy tree. Fig. 3. Transmission electron micrograph of a radial section of *P. contorta* showing wood ray parenchyma cells. Storage product is in the form of lipid globules (L). Thin primary cell walls (CW) possess numerous plasmodesmata. Sample was taken from an apparently healthy unattacked tree 26 September 1980. Fig. 4. Light micrograph of radial section of infected *P. contorta* sapwood showing proliferation of fungal hyphae (FH) within ray parenchyma cells (RP). Note the appressoriumlike structures (arrows) at tangential cell walls. Axial tracheids (T) intersect with the ray via large diameter pinoid half bordered pits. Sample was taken 26 September 1980.

cheids of blue-stained southern pines and reported a high percentage of bordered pits of these cells to be aspirated. With aspiration, water conduction through that bordered pit pair ceases. Unattacked trees showed a much lower percentage of aspirated bordered pits. Nelson (1934) suggested that aspiration of bordered pits of tracheids in blue-stained sapwood was due to incrustation products, leaking from dead ray parenchyma cells and lodging against pit membranes (margo) of bordered pits. These incrustation products would slow and eventually stop the flow of water through tracheid bordered pits. Bramble and Holst (1940) looked for this incrustation product and found oleoresin globules. Mathre (1964), studying blue-stained ponderosa pines, and Basham (1970), studying blue-stained southern pines, performed numerous histochemical tests and found no incrustations in blue-stained sapwood of pines. We found no evidence of incrustations apparent in this study. Therefore, it would seem that the evidence presently available would not support blockage by incrustation.

Fares *et al.* (1980) have proposed, and the results of Liese and Schmid (1961), Wong and Berryman (1977), and our early work (Ballard *et al.* 1982) suggested that hyphal penetration of tracheids may be responsible for introducing embolisms and bordered pit aspiration. Earlier work (Nelson 1934; Rumbold 1941) and the present study confirm that fungal hyphae are initially confined to the rays. In fact, only 5–18% of the tracheids at the blue-stain margin are actually occupied

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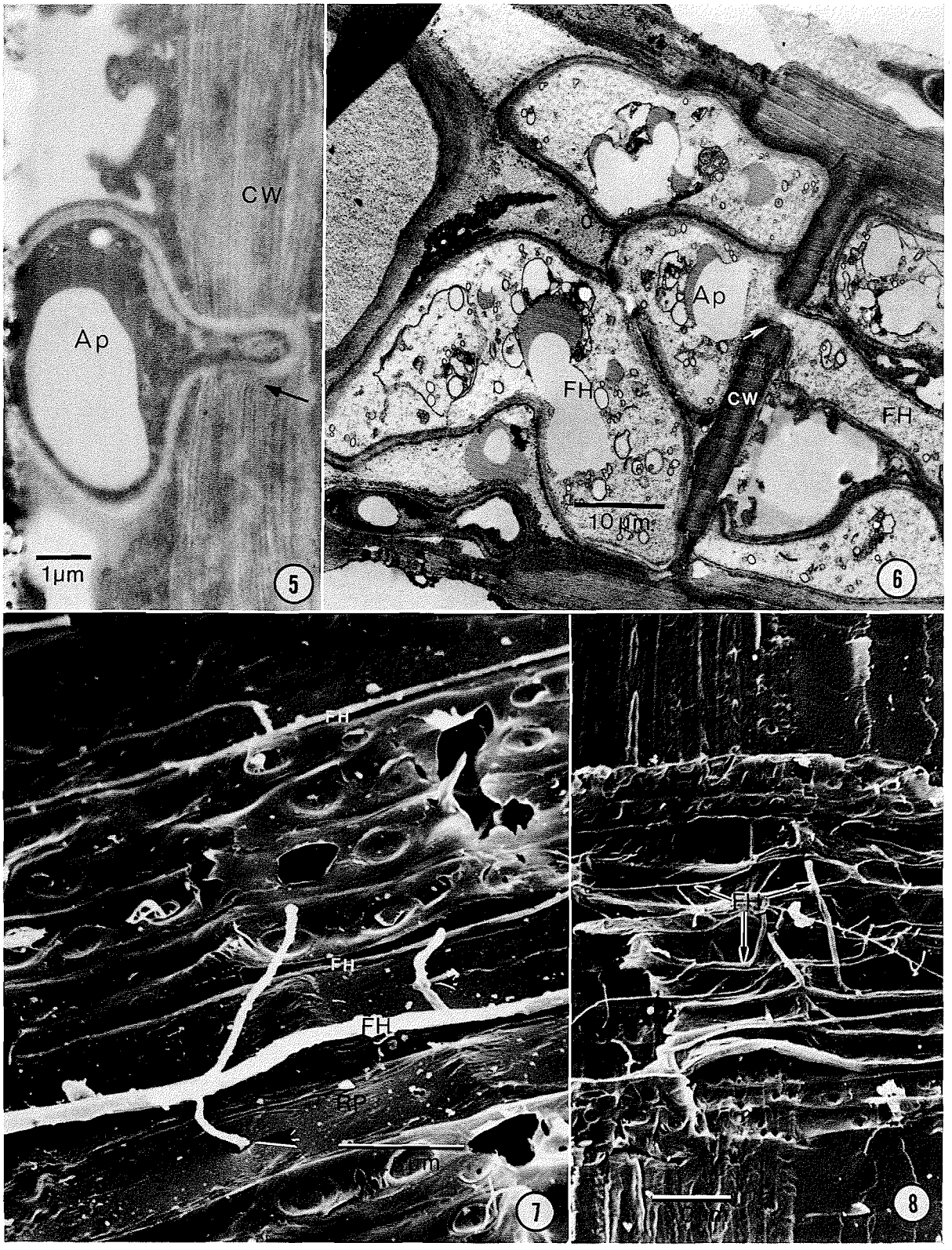

FIGS. 5–8. Transmission electron micrograph of fungal penetration peg originating from appressoriumlike structure (Ap) pushing through cell wall of ray tracheid (CW). Note the slight deformation of cell wall lamellations near penetration peg (arrow). Fig. 6. Transmission electron micrograph of fungal hyphae (FH) passing through wall of ray parenchyma cell (CW). Penetration peg originates from an appressoriumlike structure at left (Ap). Fungal hypha remains constricted at cell wall passage point; however, wall irregularities at this point may indicate some enzymatic digestion at work. Fig. 7. Scanning electron micrograph of hyphal penetration of ray parenchyma cell walls. The small arrow indicates appressoriumlike structure where hypha enters cell. The large arrow indicates point of exit by hypha. Note morphological differences of hyphae; large segment is probably pigmented. Fig. 8. Scanning electron micrograph of hyphal (FH) proliferation in the middle lamella region of the rays. Note intact, though slightly collapsed, ray parenchyma cells. Sample was collected 26 September 1980; taken near the inner margin of developing blue stain.

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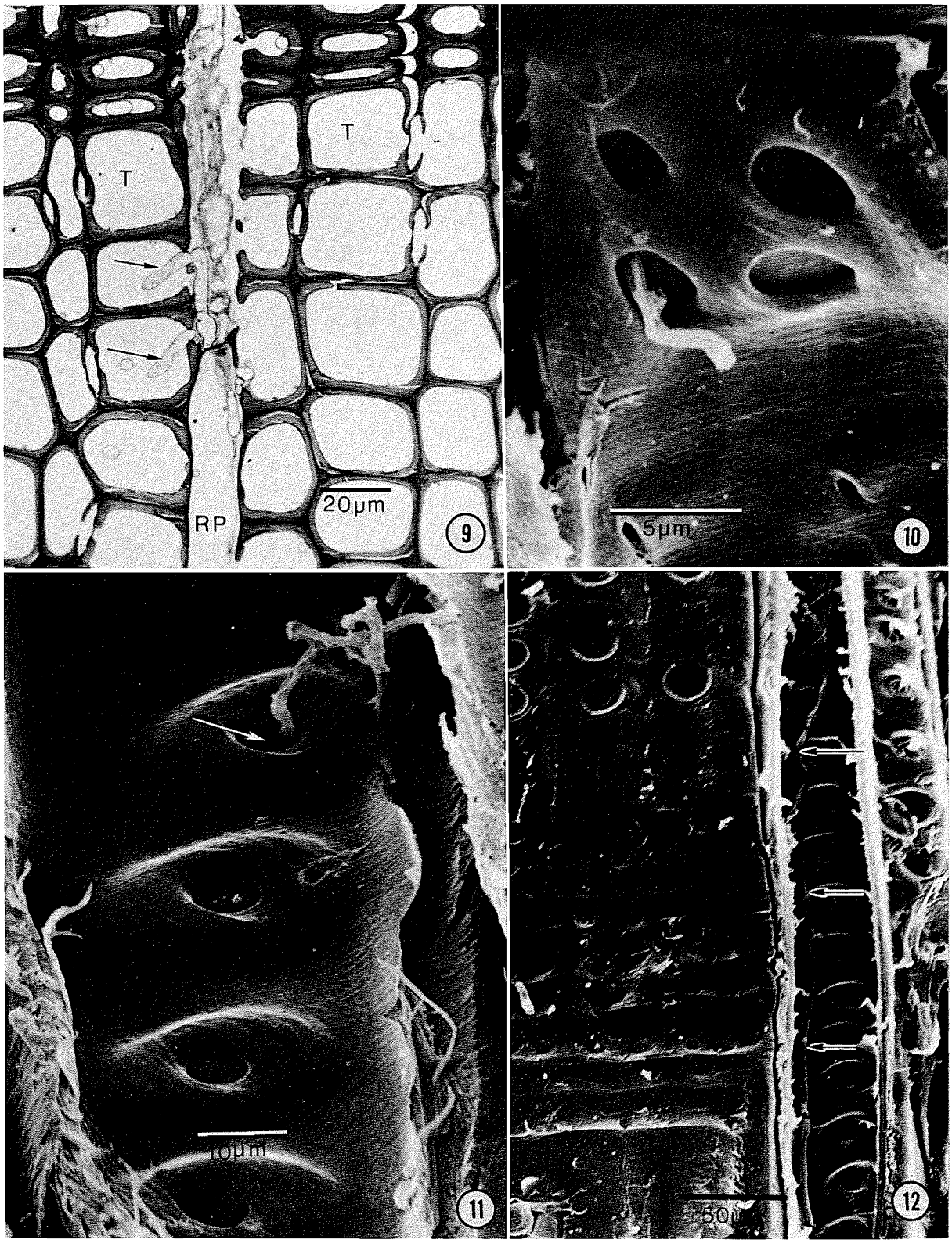

FIGS. 9–12. Light micrograph of transverse section of blue-stained sapwood. Arrows indicate penetration into tracheid by fungal hyphae via pinoid half-bordered pits. Sample was taken 26 September 1980 in region a few millimetres behind margin of developing blue stain. Fig. 10. Scanning electron micrograph showing fungal hyphae emerging from a pinoid half-bordered pit into the lumen of axial tracheid. Fig. 11. Scanning electron micrograph of fungal hypha (FH) penetrating torus of an aspirated bordered pit membrane in an axial tracheid. Note the inward deformation of torus where the hypha pushed its way through (white arrow). Fig. 12. Scanning electron micrograph showing longitudinal growth of fungal hyphae (arrows) in lumen of sapwood tracheid. At top of micrograph branch penetrates bordered pit of tracheid. Axial growth of hyphae in tracheids is common.

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(Ballard 1982).

Though little is known about the exact physiological nature of the relationship between sapwood rays and axial tracheids, it may be arguable that one may not function well without the other. Rays are thought to be responsible for storage and radial transport of nutrients and water (Zimmerman and Brown 1977). According to Carlquist (1975): "though rays account for only 10% of the total tissue of conifer wood, tracheids are so long and rays so numerous that contact by each tracheid with at least one ray is assured." Kramer and Kozlowski (1979) have suggested that rays may have a function in the conductive process. The close association between rays and tracheids, both developmentally and anatomically (Braun 1970), recommends ray parenchyma destruction by blue-stain fungi as a possible mechanism for transpiration stream dysfunction.

In summary, these observations help to better understand the role of the fungus complex that colonize trees in tandem with bark beetle attacks. Because of the necessary beetle implication and the apparent number of fungal species involved (from our material we have isolated mainly *Hyalorhinocladiella* Upadhyay and Kendrick, *Verticicladiella* Hughes, and *Leptographium* Lagerb. and Melin. at the inner margin of developing sapwood stain (R. G. Ballard, M. A. Walsh, and W. E. Cole, unpublished observation)), it seems difficult to reproduce by artificial inoculation alone the whole disease syndrome. Until this type of experiment can be done it is not possible to clarify further the individual or mutual action of these fungi in the disease.

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