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1. Introduction

When a swinging drawbridge over the Milwaukee River was dismantled in 1974, an array of 197 foundation pilings were found to have been supporting the stone block pier upon which the center of the bridge rested. From this array 14 red pine (*Pinus resinosa* Ait.), 11 white pine (*Pinus strobus* L.), and 10 tamarack (*Larix laricina* (Du Roi) K. Koch) pilings, which had been totally submerged in river water for 85 years, were obtained for study. Samples removed from these pilings were used to determine: (a) piling strength losses, (b) the microorganisms associated with the different piling tree species, and (c) the microscopical and chemical changes occurring in representative piling sections. The effect of long-time submersion in river water on wood strength has already been reported (W. E. ESLYN and J. W. CLARK, 1976). Our objectives here are to detail the findings pertaining to parts b and c above.

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2. Materials and Methods

2.1 Sampling techniques

Three discs, each roughly 15.2 cm (6 in.) long in the grain direction, were removed from each of the 35 pilings. The discs, which were located 1.22 m (4 ft) and 2.44 m (8 ft) down from the tops of the piles and 0.61 m (2 ft) from the bottoms of the piles, were designated "top", "mudline", and "bottom", respectively. A radial segment was removed from each disc (Fig. 1); each segment was subsequently divided radially into three equal parts to provide material for sampling from the sapwood and middle and inner heartwood of each disc. From the center of each part a 2.54. cm (1 in.) square, 15.2 cm long, piece was removed for use in strength tests, culturing, microscopial examination, and chemical analyses. For an illustration of this sampling technique, see Figure 1 in the earlier report by W. E. ESLYN and J. W. CLARK (1976).

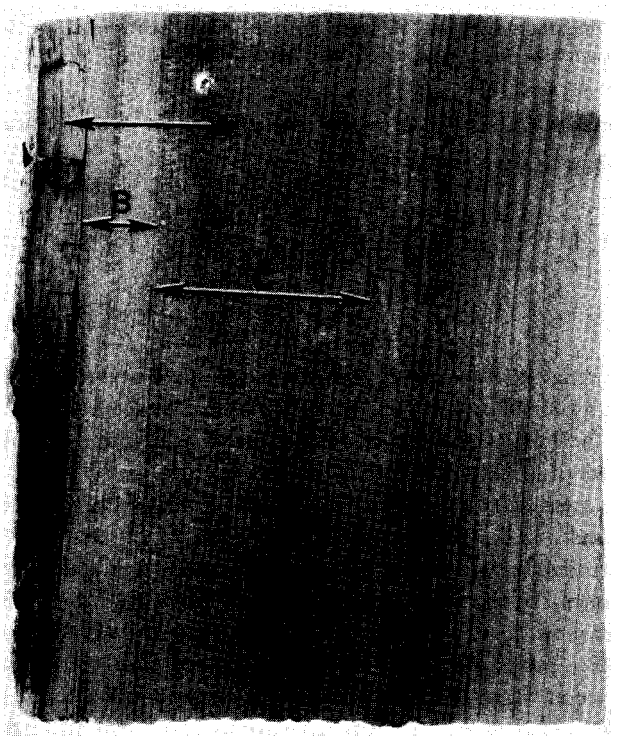

Fig. 1. Radial segment from top disc of white pine piling. Note checking and obvious deterioration of exterior (A), bleaching of the underlying area to a depth of about 3.0 cm (B), and sound heartwood (C).

2.2 Isolation and identification of microorganisms

The media used in isolation attempts, including their chemical composition per liter of distilled water, were as follows:

(a) Malt agar: 20 g Difco[2] malt extract and 15 g agar.
(b) Casamino acid: 3 g Difco casamino acids, 3 g Difco yeast extract, 1 g dextrose, and 2 g agar.
(c) Difco thioglycolate medium: 40.5 g to which was added 2.5 g dextrose and 2 g agar.
(d) Corn meal mash.

The malt agar and casamino acid media were included for the purpose of isolating both fungi and aerobic bacteria, and the thioglycolate and corn meal mash media were used to isolate anaerobic bacteria. The first two media were used in isolations from all piles, the thioglycolate and the corn meal media were used in isolations from only 14 of the piles.

To ensure that the bacterial cultures obtained were pure, we streaked loops from each culture onto tryptone-yeast extract-glucose agar and then incubated these under both aerobic and anaerobic conditions. Once new growth ensued from these, individual colonies were picked out and transplanted to fresh media.

The scheme followed for identification of bacterial isolates was generally that described by S. T. COWEN and K. J. STEEL (1970). The purified cultures were run through a number of primary tests, such as gram reaction, catalase, oxidase, O-F, motility, etc., generally enabling identification of the unknowns to genus. Secondary tests - the particular tests used depending upon the isolate involved - were conducted to determine the species involved.

2.3 Microscopical observations

Choice of samples for microscopical examination and chemical analysis was based upon the results of strength tests and bacterial isolations and identifications. In this way, we were able to include in this work piling samples in varying stages of deterioration and/or infected with different species of bacteria.

Microscopical examinations were conducted with both the light microscope and the scanning electron microscope (SEM). Slides produced for use with the light microscope consisted of piling material imbedded in celloidin, sectioned at 15 - 20 μ, and stained with saffranin-picroaniline blue. In our SEM work, air-dried piling material was coated with gold and viewed with a Cambridge Mark 2A SEM at 20 kV.

2.4. Chemical analyses

Chemical analyses were conducted on material from top, mudline, and bottom exteriors, and from bottom disc interiors (heartwood), of a red pine, white pine, and tamarack piling, to ascertain the order and magnitude of lignin and sugar depletion in samples having undergone varying degrees of deterioration. As a basis

[2] The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not consitute an official endorsement or approval by the U.S. Department of Agriculture of any product or service to the exclusion of others that may be suitable.

for comparison, similar analyses were run on fresh red and white pine and tamarack controls. Individual sugars were determined by use of high-performance liquid chromatography (F. E. WENTZ et al., 1982). Total sugars and lignin were obtained by the procedure of M. J. EFFLAND (1977).

3. Results

3.1 Bacterial isolations

A total of 115 bacterial isolates were obtained - 60 from red pine, 39 from white pine, and 16 from tamarack pilings (Table 1). These isolates included 10 different species of Pseudomonas, five of Bacillus, three of Alcaligenes, two of Flavobacterium, and one each of *Acinetobacter, Chromobacterium,* and *Micrococcus. Clostridium* species were also included among these isolates; however, the number involved is uncertain as we were able to identify Clostridium isolates to genus only. Mold fungi were isolated only a few times and no attempt was made to identify them or to categorize them according to host wood or to location within the piles.

Pseudomonas fluorescens was the species most frequently isolated from piling of all wood species, followed by *Bacillus pumilus* and, dependent upon the number of species involved, by Clostridium species (Table 1). Based upon frequency of success in isolating, tamarack piling supported lesser populations of bacteria than did the red and the white pine pilings.

Aerobic bacteria in the genera Pseudomonas, Acinetobacter, Alcaligenes, and Micrococcus, and facultatively anaerobic bacteria, such as Bacillus, Chromobacterium, and Flavobacterium, were most frequently isolated from the outer third of the top disc of the piles (Table 2) were aeration would have been at its highest. Deviations from this trend by individual species within some of these genera did occur however. Bacillus cereus, for example, was isolated from mudline and bottom discs, but not from top ones. Also, *P. fluorescens,* which was isolated in greatest numbers from the top discs, was also well represented in isolations from the two lower discs (Table 2). Anaerobic bacteria in the genus Clostridium were dominant in the lower portions of the piles, particularly if one considers that anaerobic isolation techniques were conducted on fewer than half of the piling samples.

3.2 Microscopical appearance

3.2 Microscopical appearance

3.2.1 Light microscopy

In cross sections of severely deteriorated wood, cell walls were thinned to the extent that only the compound middle lamella remained, or the cell

Table 1: Identification and frequency of isolation of bacteria inhabiting red pine, white pine, and tamarack piling.

Bacterial species	Frequency of isolation		
	Red pine	White pine	Tamarack
Acinetobacter sp.	1	0	0
Alcaligenes faecalis Castellani and Chalmers	1	0	0
Alcaligenes viscolactis (?)	1	0	0
Alcaligenes sp.	0	0	1
Bacillus badius Batchelor	2	0	1
Bacillus cereus Frankland and Frankland	3	2	0
Bacillus circulans Jordan	1	0	0
Bacillus firmus Bredemann and Werner	0	1	0
Bacillus pumilus Meyer and Gottheil	6	4	2
Chromobacterium violaceum Bergonzini	1	3	1
Clostridium spp.	9	6	4
Flavobacterium solare Lehmann and Neumann	0	1	1
Flavobacterium sp.	1	3	0
Micrococcus roseus Flügge	0	2	0
Pseudomonas acidovorans den Dooren de Jong	1	0	0
Pseudomonas cepacia Burkholder	2	1	0
Pseudomonas fluorescens Migula	22	10	4
Pseudomonas fluorescens (achromatic variety?)	3	1	1
Pseudomonas mallei (Zopf) Redfearn, Palleroni und Stanier	1	0	0
Pseudomonas maltophilia Hugh and Ryschenkov	0	1	0
Pseudomonas pseudomallei (Whitmore) Haynes	1	0	0
Pseudomonas putida (Trevisan) Migula	1	2	0
Pseudomonas stutzeri (Lehmann and Neumann) Sijderius	0	1	0
Pseudomonas sp. A	1	1	0
Pseudomonas sp. B	2	0	1
Total	60	39	16

T a b 1e 2: Frequency of isolation of different bacterial genera from various positions within the piles.

Radial position of samples	Aerobes		Facultative anaerobes			Obligate anaerobes
	Pseudomonas	Miscellaneous[a)]	*Bacillus*	*Chromobacterium*	*Flavobacterium*	*Clostridium*
			Top Disc			
Outer Third	22	5	4	2	4	0
Middle	9	0	6	0	0	0
Inner Third	1	0	1	0	0	3
			Mudline Disc			
Outer Third	9	1	5	0	1	6
Middle	4	0	2	2	0	0
Inner Third	2	0	0	0	0	0
			Bottom Disc			
Outer Third	2	0	3	0	1	9
Middle	6	0	1	1	0	1
Inner Third	2	0	0	0	0	0

a) The miscellaneous grouping includes the genera *Acinetobacter*, *Alcaligenes*, and *Micrococcus*, all of which were isolated in small numbers.

interiors were so disorganized that they appeared granular (Fig. 2). Rays were destroyed (Fig. 3) and tracheid cell walls were almost wholly eroded. Where degradation was less advanced, conical to variably shaped erosion

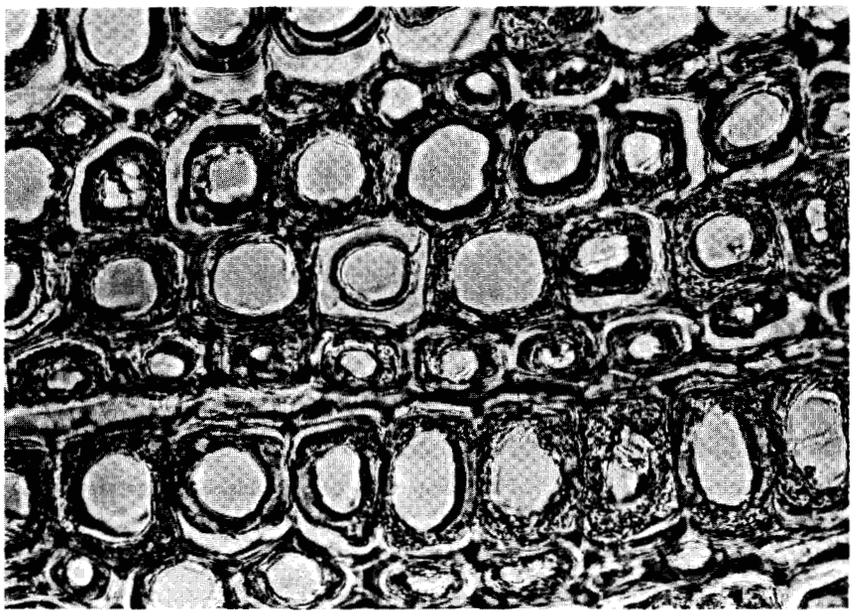

Fig. 2. Granulated appearance of cross section of tracheids from deteriorated edge of red pine piling.

patterns were commonly seen (Fig. 3). Pencil-shaped cavities aligned with the microfibril angle were also present in tracheid cell walls. Pitting of the cell wall was also observed (Fig. 4).

3.2.2 Scanning electron microscopy

Tracheid cell walls, removed from piling exteriors, appeared to be severely corroded beneath a layer of bacterial slime and debris (Figs. 5 and 6). With increasing depth into the piling and with progression from pile top to bottom the extent of deterioration lessened (Figs. 7 and 8), taking on the appearance of individual narrow erosion troughs (Fig. 9), or coalesced troughs (Fig. 10), and finally appearing sound (Fig. 11). Comparison of cross sections of sound (Fig. 12) and deteriorated (Fig. 13) sections of piling revealed tracheids of the latter to be either thinned or eroded from the lumens inwardly or, in the case of the granulated-appearing tracheids

Fig. 3. Deteriorated ray cells (A) and diamond- to oval-shaped eroded areas (B) in tangential section of red pine piling.

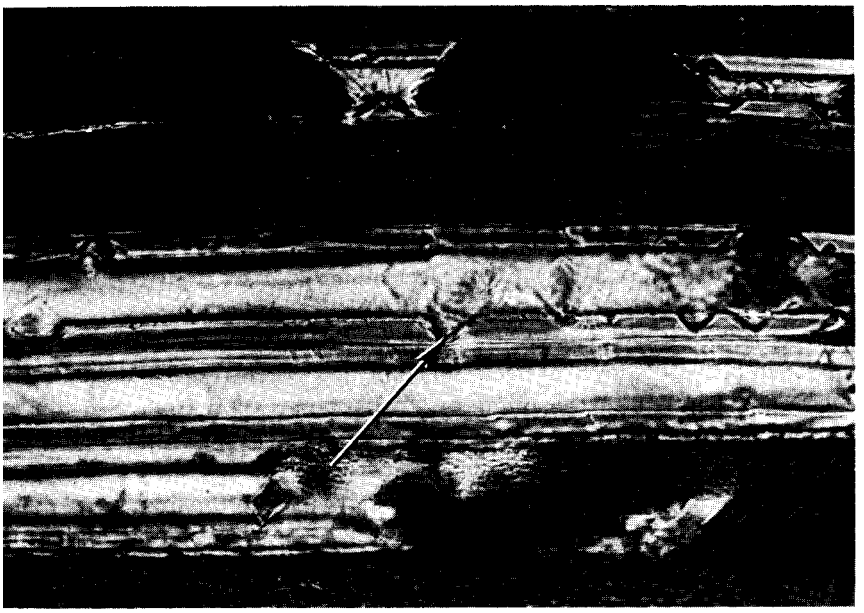

Fig. 4. Radial view of pitting in red pine tracheids, which may be seen to extend down to the middle lamella (arrow).

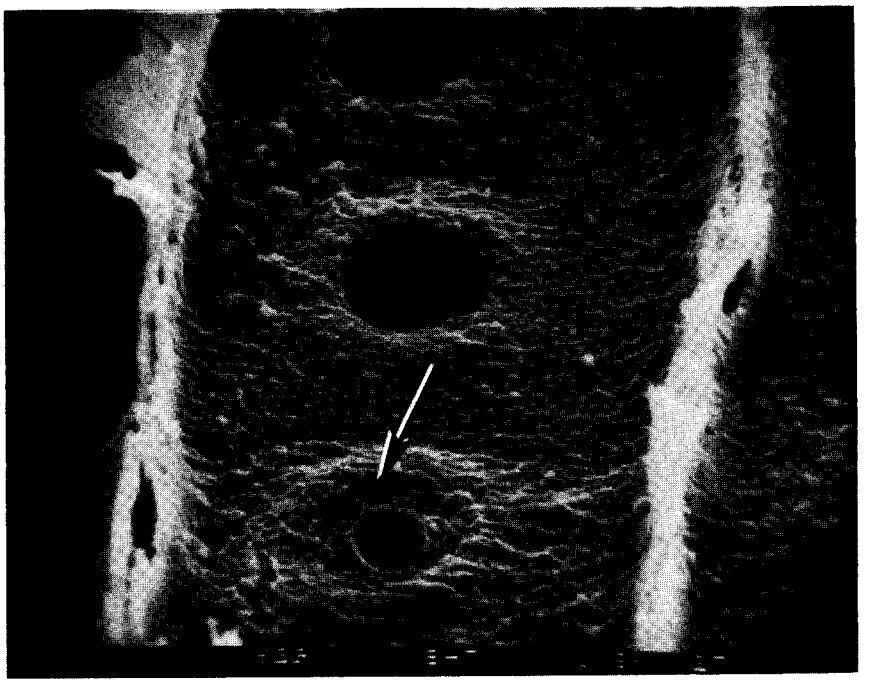

Fig. 5. Severely deteriorated tracheid, coated with bacterial slime and cell debris, from the outer edge of a bottom disc from a red pine piling. Note the evident erosion of the pit torus and border (arrow) (× 1800).

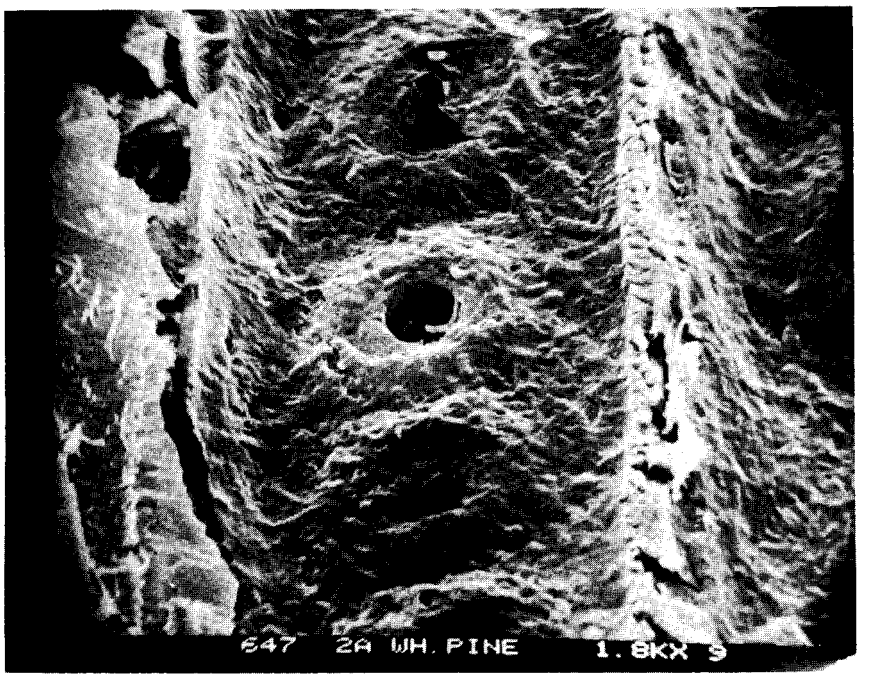

Fig. 6. Severe erosion and bacterial slime in tracheid from the outer edge of a top disc from a white pine piling (× 1800).

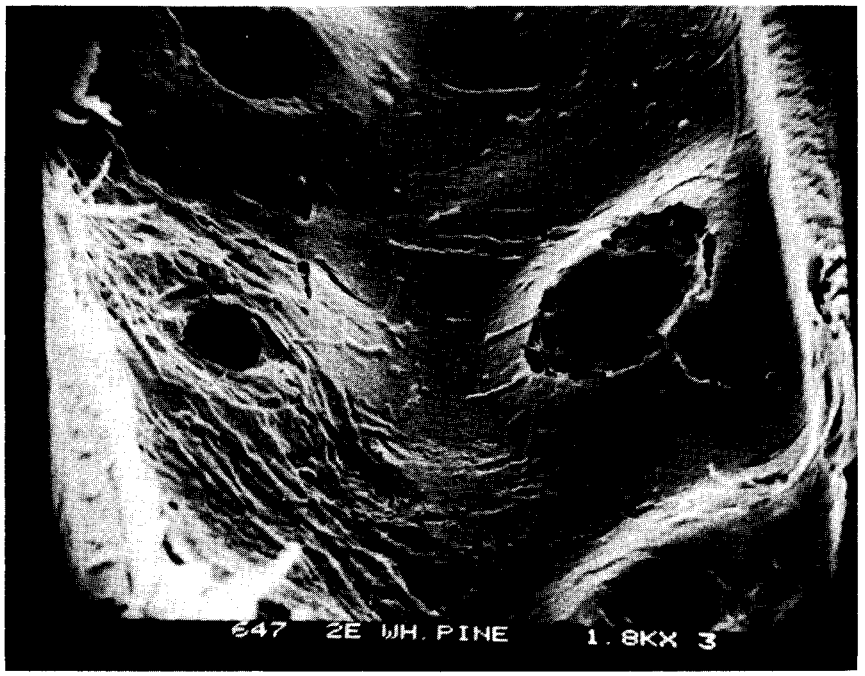

Fig. 7. Erosion of bordered pits and tracheid cell wall in top disc of a white pine piling (× 1800).

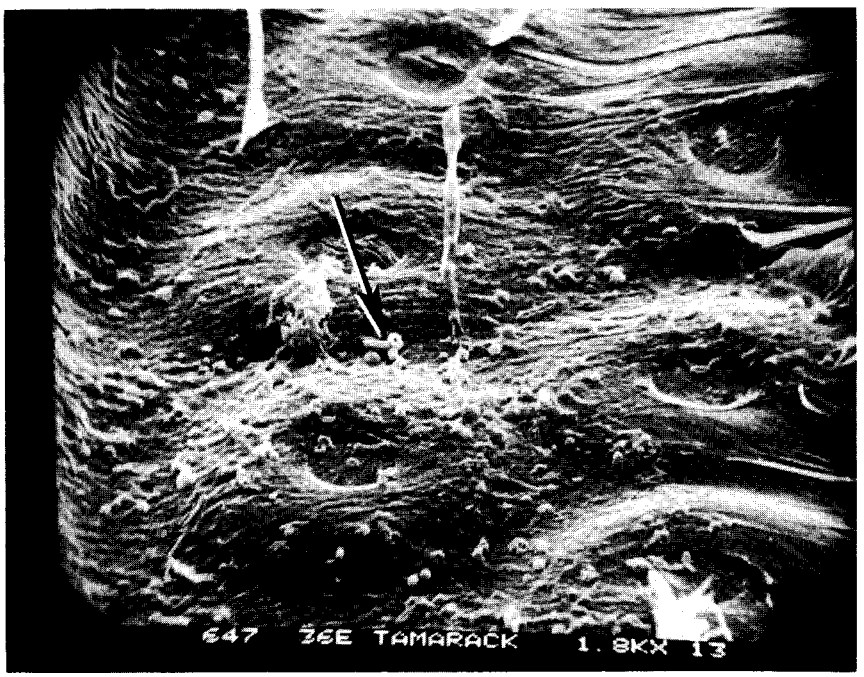

Fig. 8. Deteriorated tracheid from outer edge of top disc from a tamarack piling. Note the rod and cocci bacteria (× 1800).

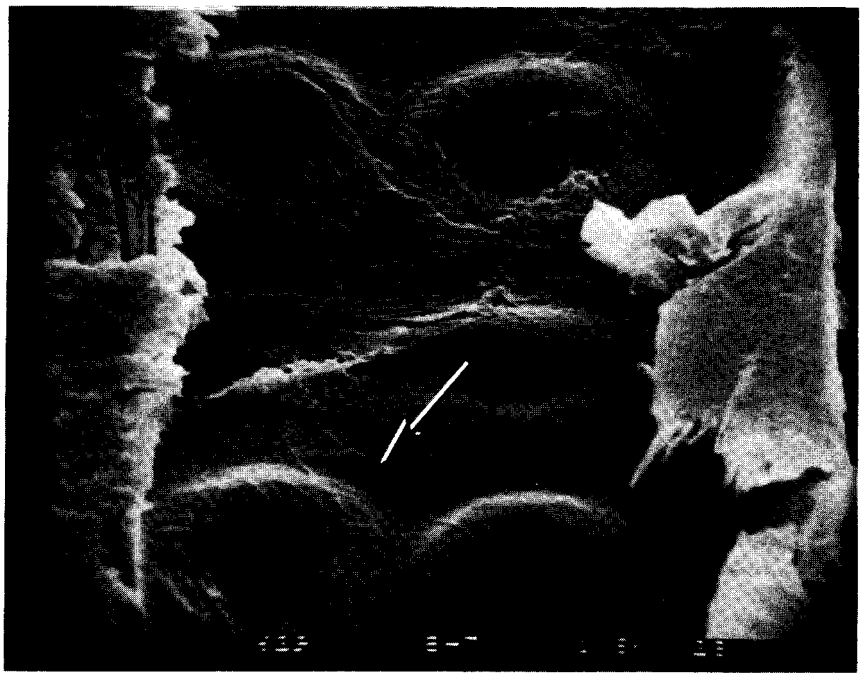

Fig. 9. Erosion troughs, hyphae (arrow) - probably of an actinomycete - and rod bacteria in outer third of bottom disc from a red pine piling (x 1800).

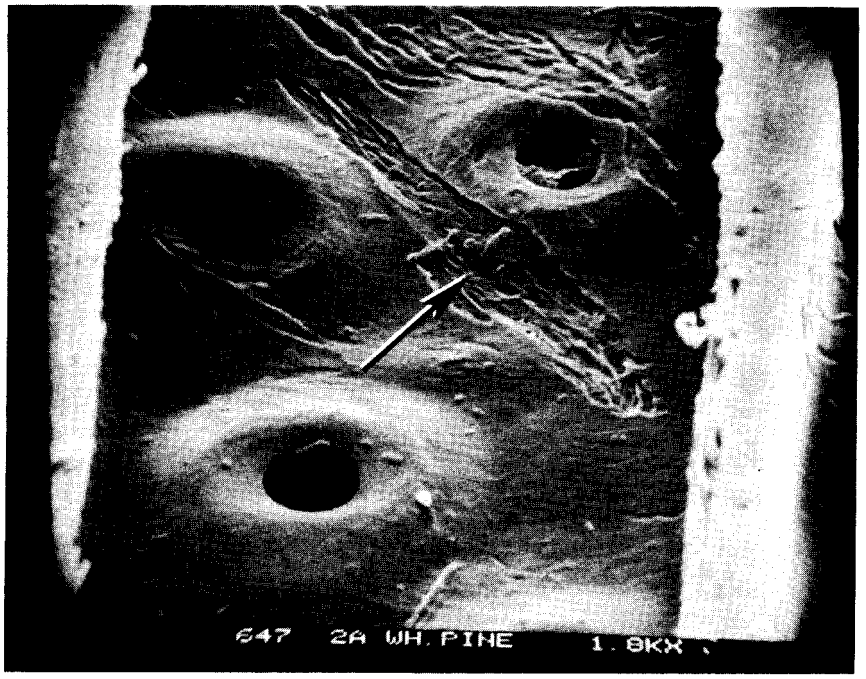

Fig. 10. Coalesced erosion troughs (arrow) and rod bacteria in top disc of a white pine piling (× 1800).

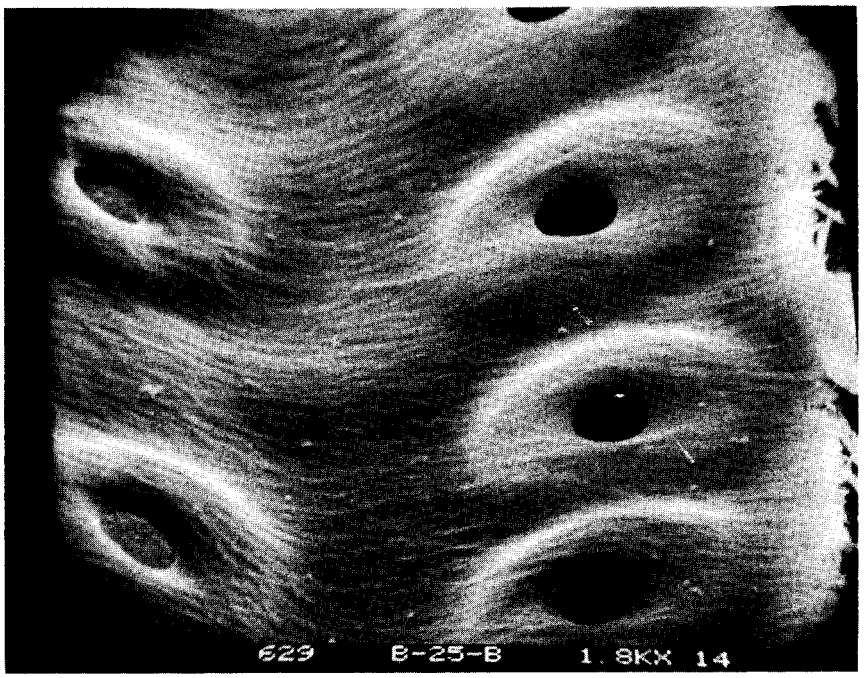

Fig. 11. Sound tracheid from interior of bottom disc from a tamarack pile (× 1800).

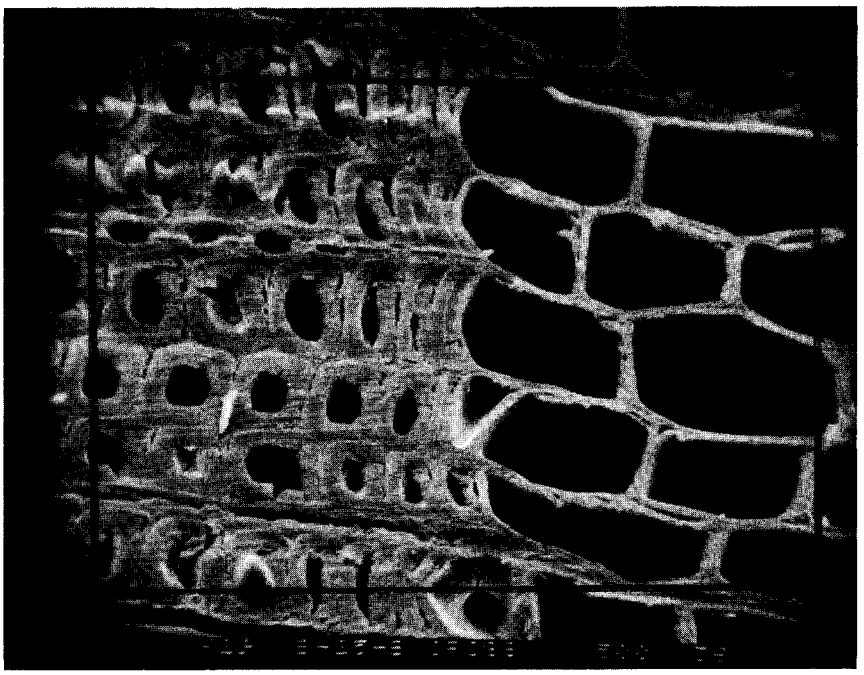

Fig. 12. Cross section of sound summerwood (left) and springwood (right) tracheids from the bottom disc of a tamarack piling (× 500).

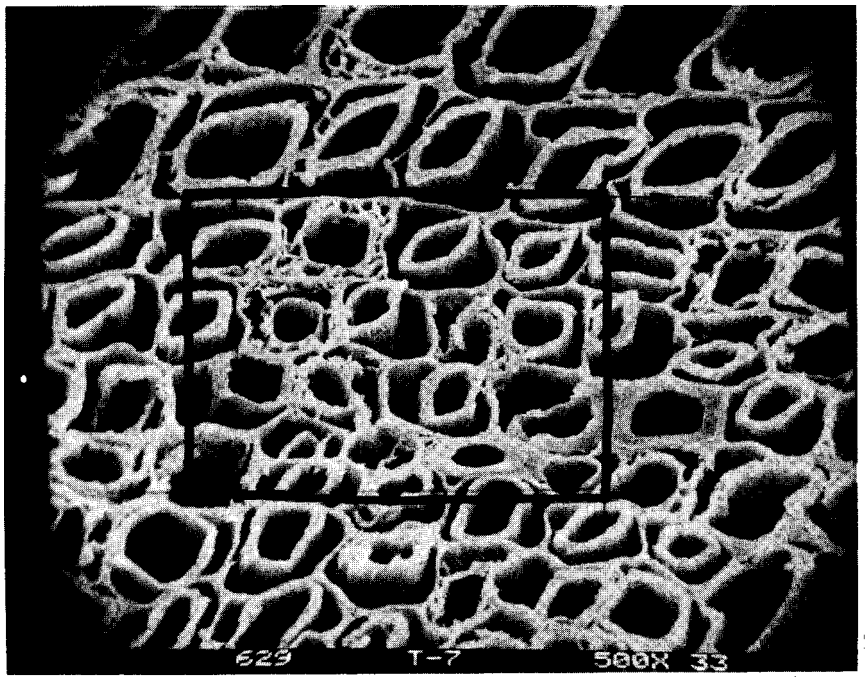

Fig. 13. Cross section of summerwood tracheids from the top disc of a red pine piling illustrating breakdown of S_2 and, possibly, S_1 layers and resultant delamination (× 500).

(Fig. 2), to contain deteriorated S_2 and, possibly, S_1 layers. Very narrow hyphae (Fig. 9), presumably of actinomycetes, and rod (Figs. 8, 9, and 10) and cocci bacteria (Figs. 8 and 14) were found in various sections of the pilings.

3.3 Chemical analyses

Decreases in total sugars of 15 (tamarack), 28 (red pine), and 35 (white pine) percent, with correspondingly large increases in lignin of 31, 64, and 72 percent, were encountered when top disc-edge samples from these pilings were compared chemically to their respective controls (Table 3). Glucose and mannose were preferentially degraded in the pines, while glucose, galactose, mannose, and arabinose were most depleted in the tamarack sample.

When compared with the controls little change in total sugars and lignin was found to occur in all samples removed from the exteriors of mudline and bottom discs and from bottom disc interiors (Table 3).

Fig. 14. Cocci bacteria on tracheid cell wall from the outer third of the top disc of a tamarack piling (× 2000).

4. Discussion and Conclusions

J. B. BOUTELJE and B. GÖRANSSON (1975) investigated the microbiology of pilings in use below the water table in Stockholm and found the greatest variety of microorganisms, including aerobic and anaerobic bacteria, actinomycetes and molds, concentrated in the outer edges of the pilings. Deeper into the piling sapwood the number of different organisms encountered decreased, and Clostridium sp. and Bacillus cereus were prevalent. These bacteria were also widespread in the less aerobic portion of the Milwaukee River pilings. Other bacteria isolated from pilings included in both studies were Bacillus pumilus and Pseudomonas spp. No bacteria were found in the heartwood of piles in place for 50 or 60 years in Hamburg harbor (W. LIESE and G. KARNOP, 1968)nor in the pilings studied by J. B. BOUTELJE and B. GÖRANSSON (1975). The latter thought this might be due to the timber species involved. In the present study and in that by T. C. SCHEFFER et al.

(1969), however, bacteria were isolated from piling heartwood, although the numbers isolated were far smaller than those obtained in the sapwood. Actinomycetes were isolated from piling by. J. B. BOUTELJE and B. GÖRANSSON (1975) and by L. HARMSEN and T. V. NISSEN (1965) but none were obtained in the present study due, possibly, to our not including special actinomycete media in our isolation procedures.

The surfaces of the Milwaukee River pilings were generally discolored while beneath the wood was softened and bleached to depths – at least in the top and middle discs – of up to 3.0 cm (Fig. 1). Under the light microscope the softened wood often appeared granular (Fig. 10), conforming closely to the descriptions of similar areas provided by J. B. BOUTELJE and A. F. BRAVERY (1968), J. B. BOUTELJE and B. GÖRANSSON (1975), J. KOHLMEYER (1980), and L. E. LEIGHTLEY and R. A. EATON (1980). The variously shaped erosion patterns encountered herein in tracheid cell walls have been widely reported (J. B. BOUTELJE and A. F. BRAVERY, 1968; J. B. BOUTELJE and B. GÖRANSSON 1975; H. GREAVES, 1969; H. GREAVES, 1970; L. HARMSEN and T. V. NISSEN, 1965) while pitting has been described by J. B. BOUTELJE and A. F. BRAVERY (1968) as "type 1 attack".

Ultrastructurally, two types of bacterial attack in wood have been distinguished – i.e., cell wall erosion and cavity formation within the S_2 layer (D. M. HOLT, 1983). In the former, a "rod-like" bacterium orients itself on the S_3 layer so that its main axis is parallel to the cellulose microfibrils. It erodes the cell wall causing a narrow trough to appear which elongates as the bacterium divides. Where several bacteria are in proximity their erosion troughs merge and the S_3 and S_2 layers are eventually removed. This is the type of attack depicted in our Figures 9 and 10. The second type of attack entails penetration of the S_3 layer by bacteria which then, through elongation and division, branch out into the S_2 layer. These have been termed "tunnelling bacteria" by T. NILSSON and G. DANIEL (1983). We have not seen tunnelling, as depicted by these authors, in our piling samples, although we have noted a seemingly preferential destruction of the S_2 layer in cross sections of some tracheid cell walls (Fig. 13) which may be attributable to the action of such bacteria. J. KOHLMEYER (1980) describes destruction of the S_2 layer, which becomes "granular in appearance", while the compound middle lamella and the S_3 layer retain their shape for some time thereafter. This deterioration has been attributed by D. M. HOLT (1983) and T. NILSSON and G. DANIEL (1983) to the action of tunnelling bacteria.

Earlier tests conducted on the Milwaukee River pilings generally showed greatest strength losses to have occurred in the outer third of their boles during long-term submergence (W. E. ESLYN and J. W. CLARK, 1976). While high strength losses in such obviously deteriorated pile areas were to be expected, similar losses were also registered for interior sound-appearing

Table 3: Lignin and sugar components of red pine, white pine, and tamarack piling following 85 years submersion in river water.

Sample	Origin in piling	Chemical composition (% of oven-dried sample)						
		Lignin	Total sugars	Glucose	Xylose	Galactose	Arabinose	Mannose
Red pine								
Sapwood (control)[a]	—	28	65	46	5.6	1.8	1.5	11.8
Heartwood (control)[a]	—	35	58	40	6.3	2.7	1.4	10.1
Piling # 7	Top, outer edge	46	47	34	6.0	4.1	2.6	9.9
		[b](+64)	(−28)	(−26)	(+7)	(+128)	(+73)	(−16)
	Mudline, outer edge	28	70	52	7.0	2.9	2.0	13.9
		(0)	(+8)	(+13)	(+25)	(+61)	(+33)	(+9)
	Bottom, outer edge	29	69	52	6.7	4.6	2.1	13.2
		(+4)	(+6)	(+13)	(+20)	(+156)	(+40)	(+12)
	Bottom, interior (heart)	32	63	40	7.8	3.1	1.5	10.4
		(−9)	(+9)	(0)	(+24)	(+15)	(−7)	(+3)
White pine								
Sapwood (control)[a]	—	29	65	47	4.5	1.6	1.6	12.3
Heartwood (control)[a]	—	34	59	42	6.2	2.7	1.2	11.1
Piling # 22	Top, outer edge	50	42	28	5.2	2.9	2.2	8.0
		(+72)	(−35)	(−40)	(+16)	(+81)	(+38)	(−35)
	Mudline, outer edge	30	67	50	6.8	3.4	2.6	12.9
		(+3)	(+3)	(+6)	(+51)	(+113)	(+63)	(+5)
	Bottom, outer edge	33	64	49	6.7	4.4	2.3	13.0
		(+14)	(−2)	(+4)	(+49)	(+175)	(+44)	(+6)
	Bottom, interior (heart)	32	64	46	6.1	3.8	1.9	12.0
		(−6)	(+8)	(+9)	(−2)	(+41)	(+58)	(−8)

T a b 1e 3: Lignin and sugar components of red pine, white pine, and tamarack piling following 85 years submersion in river water. – con.

Sample	Origin in piling	Chemical composition (% of oven-dried sample)						
		Lignin	Total sugars	Glucose	Xylose	Galactose	Arabinose	Mannose
Tamarack								
Sapwood (control)")	—	29	65	46	5.3	3.5	1.6	12.4
Heartwood (control)")	—	28	67	40	5.1	13.5	3.5	10.8
Piling # 25	Top, outer edge	38 (+31)	55 (−15)	38 (−17)	5.2 (−2)	2.1 (−40)	1.3 (−19)	9.6 (−23)
	Mudline, outer edge	29 (0)	68 (+5)	50 (+9)	7.1 (+34)	4.3 (+23)	3.0 (+88)	13.0 (+5)
	Bottom, outer edge	29 (0)	67 (+3)	52 (+13)	6.9 (+30)	4.0 (+14)	3.0 (+88)	13.4 (+8)
	Bottom, interior (heart)	27 (−4)	70 (+4)	46 (+15)	7.2 (+41)	10.5 (−22)	3.2 (−9)	12.9 (+19)

a) All control data are based upon averages of analyses of material obtained from two trees.
b) Numbers in brackets show the extent, in percent, to which the piling sample values differ from those of the controls.

sections of the pilings. High strength losses in the interior of the pilings were generally attributed to the smaller amounts of dense summerwood found therein. The results of present chemical analyses conducted on these pilings indicate considerable alteration of the total sugars/lignin ratios only in their top disc exteriors (Table 3). This supports the contention of W. E. ESLYN and J. W. CLARK (1976) that the high strength losses registered for lower piling sections were due to other than deteriorating agents.

The question arose during conduction of this study as to what extent chemicals present in the polluted Milwaukee River were responsible for the deterioration of the test pilings. Although we cannot answer this question directly, the literature reviewed and the present work leaves little doubt that bacteria play a major role in the deterioration of long submerged wood.

5. Summary

Pseudomonas fluorescens, Bacillus pumilus, and one or more species of *Clostridium* were most frequently isolated from red pine, white pine, and tamarack pilings that had been submerged in the Milwaukee River for 85 years. The exteriors of the piles were softened and discolored to a maximum depth of 3.0 cm. Viewed transversely under the light microscope, cells within the deteriorated areas were thinned or their interior were disorganized and granular in appearance. In tangential or radial view, the ray cells were destroyed and the tracheids were eroded or pitted. Viewed under SEM the dominant feature was the presence of narrow erosion troughs or wide, coalesced erosion troughs in tracheid walls. Considerable decreases in total sugars and correspondingly high increases in lignin were found in the upper pile exteriors. Based on chemical analyses, degradation was greatest in the white pine and least in the tamarack. Glucose and mannose were preferentially degraded in the pines whereas glucose, galactose, arabinose, and mannose were more depleted than xylose in the tamarack samples.

Zusammenfassung

Schädigung von Brückenpfeilern durch Bakterien

Von Pfeilern aus *Pinus resinosa* Ait., *P. strobus* L. und *Larix laricina* (Du Roi) K. Koch, die seit 85 Jahren im Milwaukee River standen, wurden Bakterien isoliert; *Pseudomonas fluorescens, Bacillus pumilus* und eine oder mehrere Arten von *Clostridium* waren am häufigsten vertreten. Das Äußere der Pfeiler war erweicht und bis zu einer Tiefe von 3 cm verfärbt. Unter dem Lichtmikroskop wurde festgestellt, daß die Zellen in den befallenen Stellen verringert waren und daß das Zelleninnere desorganisiert und körnig aussah. In tangentialer und radialer Richtung waren die Zellen zerstört und die Tracheiden zerfressen oder durchlöchert. Im Rasterelektronenmikroskop waren hauptsächlich enge Erosionsrinnen oder weite verschmolzene Erosionsrinnen in den Tracheidwanden erkennbar. An den Außenwänden des oberen Pfahlbereichs hatte die Gesamtzuckermenge erheblich ab- und der Ligningehalt dem-

entsprechend zugenommen. Chemische Analysen zeigten, daß der Abbau bei *P. strobus* am starksten, bei *L. laricina* am geringsten war. In den Kiefernarten wurden hauptsachlich Glukose und Mannose abgebaut, in der Larchenart Glukose, Galactose, Arabinose und Mannose mehr als Xylose.

Résumé

Les bactéries accompagnant la deterioration de pilotis de rivière

Le *Pseudomonas fluorescens,* le *Bacillus pumilus* et une ou plusieurs espèces de Clostridium ont été le plus souvent isolés des pilotis de pin rouge et blanc et de mélèze qui avaient été immerges pendant 85 ans dans la rivière Milwaukee. Pseudomonas fluorescens, Bacillus pumilus et une ou plusieurs espèces de *Clostridium* étaient les plus frequents. Les parties externes des pilotis étaient ramollies et décolorées sur une profondeur maxima de 3,0 cm. Vues transversalement sous le microscope optique, les cellules des zones détériorées étaient amincies et leur contenu desorganisé et d'apparence granulaire. Dans les vues tangentielle ou radiale, les cellules rayonnantes étaient détruites et les tracheides érodées ou piquées. Sous microscope électronique, les faits dominants étaient la présence de creux d'érosion étroits ou de creux larges et coalescents dans les parois des tracheides. On a trouvé dans les parties externes et supérieurs des pilotis des diminutions considérables de sucres totaux et, en contrepartie, des augmentations élévées de lignine. Sur la base des analyses chimiques, la degradation était la plus forte chez le pin blanc et la plus faible chez le mélèze. Le glucose et le mannose étaient préférentiellement dégradés chez les pins tandis que chez le mélèze, le glucose, la galactose, l'arabinose et la mannose étaient plus détériorés que le xylose.

Resumen

Daños por bacterias en pilares de puentes

Se procedió a aislar bacterias de pilares de *Pinus resinosa* Ait., P. strobus L. y Larix laricina (Du Roi) K. Koch sumergidos durante 85 años en aguas del río Milwaukee, siendo *Pseudomonas fluorescens, Bacillus pumilus,* así como una o varias especies de *Clostridium,* las más frecuentes. El exterior de los pilares estaba reblandecido y decolorado hasta una profundidad maxima de tres centímetros. Estudios transversales con microscopio óptico demonstraron que, en las areas deterioradas, las células estaban adelgazadas y su interior aparecía desorganizado y de aspecto granuloso. Estudios tangenciales y radiales mostraron células destruidas y traqueidas erosionadas u horadadas. Bajo el microscopio electrónico de barrido aparecieron, predominantemente, surcos estrechos, o bien surcos concrescentes causados por la erosion en las paredes traqueidales. En las paredes exteriores de la parte superior de los pilares los azúcares totales habían disminuido considerablemente, con el consiguiente incremento del contenido de lignina. Análisis químicos demostraron que *P. strobus* había sufrido la mayor degradación, mientras que *L. laricina* acusaba la menor degradation. En las especies de pino fueron degradadas, principalmente, glucosa y manosa, y en las muestras de alerce, glucosa, galactosa, arabinosa y manosa en mayor grado que xilosa.

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