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A proposed model of the tracheid cell wall of southern yellow pine having an inherent radial structure in the S_2 layer

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1. Introduction

I. W. BAILEY (1954) and E. B. COWLING (1964) advocated the use of micro-organisms to elucidate the physico-chemical structure of wood, providing a more fundamental understanding that eventually would enhance capabilities to prevent or control decay of wood in service. F. GREEN et al. (1989), in a scanning electron microscope (SEM) study, stated that the selective nature of the brown-rot process of *Postia placenta* (Fr.) M. Lars. et Lomb. apparently reveals underlying physical or chemical structures not evident in undecayed wood, and that penetration by the fungal decay agents appeared radial and perpendicular to the axis of the tracheid.

The generally accepted theory of tracheid cell wall structure is that the S_2 layer consists of layers of concentric lamellae (H. MEIER and K. C. B. WILKIE, 1959; C. E. DUNNING, 1968; J. E. STONE et al. 1971; A. J. KERR and D. A. I. GORING, 1975). Earlier reports of a radially-orientated S_2 layer were proposed by I. W. BAILEY (1938) and A. B. WARDROP and H. E. DADSWELL (1950). However, I. W. BAILEY (1938), using light microscopy, was apparently examining conifer compression wood. His images are strikingly similar to those of W. A. COTE (1964), where compression wood was viewed by TEM. A. B. WARDROP and H. E. DADSWELL (1950) also stu-

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died compression wood. However, compression wood is chemically and structurally different from the conventional secondary wall thickenings (S_2) found in conifer tracheids (R. A. BLANCHETTE et al., 1994). Recently, evidence for a radial, instead of concentric, structural configuration of the S_2 cell wall, was proposed by J. SELL and T. ZIMMERMAN (1993a, b) and J. SELL (1994a, b) while studying the influence of various temperatures and relative humidities on tension-induced transverse fracturing. They theorized that the more crystalline regions of the S_2 cell wall are orientated in radial agglomerations of microfibrils.

Our purpose here is to propose that our earlier (F. GREEN et al., 1989) and present observations and those of J. SELL and T. ZIMMERMAN (1993a, b) and J. SELL (1994a, b) on wood cell wall structure, using different methodologies, support a new hypothesis: that while concentric layering in the S_2 may indeed exist, there are also thin radial bands of hemicellulose adjacent to the crystalline microfibril bundles that act as an inherent plane of weakness within the ultrastructure of the S_2 cell wall. Fungal and thermochemical agents can exploit this radial organization of hemicellulose. We propose that radially aligned low molecular-weight hemicellulosic bands are interspersed between highly ordered concentric layers of cellulose (evident as microfibril bundles) and the matrix-like agglomeration of hemicellulose/lignin. We believe our observations of variously degraded wood cells provide further insight into the ultrastructure of the S_2 layer of conifer tracheids and partially explain previously reported observations of radial channels in degraded cell walls (F. GREEN et al., 1989; T. L. HIGHLEY and L. L. MURMANIS, 1985; W. A. COTÉ, 1964; I. B. SACHS et al., 1963; M. STOLL and D. FENGEL, 1977; A. B. WARDROP and H. HARADA, 1985).

2. Materials and methods

Southern pine *(Pinus* spp.) wood blocks (8 mm × 8 mm × 4 mm) were exposed to the brown-rot fungus *Postia placenta* isolate (MAD 698) according to the ASTM soil-block decay procedure (ASTM, 1991) except that each block was only allowed to incubate at 24°C from 14 to 28 days, and removed at various intermediate times. This protocol allowed decay to be progressively monitored. Individual wood blocks were cryofixed by rapid quenching in precooled (1.4kPa -210°C) liquid nitrogen, followed by lyophilization (–55°C for 12h) without chemical fixation.

In a second experiment, undecayed wood blocks (8 mm × 8 mm × 4mm) were placed in a solution of oxalic acid (pH 1.7) in an Erlenmeyer flask and shaken gently for one week. Specimens were removed from oxalic acid solution, washed in distilled water, and air dried. Specimens were split longitudinally and prepared for SEM. A third set of undecayed southern yellow pine wood blocks (20 cm × 0.8 cm × 0.8cm, controls) were placed in a Dewar flask containing precooled liquid nitrogen for ten minutes and immediately broken transversely and prepared for SEM.

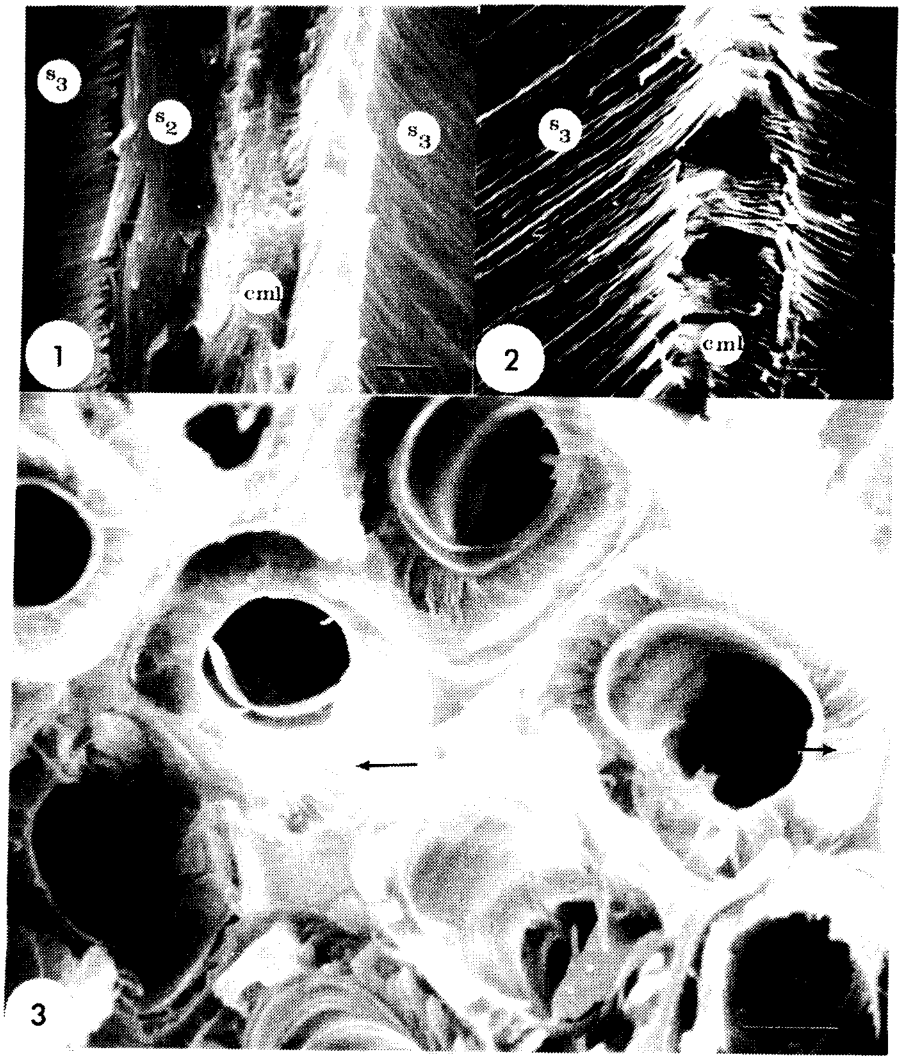
Specimens were coated with gold in a Polaron sputter-coater for approximately 22 s, resulting in a 6.5- to 7.5-nm-thick gold layer, and examined with a Hitachi S-530 scanning electron microscope at an accelerated voltage of 25kV with working distances between 5 and 10mm. Whenever it was deemed necessary, stereo images were prepared to aid in the accuracy of our interpretations.

3. Results

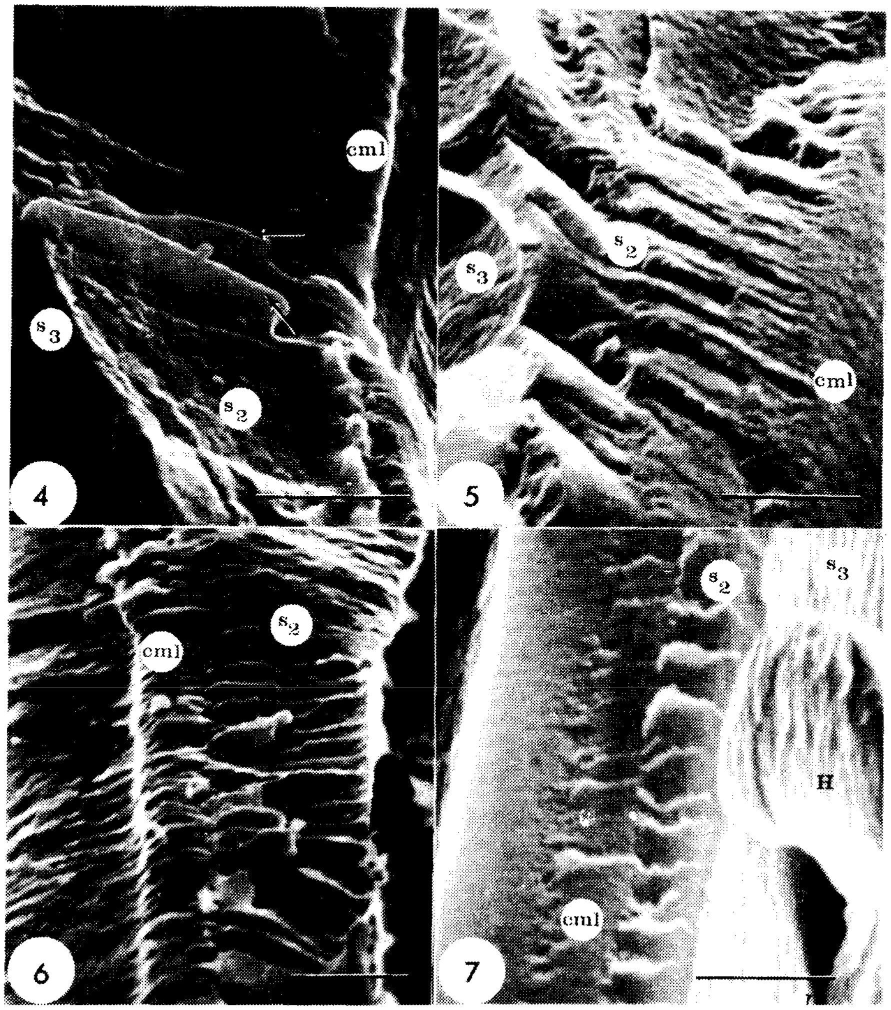
Our SEM micrographs of degraded wood cell walls repeatedly demonstrated what appeared to be an inherent radially oriented structure whose presence was enhanced after treatment with the brown-rot decay fungus *Postia placenta* or oxalic acid (Figs. 2-11). In Fig. 1 (control specimen), the S_2 layer of the right tracheid presented a surface that possessed many flat, square, or cubical structures, indicating an inherent radially oriented structure associated with the fiber angle. The longitudinal face of the cell wall between two adjacent tracheids (Fig. 2) treated with oxalic acid revealed a highly grooved and linear S_3 (compare to smooth S_3 in Fig. 1); the exposed S_2 clearly bears radial grooves (exposed surface of radially oriented planes) that partially to completely traverse the compound cell wall (S_2 to S_2). However, in our micrographs, we found no evidence that these radially oriented planes were continuous the full length of the tracheids. Curvilinear radial configurations in the S_2 were clearly seen (Fig. 3) in cross-section of partially decayed southern pine (weight loss ca. 1%). Specifically, note that no visible connection between these structures from cell to cell exists and that all cell wall layers are clearly identifiable. In decayed wood at various advanced stages (Figs. 4-7), radial configurations were clearly seen (Figs. 5-7) and traverse the S_2, compound middle lamella, and into the adjacent cell wall (Figs. 6-7). Figure 5 clearly shows a "stacking" appearance of individual plate-like layers. Figures 8-11 all reveal configurations from frozen and transversely fractured surfaces that are radial (Fig. 11), somewhat curvilinear (Figs. 8-9), and one (Fig. 10) with structures that appear to radiate from a point in the cell corner.

4. Discussion

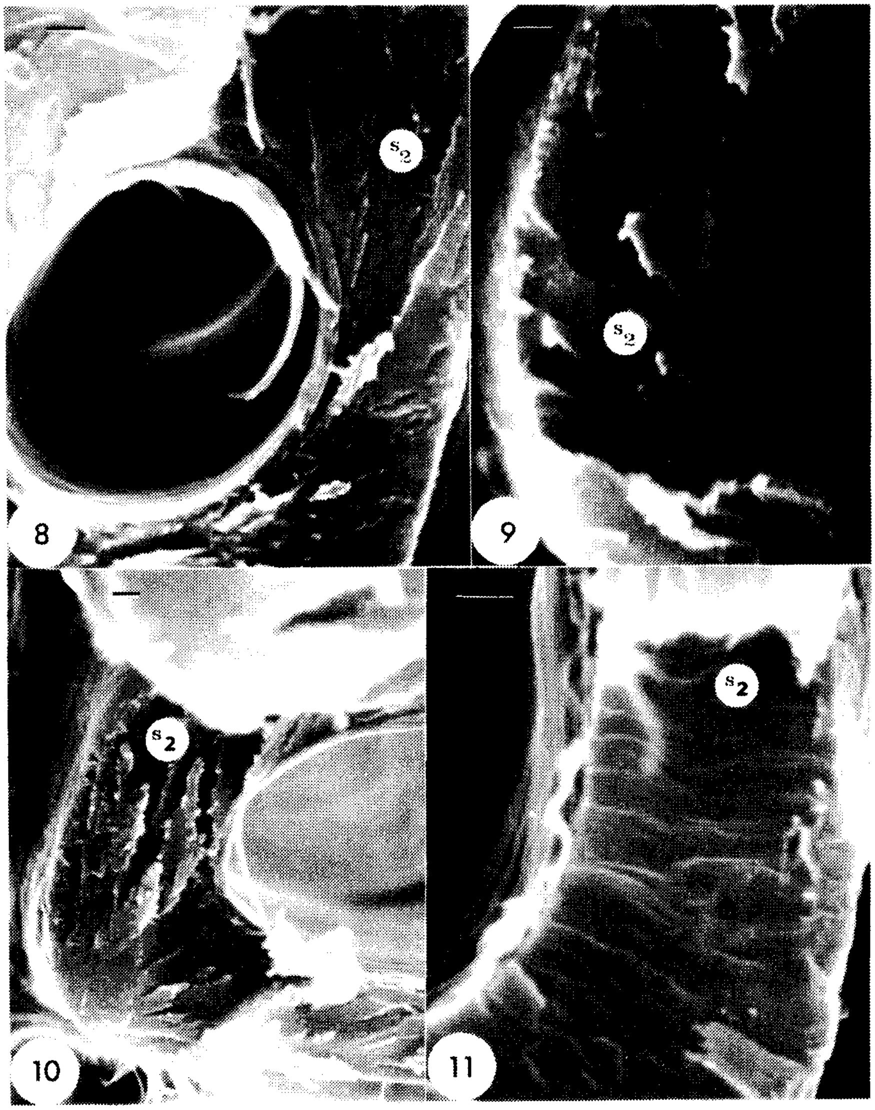
The results presented here indicate that a radial (chemical) structural organization in the S_2 layer of the tracheid wood cell wall coexists with the commonly accepted concentric lamellar model. We have also observed in our micrographs and from the reported literature (J. SELL and T. ZIMMERMAN, 1993a, 1994b; F. GREEN et al., 1989) that the radial configurations are not consistent in form. J. SELL and T. ZIMMERMANN'S (1993 a,b) model shows only straight radial configurations, but in their



Figures 1-3: Scanning electron micrographs of southern yellow pine wood. Fig. 1. Experimentally untreated control, depicting S_3 and S_2 wall layers and cml (compound middle lamella), Note the smoothness of the S_3 and fairly unstructured nature of the S_2 (longitudinal section). Fig. 2. Sample exposed to oxalic acid. Note the highly ridged surface of the S_3 and what appear to be grooves/lines (arrow) that extend partially to completely from lumen to lumen [S_2 to S_2 and across the cml (longitudinal section)]. Fig. 3. Sample decayed by *Postia placenta* for one week, Note the curvilinear configurations (arrows) in the S_2 of several tracheids (cross-section). All scale bars equal one micrometer.



Figures *4-7:* Scanning electron micrographs of longitudinal sections of southern yellow pine wood decayed by *Postia placenta.* Fig. 4. Fractured longitudinal surface showing a “benched” area (b) of the S_2 from which two radially linear structures protrude (arrow). Fig. 5. Individual radially-oriented plate-like structures in S_2 and extending partially into the compound middle lamella (cml). Note that the angle of plate-like structures is coincident with the fiber angle of residual microfibrils. Figs. 6-7. Longitudinal sections of cell wall between two contiguous tracheids demonstrating radial configurations traversing both the S_2 and cml. A collapsed fungal hypha (H) appears on the surface of the S_3 at the right. All scale bars equal one micrometer.



Figures 8-11: Scanning electron micrographs of cross sections of southern yellow pine wood frozen in liquid nitrogen. All figures clearly demonstrate S_1, S_2, and S_3 layers of tracheid walls. Note the variability in orientation of configurations in the S_2. All scale bars equal one micrometer.

micrographs there is considerable deviation from their model. In fact, many of their images are similar to our Figure 10. We believe that these radially oriented zones or bands (Fig. 3) represent alternating areas of higher and lower concentrations of hemicellulose or a hemicellulose-lignin matrix (A. BJÖRKMANN, 1988). Furthermore, though we see radial curvilinear configurations in cross-section, there is no evidence that each configuration is continuous the full length of each tracheid.

Brown rot decay is a diffuse process which rapidly depolymerizes polysaccharides, similar to mild acid hydrolysis, and modifies lignin by removing methoxyl groups (P. ANDER et al., 1988; F. GREEN et al., 1992a). Hemicellulose is very susceptible to acid-catalyzed hydrolysis (N. I. NIKI. TIN, 1966). It has been clearly shown that significant hemicellulose degradation occurs almost exclusively in the early stages of brown-rot decay (J. E. WINANDY and J. J. MORRELL, 1993) and in thermal acid-mediated degradation (S. L. LEVAN et al., 1990; J. E. WINANDY, 1994; J. E. WINANDY, 1995). Though we consistently observe radial channels in decayed and acid treated wood, our results by themselves do not indicate whether pre-existing channels are present and exploited or new channels are created by chemical or fungal modification of the cell wall.

Others have also reported, but not explained, radial channels in decayed or thermochemically degraded tracheid walls. A reexamination of transmission electron micrographs (TEM) of T. L. HIGHLEY and L. L. MURMANIS (1985) also provided strong evidence for a radial decay pattern, but they did not explicitly interpret their TEMs as such. The TEMs of hydrofluoric acid treated wood published by W. A. COTÉ (1964) also revealed a pattern of radial channels or residual plates similar to that seen by F. GREEN et al. (1989) in brown-rotted wood. Similarly, I. B. SACHS'S et al. (1963) micrographs of hydrofluoric and periodic acid treated wood also showed a radial orientation in S_2 structure in post-treatment cross-sections of *Picea* sp. tracheid walls. L. L. MURNIANIS et al. (1983), using SEM, reported that there were many radial cracks in the S_2 layer of tracheids of Douglas-fir *[Pseudotsuga menziesii* (Mirb.) France], but provided no further comment on their observations except that the walls had been greatly damaged. M. STOLL and D. FENGEL (1977) and A. B. WARDROP and H. HARADA (1965) also provided some micrographs that depicted a radial fibrillar orientation of the S_2; they also offered no explanation as to the cause or source of the radial configuration.

When these often-cited radial channels in decayed wood are considered in conjunction with the observations of J. SELL and coworkers (1993a, b, 1994a, b) of distinct radial configurations in unmodified wood, we are lead to postulate that the brown rot fungus *P. placenta* actually exploits a pre-existing radial conformation inherent in these cell walls rather than modifying a concentric conformation into a radial conformation.

A. J. KERR and D. A. I. GORING (1975) presented a cell model having hemicelluloses arranged in between cellulose and lignin. A. BJÖRKMANN (1988) later defined this matrix between the cellulose microfibril bundles as a lignin-hemicellulose matrix. If our interpretations are correct, then minor modification of the A. J. KERR and D. A. I. GORING model to include a radial linear/curvilinear zone of high hemicellulose content would provide a continuous radial avenue for the rapid penetration of the low molecular weight hydronium ion into the cell wall (M. W. JENNISON, 1952; E. B. COWLING, 1961; F. GREEN et al., 1991). This radial layer of hemicellulose then could account for the directionality and rapidity of the brown-rot decay process. A radially orientated hemicellulose configuration in the S_2 would also account for the radial penetration of hyphal sheath structures subsequent to the rapid penetration of the hydronium ion (F. GREEN et al., 1989; F. GREEN et al., 1991; M. J. LARSEN and F. GREEN, 1992). Later in the decay process brown-rot fungi produce hemicellulases, in addition to pectinases, cellulases and lignin-modifying systems which also chemically modify the S_2 cell wall structure during decay, further exploiting the existing radial organization of hemicellulose.

We have compared our observations with those of J. SELL and T. ZIMMERMANN (1993a, b), who used wood substrates that were undecayed, but which were subjected to a variety of static bending tests at three temperatures (-20°, 20°, and 60°C) and moisture contents (7, 12, 25%). Furthermore, their *(loc. cit.)* model is substantially different from the perspective of C. E. DUNNING (1968), A. J. KERR and D. A. I. GORING (1975), K. RUEL et al. (1978), A. J. KERR (1977), J. E. STONE et al. (1971), who illustrate concentric, tangentially arranged alternating regions of lignin, hemicellulose, and cellulose.

A major argument for the “concentrically-wound” cell wall model was presented by J. E. STONE et al. (1971) in an attempt to address the question of whether the S_2 cell wall was radially or concentrically constructed. Their experimental methods included measuring the shrinkage of many individual wood cells in small wood blocks. J. E. STONE et al. (1971) concluded that since there was more shrinkage in cell wall diameter from the inside rather than outside, then the cell wall had a concentrically organized laminated structure. However, because they (J. E. STONE et al., 1971) studied wood cells in small blocks rather than separated individual tracheids, they appear to have biased their results because the outer diameter of each cell was constrained from shrinking independently.

Additional evidence for the concentrically layered cell wall theory is provided by A. J. KERR and D. A. I. GORING (1975). Building on the earlier results of J. E. STONE et al. (1971), A. J. KERR and D. A. I. GORING (1975) measured the variation in density parallel, and perpendicular to, the middle lamella. These results (Fig. 4 of A. J. KERR and D. A. I. GOR. ING, 1975) are then interpreted to justify a concentrically-wound cellulose-hemicellulose-lignin structure (Fig. 5 of A. J. KERR and D. A. I. GORING, 1975) consistent with the J. E. STONE et al. (1971) model of concentrically-wound S_2 wall layers. The A. J. KERR and D. A. I. GORING (1975, Fig. 4) densitometric profiles "parallel to middle lamella" show greater variation in the magnitude of density change while the profiles "perpendicular to middle lamella" show a greater frequency of density variation with a lower magnitude of change. We interpret this to mean that alternating radial bands of lower density, non-crystalline hemicellulose and lignin are interspersed between higher density cellulose bands. Thus, the A. J. KERR and D. A. I. GORING data may also be interpreted to support an underlying radial channel structure in the S_2 cell wall. Thus, we propose a new ultrastructural model for the arrangement of cellulose, lignin, and hemicellulose within the S_2 layer of the conifer tracheid (Fig. 12). This ultrastructure may co-exist as a sublevel with the concentric laminar structure (Fig. 12). This type of ultrastructure would have radial planes of symmetry. These radial planes could easily be exploited by fungal and thermochemical agents of degradation. In our opinion, such a model would better represent our interpretations of the densitometric cell wall data presented by A. J. KERR and D. A. I. GORING (1975).

We conclude from the present study and previous ones (F. GREEN et al., 1989; M, J. LARSEN and F. GREEN, 1992; F. GREEN et al., 1992b; J. SELL and T. ZIMMERMANN 1993a, b; J. SELL 1994a, b) that a radial structural arrangement coexists across the secondary wall (S_2) in southern yellow pine tracheids with a concentric laminar structure. The easily-hydrolyzable nature of this radial ultrastructural element can be exploited by selected brown-rot fungi which produce copious amounts of oxalic acid. Oxalic acid has been shown to hydrolyse hemicelluloses in the incipient stages of decay (J. BECH-ANDERSON, 1987; F. GREEN et al., 1991; M. SHIMADA et al., 1991). This hydrolytic attack on low molecular-weight hemicelluloses eventually results in what appears to be a radial configuration. This radial configuration can also be revealed after exposure *in vitro* to prepared solutions of oxalic acid (F, GREEN et al., 1991). This revised perspective of the cell wall would largely account for:

(1) the rapidity of decay and rapid strength loss in brown-rotted wood (J. E. WINANDY and J. J. MORRELL, 1993), and

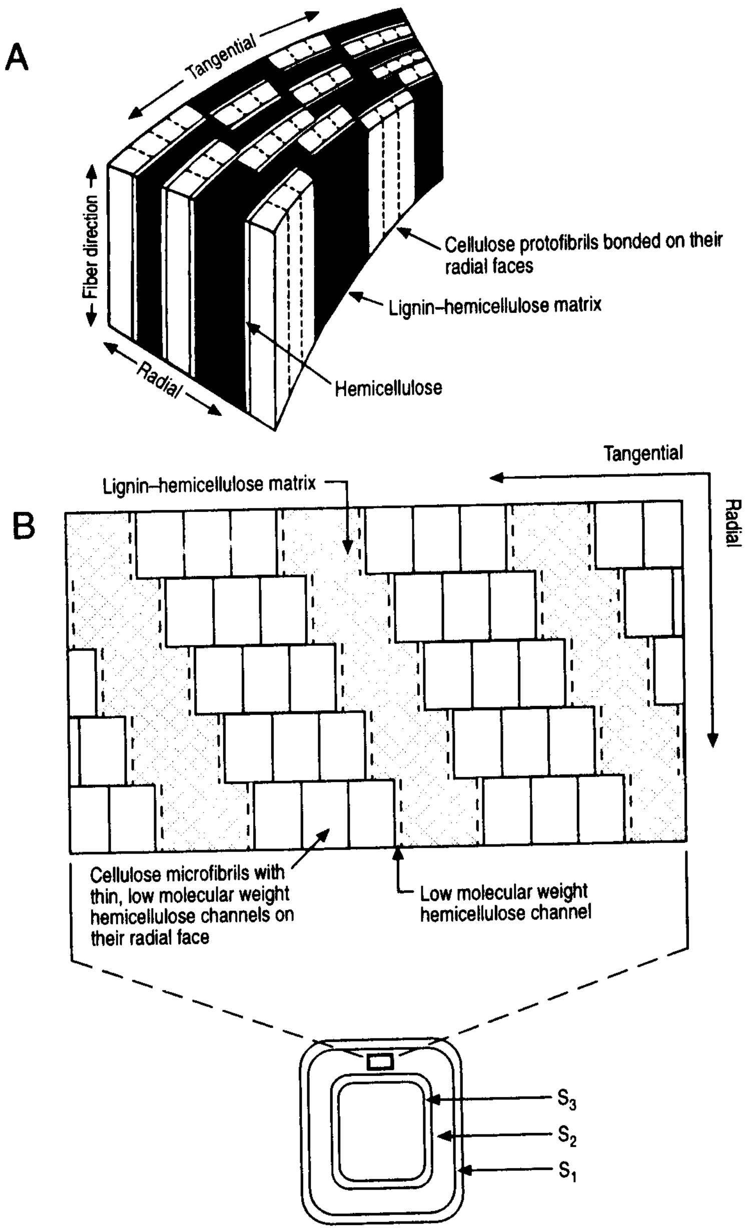


Figure 12: Representations of proposed ultrastructural models of the arrangement of lignin, cellulose, and hemicellulose in S_2 layer of the wood cell wall.
A. Model proposed by A. J. Kerr and D. A. I. Goring (1975).
B. Model proposed in this report.

(2) the rapid hydrolytic action of acidic chemicals on wood structure and strength (S. L. LEVAN et al., 1990; J. E. WINANDY, 1994; J. E. WINANDY, 1995).

5. Summary

During our many SEM studies on brown-rot decayed or oxalic acid-treated wood blocks, our observations consistently showed that the S_2 layer of degraded tracheid cell walls possessed an underlying structural configuration perpendicular to the lamellae. We hypothesized that fungal decay and/or acid attack had revealed, rather than modified, the underlying wood chemical composition and ultrastructure which is not evident in undecayed wood. From this we conclude that there are radial planes of low molecular-weight hemicellulose across the S_2 layer, in addition to the previously recognized concentric layering of cellulosic microfibrils. These radial planes of hemicellulose can be exploited by acid-mediated fungal and thermochemical agents that reveal the radial ultrastructural organization in degraded cell wall remnants.

Zusammenfassung

Vorgeschlagenes Modell der tracheidalen Zellwand mit einer spezifischen Feinstruktur in der S_2-Schicht von *Pinus* spp.

In unseren zahlreichen rasterelektronenmikroskopischen Untersuchungen an Holzklötzchen, die von Braunfäulepilzen befallen oder mit Oxalsäure behandelt waren, haben wir ausnahmslos festgestellt, daß die S_2-Schicht der angegriffenen tracheidalen Zellwände eine besondere Struktur senkrecht zu den Lamellen aufwies. Unsere Hypothese ist, daß der Pilzbefall und/oder der Säureangriff den eigentlichen chemischen Holzaufbau und die Feinstruktur des Holzes nicht verändert, sondern erst deutlich erkennen läßt, was in nicht befallenem Holz nicht sichtbar ist. Wir schließen daraus, daß eine radiale Struktur von Hemizellulosen mit niedrigem Molekulargewicht quer durch die S_2-Schicht verläuft, zusätzlich zu den vorher bekannten konzentrischen Schichten der Zellulose-Mikrofibrillen. Die radiale Struktur der Hemizellulose kann durch Pilze unter Zuhilfenahme eines Säurevermittlers und durch thermochemische Agenzien, die die radiale Feinstruktur der angegriffenen Zellwandreste freilegen, verwertet werden.

Résumé

Proposition de modèle de cellules trachéidales de paroi ayant une ultrastructure inhérente dans la couche S_2 de *Pinus* spp.

Lors de nos nombreuses études de microscopie électronique à balayage de blocs de bois traités par la pourriture brune ou l'acide oxalique, nos observations ont constamment montré que la couche S_2 de cellules trachéidales de la paroi possédait une configuration structurale sousjacente perpendiculaire à la lamelle. Nous avons émis come hypothèse que la pourriture fongique et/ou l'attaque acidique ont révélé, au lieu de modifier, la composition chimique du bois sousjacente et l'ultrastructure ce qui n'est pas évident dans le bois non pourri. De ceux-ci nous

concluons qu'il y a un plan radial semi-contenu de bas poids moléculaire d'hémicellulose d'un côté à l'autre de la couche S_2, qui vient s'ajouter à la couche concentrique mise en évidence précédemment. Ce plan radial d'hémicellulose peutêtre exploité par un champignon qui a un médiateur acidique et des agents thermochimiques qui révèlent l'organisation ultrastructurale dans les parois cellulaires restantes.

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