ORGANISM INTERACTIONS

In Decay and Discoloration In Beech, Birch, and Maple

by Alex L. Shigo

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Look to the Living Tree

HYMENOMYCETOUS FUNGI are the principal organisms that have been considered in past research on wood decay (Boyce 1961). Indeed few other organisms, except some of the Xylariaceae (Merrill *et al* 1965) and a few non-hymenomycetes (Savory 1954; Duncan 1960), produce enzymes capable of digesting wood. The existing information is mainly about decay by fungi of sterilized wood blocks in the laboratory.

But very little information is available about decay processes in living trees. What is known concerns mainly the final stages. Studies typically have dealt with cull following fire injuries (Toole 1959; Hepting 1935), logging wounds (Wright and Isaac 1956; Hesterberg 1957), pruning wounds (Roth 1948; Skilling 1958), and wounds caused by thinning of sprouts (Roth 1956).

Even less attention has been given to discolorations in living trees. Although many reports mention discoloration in living trees

(Nordin 1954; Hepting *et al* 1949), further research was not conducted. Discolorations have been primarily the research responsibility of the products pathologists (Scheffer and Lindgren 1940). Yet anyone who has ever cultured organisms from decayed areas in living trees has encountered many bacteria and non-hymenomycetous fungi along with hymenomycetes. Recognition of the possible importance of other wood-inhabiting organisms is increasing (Etheridge 1957; Good and Nelson 1962; Shigo 1963).

More emphasis needs to be given to the earlier stages of the decay and discoloration processes as they occur in living trees. Attempts have been made to determine the growth rate of hymenomycetes in living trees (Hirt 1949; Silverborg 1959). In these studies, only those fungi used as inoculum were considered in the results. If other organisms are involved, what are they and what role do they play in the discoloration and decay process?

Our studies indicate that interactions of many organisms besides hymenomycetes are involved in these processes. The purpose of this paper is to point out some of these interactions and to illustrate that bacteria, non-hymenomycetes, and hymenomycetes are all important in the processes that lead to decay and discoloration in beech, birch, and maple. Data from several studies are summarized.

Materials and Methods

From 1959 to 1964 investigations were conducted in New Hampshire of decay and discoloration in more than 1,000 northern hardwood trees: American beech *(Fagus grandifolia* Ehrh.); yellow birch *(Betula alleghaniensis* Britt.); paper birch *(B. papyrifera* Marsh.); sugar maple *(Acer saccharum* Marsh.); and red maple *(A. rubrum* L.). Most of the trees were more than 6 inches d.b.h., and all bore obvious infection courts, including branch stubs, stem stubs, parent stumps of sprouts, cracks, and wounds caused by logging, fire, squirrels, insects, and sapsuckers.

The trees were studied carefully both before they were cut, and later during and after dissection. The larger trees were dissected

longitudinally with a one-man chainsaw (fig. 1). More than 70,000 isolations for microorganisms were made from healthy and diseased tissues on a 2% agar medium consisting of 10 g malt extract and 2 g yeast extract/liter.

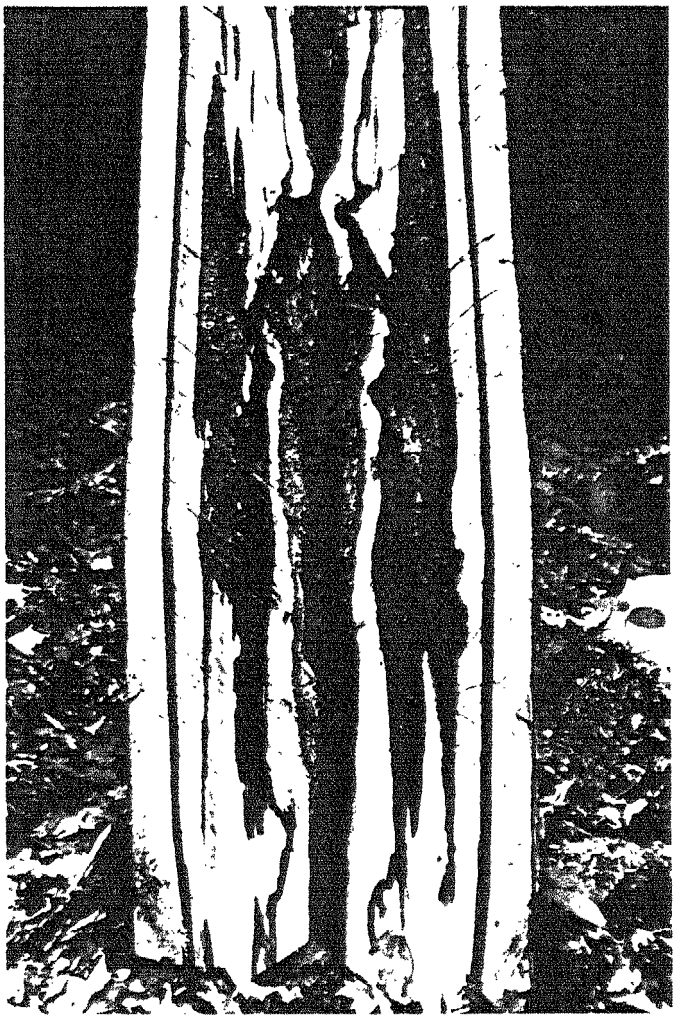

Figure 1. — Dissection of a red maple showing a column of dark decay, which yielded **F. connatus**, advancing through a column of light decay that yielded **F. igniarius**, which was surrounded by moist, dark discolored tissues that yielded bacteria and non-hymenomycetes.

Results

Data showing the associations of bacteria, non-hymenomycetes, and hymenomycetes in the decay and discoloration processes in living trees are presented in tables 1 to 8. These tables also indicate the relative frequency with which organisms were cultured from different types of infection courts.

Table 1 shows the numbers of squirrel wounds that yielded organisms. The squirrels wounded the trees from February to April during sapflow. The surfaces of the fresh wounds were colonized by many organisms. Yeasts were associated only with fresh wounds having moist surface tissues, while *Hypoxylon* spp. and *Phialophora* spp. were cultured only from older wounds with discolored tissues. These discolorations varied from green-black to bright green. Bacteria were cultured frequently from all the wounds.

Branch stubs were the principal infection courts on sprouts of *A. rubrum* (table 2). Non-hymenomycetes were associated more frequently with the pith and surrounding tissues in young stems of *A. rubrum* than with *A. saccharum* (table 3). Non-hymenomycetes also were the principal organisms cultured from *A. rubrum* sprouts over 10 years old (table 4). The principal non-hymeno-

Table 1. — Number of squirrel-caused wounds that yielded organisms

Organisms	*Acer saccharum*		*Acer rubrum*	
	Wounds less than 4 months old	Wounds over 1 year old	Wounds less than 4 months old	Wounds over 1 year old
Bacteria	29	20	20	7
Yeasts	20	0	15	0
Verticillium sp.	13	1	2	1
Cephalosporium sp.	15	6	2	2
Cladosporium sp.	5	1	1	0
Fusarium sp.	11	1	4	0
Hypoxylon spp.	0	4	0	3
Phialophora spp.	0	14	0	8
Wounds sampled	30	20	20	9

Table 2. — Principal infection courts on 261 sprouts of *A. rubrum*

Infection court	Number of sprouts	Percentage of sprouts
Branch stubs	126	48
Stump wounds	53	20
Branch stubs and stump wounds	47	18
Mechanical wounds	10	4
Sprouts clear to 8 feet above ground	25	10

Table 3. — Sprouts of *Acer* spp. approximately 1 inch in diameter and less than 15 years old that yielded organisms from the pith and surrounding tissues associated with small branch stubs

Organism	*A. rubrum*		*A. saccharum*	
	No.	%	No.	%
Bacteria	19	45	45	47
Non-hymenomycetes:	42	100	30	32
Cytospora decipiens	28	67	0	0
Phialophora spp.	17	41	16	17
Hypoxylon spp.	10	24	2	2
Trichocladium canadense	4	10	0	0
Hymenomycetes	4	10	9	9
No organisms isolated	0	0	42	44
Total, isolations	420	—	950	—
Total, sprouts sampled	42	—	95	—

mycetes cultured from discolored tissues associated with all types of infection courts on all species of northern hardwoods were *Phialophora* spp., especially *P. melinii* (Nannfeldt) Conant; *Trichocladium canadense* Hughes, and *Hypoxylon* spp., especially *H. rubiginosum* Per. ex Fries (tables 3, 4, 5, and 6). *Cytospora decipiens* Sacc. was cultured frequently, but only from discolorations in *A. rubrum* (tables 3, 4, and 5). *C. decipiens* was cultured frequently from the central column of discoloration in mature, vigorous trees with little decay. Tissues that yielded these fungi usually were red-brown to tan *(Hypoxylon* spp.), tan to green-black *(Phialophora* spp.), tan to red-brown *(T. canadense)*, and pink to pink-brown *(C. decipiens)*.

Table 4.—Red maple sprouts from 210 sampled that yielded organisms. The sprouts ranged from 10 to 75 years old

Organism	Number	Percentage
1. Bacteria	107	51
2. Non-hymenomycetes	183	87
3. *Cytospora decipiens*	85	40
4. *Phialophora* spp.	90	43
5. *Hypoxylon* spp.	52	25
6. *Trichocladium canadense*	52	25
7. Hymenomycetes	82	39
1 & 2	101	48
1 & 3	39	19
1 & 4	57	27
1 & 5	24	11
1 & 6	30	14
1 & 3 & 4	18	9
1 & 3 & 4 & 5	5	2
1 & 7	36	17
1 & 3 & 7	12	6
1 & 4 & 7	16	8

Table 5. — Numbers of trees wounded during logging that yielded organisms. The wounds ranged from 2 to 60 years old

Organism	Species and total number of trees sampled				
	Beech 82	Sugar maple 48	Red maple 29	Paper birch 46	Yellow birch 116
1. Bacteria	53	33	23	40	97
2. Non-hymenomycetes	72	45	29	41	115
3. *Phialophora* spp.	52	29	21	27	68
4. *Trichocladium canadense*	38	12	13	32	77
5. *Hypoxylon* spp.	34	13	9	7	33
6. *Nectria* spp.	12	8	5	5	17
7. *Coryne sarcoides*	4	2	1	2	7
8. *Graphium* sp.	3	2	1	2	7
9. *Cytospora decipiens*	0	0	6	0	0
10. Hymenomycetes	62	32	20	32	98
1 & 3	34	21	19	22	70
1 & 4	27	9	11	26	63
1 & 3 & 4	17	6	8	15	39
1 & 5	17	6	7	3	23
1 & 3 & 5	13	3	6	2	15
1 & 10	46	21	18	30	87
1 & 2	51	29	23	35	95
1 & 2 & 10	45	20	18	28	86

Table 6.—Frequency of organisms cultured from discolored tissues that surrounded decay columns caused by 4 hymenomycetes in 140 trees

Organism	Hymenomycetes			
	Fomes igniarius (All northern hardwoods)	*Polyporus glomeratus* (*Acer rubrum*)	*Poria obliqua* (*Betula* spp.)	*Pholiota squarrosa-adiposa* (*Betula* spp.)
NO. TREES THAT YIELDED HYMENOMYCETES				
Hymenomycetes	66	21	25	28
NO. TREES THAT YIELDED OTHER ORGANISMS				
Bacteria	63	21	24	27
Non-hymenomycetes:	56	20	22	26
Phialophora spp.	15	11	13	19
Trichocladium canadense	22	14	11	20
Hypoxylon spp.	25	10	3	4

The principal bacteria cultured were gram negative, motile, short rods that produced an abundance of slime. Several of these bacteria were identified tentatively as species in the genus *Pseudomonas*. Bacteria were cultured from tissues ranging in color from light yellow to dark tan.

The organisms associated with branch stubs, except *Hypoxylon* spp., first infected the pith and surrounding tissues. Microscopic examination of these tissues revealed phialophores producing spores, and bacteria (fig. 2). Tissues infected by bacteria and *Phialophora* spp. and *T. canadense* were darker and more moist than healthy tissues (fig. 1). Tissues infected by *C. decipiens* were bleached at first and later turned pink. Bacteria were associated intimately with all these fungi in the living trees, and wood chips used for isolations often yielded both bacteria and non-hymenomycetes (fig. 3).

Most isolations from discolored tissues associated with infection courts less than 5 years old yielded organisms. Histological examination of discolored tissues from living trees revealed hyphae in cells that were producing dark substances (fig. 4), especially ray cells. Usually discolored tissues not yielding organisms were those located nearest to healthy tissues.

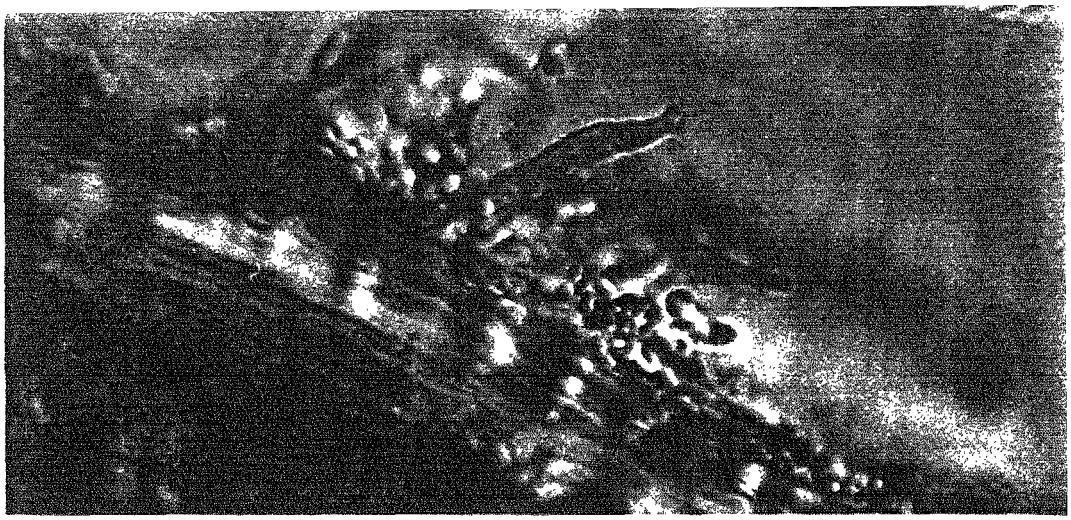

Figure 2. — Phialophores of **Phialophora** sp. producing spores in a vessel in discolored tissues from a living red maple.

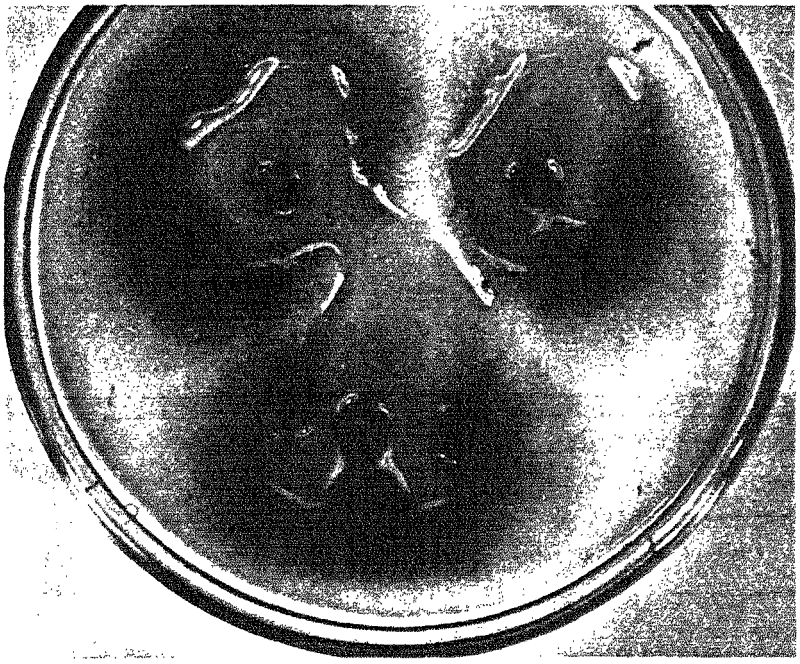

Figure 3. — Bacteria and **T. canadense** were associated intimately in discolored tissues in living trees, and they grew well together in culture.

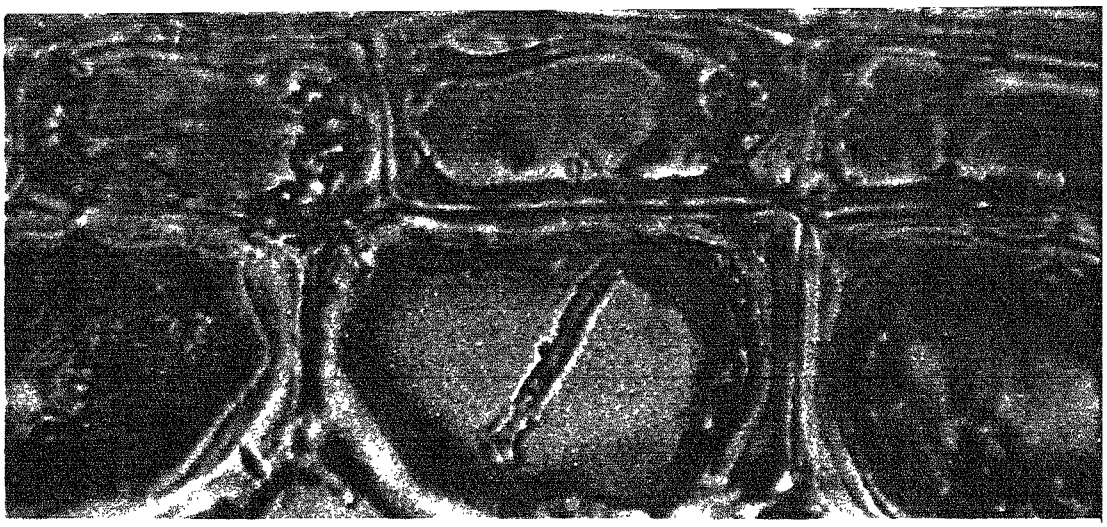

Figure 4. — Hyphae of a fungus growing through ray cells that were producing dark substances.

The rate of development of discolorations associated with a variety of infection courts on different trees varied greatly. Some large 13-year-old logging wounds on red maple trees over 10 in. d.b.h. had very little discoloration associated with them (fig. 5). In some cases, where *Nectria galligena* Bres. had infected the wounds, the discolored tissues beneath the wound surface were hard and dry. Also, some logging wounds not infected by *N. galligena* had hard, dry wound surfaces with very little associated discoloration (fig. 6). On the other hand, discoloration developed rapidly in some trees, and especially in association with branch stubs. Discolored streaks advancing from dead branch stubs often coalesced. Mature trees bearing few small infection courts contained light-colored wood from the cambium to the pith (figs. 5 and 6).

Discolored tissues formed only after an infection court was created. And — most important — wood tissues formed after the infection court was created were seldom infected. Therefore, the greatest diameter attained by the discolored column usually was the diameter of the tree when infection courts were created.

All degrees of discoloration from none to total involvement of those tissues present at the time of wounding were observed. Ob-

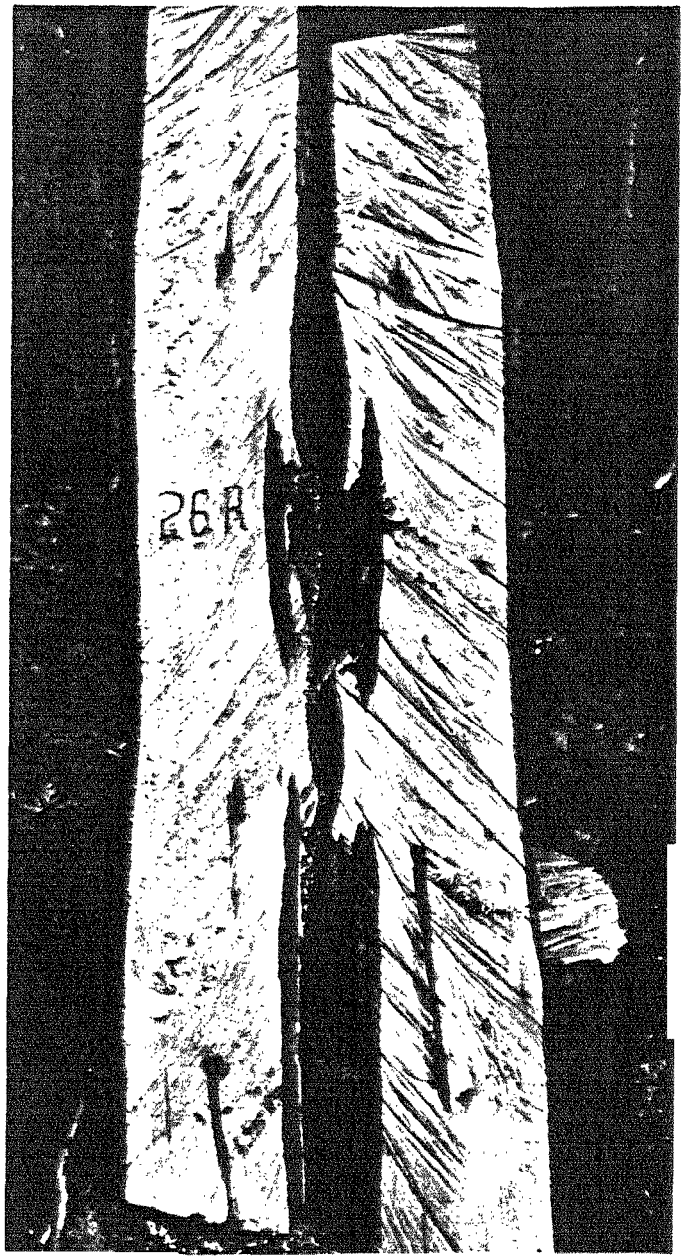

Figure 5. — Dissection of a red maple that had 2 large 13-year-old wounds. Very little discoloration was associated with the wounds. Perithecia of **N. galligena** were on the wound callus. There were few other defects in the tree, and the wood was clear from the cambium to the pith.

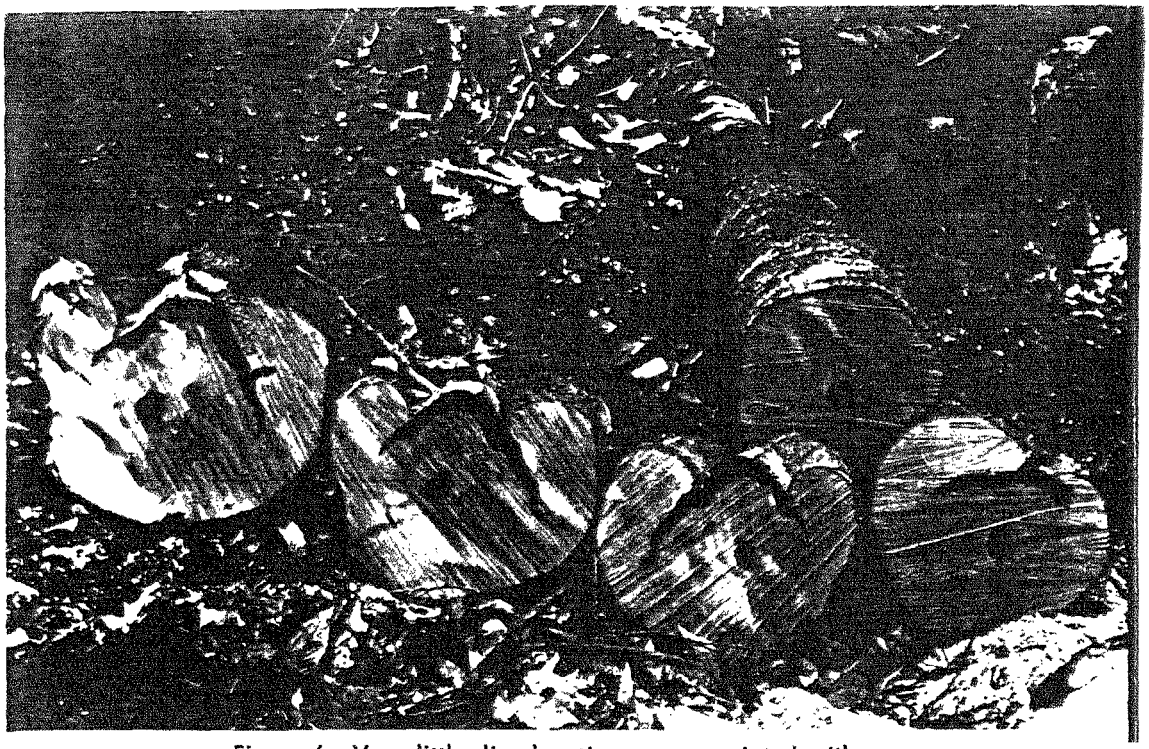

Figure 6.—Very little discoloration was associated with the hard, dry wound of this sugar maple. The branch stubs were well healed and the dark central discoloration was small.

servations and the results of statistical analyses indicated that the extent of the development depended on many factors, especially time and organisms. In the laboratory, discolorations similar to those in living trees formed in unautoclaved freshly cut stem sections inoculated with the principal non-hymenomycetes. In contrast, the controls remained clear.

Hypoxylon spp. usually were the first fungi to cause decay. These fungi were cultured frequently from a red and white mottled decay and discoloration associated with infection courts usually less than 8 years old and their stromata formed on logging wounds and branch stubs within this time. *Stereum complicatum* (Fr.) Fr. and *Polyporus versicolor* L. ex Fr. were usually the first hymenomycetes to infect logging wounds, and their sporophores were often found beside stromata of *Hypoxylon* spp. on the wounds. Stromata also occurred on wounds that bore sporo-

phores of fungi associated with more advanced decay, especially *Fomes igniarius* L. (Gill.) and *F. applanatus* (Pers. ex Wallr.) Gill.

The hymenomycetes invaded only discolored tissues already inhabited by other organisms, especially bacteria and non-hymenomycetes (tables 3, 4, and 5). The radial extent of the decay column usually was limited to this previously-formed column of discoloration (fig. 2). While the hymenomycetes were actively causing decay, the decay column was surrounded by discolored tissues that yielded either bacteria, non-hymenomycetes, or both (tables 3, 4, 5, and 6). After hymenomycetes had completely digested the discolored tissues, the walls of the hollowed column became hard and dry and yielded none of the organisms cited above. The diameters of such hollowed columns corresponded to the diameters of the discolored columns, which, in turn, corresponded to the diameters of the trees when the infection courts were created.

Exceptions to the pattern of decay and discoloration given above were encountered, especially if wounds were infected by *Poria obliqua* (Pers.) Bres. and *Polyporus glomeratus* Peck. These organisms infected the new tissues that formed around the infection courts. But, even when this occurred, the decay still was surrounded by moist discolored tissues that had a high pH, and yielded bacteria and non-hymenomycetes (table 6).

Often several hymenomycetes were cultured from the same decay column. In one tree, for example, a decay column caused by *Fomes connatus* (Weinm.) Gill. developed within the decay column caused by *F. igniarius*, which was surrounded by discolored tissues that yielded bacteria and non-hymenomycetes (fig. 1). Swollen knots formed by *P. glomeratus* occasionally bore sporophores of *F. igniarius*. Sporophores of several hymenomycetes on the same wound were common.

Organisms, especially bacteria, were cultured occasionally from the non-discolored tissues contiguous to discolorations (table 7) and from non-discolored tissues in other portions of the bole (table 8).

In culture, bacteria and non-hymenomycetes grew well together

Table 7. — Isolations that yielded bacteria from non-discolored tissues contiguous to discolorations in 27 trees

Distance in 1/16-inch units from discolored tissues that isolations were made	*Acer rubrum*		*Fagus grandifolia*		*Betula alleghaniensis*	
	Isolations made	Isolations yielding bacteria	Isolations made	Isolations yielding bacteria	Isolations made	Isolations yielding bacteria
	No.	*No.*	*No.*	*No.*	*No.*	*No.*
1	63	18	16	2	14	2
2	56	12	27	2	17	4
3	29	3	15	1	22	2
4	20	5	5	1	25	6
5	8	0	5	0	13	1
6	4	1	5	0	12	1

Table 8. — Organisms cultured from non-discolored wood

Tree	Isolations	Isolations that yielded bacteria	Isolations that yielded non-hymenomycetes
	No.	*No.*	*No.*
Fagus grandifolia	54	13	2
Acer rubrum	60	4	18
Acer saccharum	60	10	1
Betula alleghaniensis	48	1	0
Betula papyrifera	48	2	0

(fig. 7), but bacteria sometimes inhibited growth of hymenomycetes (fig. 8). *Fomes igniarius* and *P. obliqua* were not inhibited by *P. melinii* until the fungi made contact with each other. Bacteria isolated from the discolored tissues surrounding the decay caused by *F. igniarius* arrested growth of *F. igniarius* in culture even when the organisms were not growing close to each other (fig. 9). When *F. igniarius* grew alone in culture no pigment formed in the agar; but when it grew near bacteria, the agar and mycelium became dark. The bacteria isolated frequently from the discolored tissues surrounding *P. obliqua* had little effect on

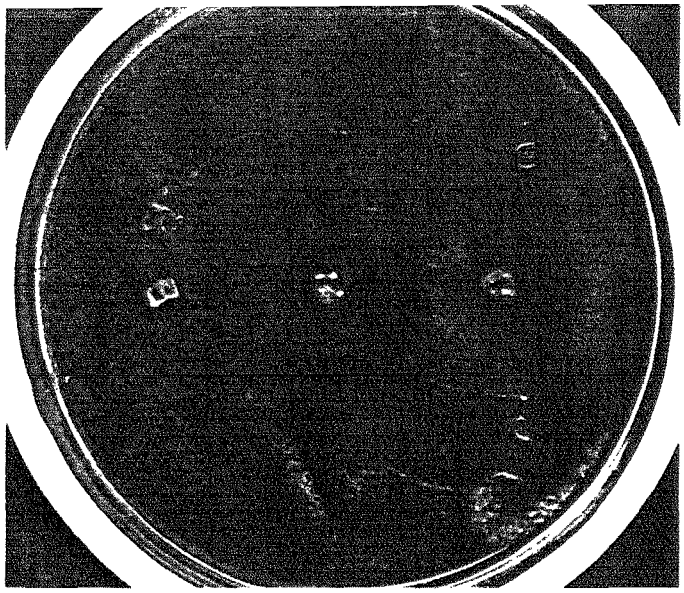

Figure 7. — Bacteria and **C. decipiens** grew well together in culture. These organisms were cultured from the same tissues.

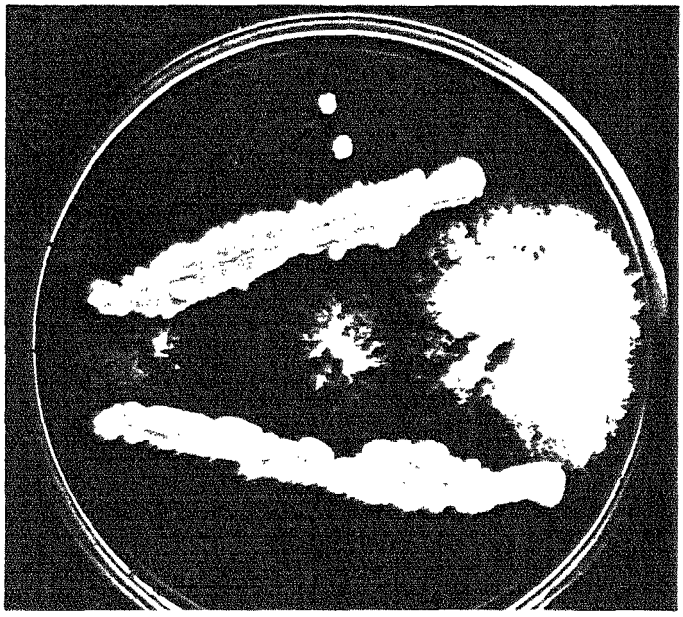

Figure 8.—Bacteria inhibited the growth of **F. igniarius** in culture. The bacterium was cultured from discolored tissues that bordered decay that yielded this fungus.

growth of the fungus. One of the most aggressive organisms in culture was *C. decipiens*. It grew well with the principal bacteria (fig. 7), and inhibited growth of many non-hymenomycetes and hymenomycetes.

Pigmentation, growth, and pH of the medium of *C. decipiens* and *P. melinii* were affected by the concentration of certain microelements in the medium (table 9). These fungi were white and the filtrate was clear in a liquid medium consisting of 5 g glucose and 1 g yeast extract/liter. But when minute amounts of manganese or calcium were added to this medium, *C. decipiens* produced a deep red pigment and *P. melinii* produced a black to green-black pigment.

Table 9. — Growth, filtrate pH, and pigmentation of *Cytospora decipiens* and *Phialophora melinii* in two liquid media: 5 g glucose and 1 g yeast extract/liter (5-1) and 5-1 plus 1 part per 100 million of manganese (5-1^{+Mn})[1] [2]

Days of growth when harvested	*Cytospora decipiens:* media				*Phialophora melinii:* media			
	5-1		5-1^{+Mn}		5-1		5-1^{+Mn}	
	mg dry wt.	*pH*	*mg dry wt.*	*pH*	*mg dry wt.*	*pH*	*mg dry wt.*	*pH*
3	4	5.4	4	5.3	5	4.9	5	4.9
4	11	4.9	12	4.8	12	4.2	12	4.2
5	20	4.3	[4]27	4.3	14	4.0	[7]16	3.9
6	23	4.1	34	4.0	15	3.8	20	3.7
7	24	4.1	[5]38	4.1	17	3.8	[8]23	3.7
10	[3]30	4.2	37	3.8	18	3.7	28	3.8
12	30	4.1	40	3.7	[6]21	3.7	36	3.9
14	35	4.0	40	3.7	25	3.7	39	4.1
17	35	4.0	39	4.4	27	3.9	47	6.1
20	35	4.2	38	5.1	38	5.0	44	6.8
24	35	5.2	40	5.5	44	6.8	40	7.5
26	35	5.8	39	5.8	41	6.6	39	7.1
28	34	5.4	37	5.9	37	7.1	38	7.4

[1] 3 flasks of each at each harvest.
[2] 5.6 initial pH of media.
[3] Filtrate clear, mycelium gray-green.
[4] Filtrate light red.
[5] Filtrate red.
[6] Mycelium and filtrate cream.
[7] Mycelium gray, filtrate clear.
[8] Mycelium green-black.

P. melinii readily utilized 7 different nitrogen sources, including potassium nitrate, but only yeast extract satisfied the growth requirements of *C. decipiens* (table 10). For *C. decipiens* the optimum pH was 3.5 with yeast extract as the nitrogen source, while *P. melinii* grew well with glutamic acid at a pH of 7.8 and with

Table 10. — Growth and pH of *Cytospora decipiens* and *Phialophora melinii* in media[1] having 7 different sources of nitrogen

Nitrogen source	*C. decipiens*			*P. melinii*		
	Greatest mycelial dry wt. attained	pH[2]	Days	Greatest mycelial dry wt. attained	pH	Days
Asparagine	36	6.1	26	51	6.0	8
Glutamic acid	34	4.8	26	59	7.8	8
Glycine	42	6.0	21	34	7.2	11
Yeast extract	85	3.5	7	62	4.5	8
Potassium nitrate	1	4.8	33	33	7.1	8
Ammonium tartrate	36	5.5	36	54	3.0	6
Ammonium nitrate	31	2.7	26	59	2.6	6
No added nitrogen	0.8	4.3	18	0.5	6.0	15

[1] Basal medium, per liter: glucose, 5 g; KH_2PO_4, 1 g; $MgSO_4 \cdot 7H_2O$, 0.5 g; Fe, 0.1 mg; Zn, 0.1 mg; Mn, 0.05 mg; Ca, 10 Mg; Thiamine, 100 ug; Biotin, 5 ug; nitrogen, equivalent to that in 1 g of Asparagine.
[2] Initial pH of all media approximately 6.

ammonium nitrate at a pH of 2.6. The growth of *C. decipiens* was jelly-like in all media except where yeast extract was used, and there was little to no pigmentation in all media. *P. melinii* formed a firm pad in all media and the mycelium was dark, especially in the medium with potassium nitrate.

Conclusion and Discussion

The wood-living bark interface is disrupted upon creation of an infection court. Mechanical wounds to stems expose wood. When branches are broken, the pith is exposed also. Certain physiological processes begin in cells following injury prior to invasion by organisms. In many plants the cellular phenols are oxidized and polymerized subsequently to polyphenols. Some of these materials are thought to cause a protective effect (Frank 1895; Zycha 1948; Jorgenson 1962). Büsgen and Münch (1931) considered this when they discussed "protective heartwood." The protective zone that formed after fire wounds may be another example (Hepting and Blaisdell 1936). Changes in air and moisture that result from wounds probably initiate the production of polyphenols (Frey-Wyssling and Bossard 1959).

It is difficult to state how far the protective processes ensue before micro-organisms become involved. The time between initiation of protective processes and arrival at infection courts of organisms capable first of competing with other organisms and second of infecting living cells may be the principal factor affecting the distructive processes. Time of year when infection courts are created may be an important factor affecting production of the protective substances. The healing of pruning wounds on oak (Roth 1948) and mechanical wounds on several hardwood species (Marshall 1931) was affected by season of year.

The fact that some mature trees heal their branch and mechanical wounds with very little associated decay and discoloration suggests that the protective barriers may be effective sometimes. On the other hand, the fact that many mature trees have extensive columns of decay and discoloration associated with infection courts suggests that the protective barriers, if formed, are not always effective. Variations in the amount of internal defect between these two extremes suggest that many different pathways may exist that lead to different types and amounts of defect.

Isolations from recent wounds yielded bacteria and many species of non-hymenomycetes. As the ages of the wounds increased, the

succession of organisms was evident. A struggle for survival on the infection courts probably occurred. Some of the organisms involved are not parasitic on trees but on other fungi. For example, on beech the parasite *Nectria coccinea* var. *faginata* Lohm. Wats. & Ayers. is attacked by the mycoparasite *Gonatorrhodiella highlei* Smith (Ayers 1941; Blyth 1949; Shigo 1964).

Many large logging wounds had very little defect related to them. *Nectria galligena* was associated with some of these. The wood behind most *Nectria* cankers is sound and is fairly resistant to decay (Brandt 1964). The fungus requires a special type of infection court (Lortie 1964); and, once it infects, apparently few other organisms can do likewise. The fungus is very pathogenic but not aggressive. This condition has been discussed by Barnett (1959).

Bacteria were cultured frequently from all ages and types of wounds. High moisture and pH were characteristic of the discolored tissues that yielded these organisms. Such zones are termed wetwood (Hartley *et al.* 1961). Duncan (1960) demonstrated that hymenomycetes grew poorly, and soft-rot fungi grew very well under such conditions. In our studies, bacteria were associated intimately with the principal non-hymenomycetes that were the first to infect the tree. Possibly hymenomycetes cannot invade until the high moisture and pH of the wood are both lowered. Hymenomycetes did not always infect discolored tissues; continued high moisture and pH may be the reason.

The principal bacteria cultured were motile, suggesting that their movement through the tissues was possible. This may account for the few isolations that yielded bacteria from non-discolored tissues contiguous to discolored tissues. But this does not explain the presence of bacteria in non-discolored tissues in trees without discolorations. The bacteria may have entered through minute wounds that healed rapidly and were not detectable when the isolations were made. The wounds made by scale insects on beech may have accounted for some of these. Regardless of how they got there, some bacteria were present in non-discolored tissues. Therefore it is possible that inoculations into supposedly organism-free wood might actually place the inoculum in the presence of

bacteria. Also, the wound made for the inoculation may stimulate the activity of the bacteria.

The discolorations in northern hardwoods are caused by processes that are initiated by wounds (Shigo 1965). Organisms caused discoloration in unautoclaved stem sections in the laboratory. In living trees organisms are associated frequently with discolorations, and the circular central discolorations found commonly in northern hardwoods are not considered true heartwood (Shigo 1965). Because organisms are associated commonly with these tissues, it is incorrect to assume that organisms inoculated into such tissues are being placed into organism-free tissues or into true heartwood. Brandt[1] (unpublished) conducted experiments similar to those of Silverborg (1959) and Hirt (1949). But, although Brandt put but one fungus into supposedly organism-free tissues, at the time of harvest he cultured bacteria and non-hymenomycetes consistently from the discolored tissues surrounding the decay tissues.

Most non-hymenomycetes and bacteria grew well together in culture, but often these organisms inhibited growth of hymenomycetes. A similar association in living trees may be operating, which would explain why decay is limited by discoloration. Indeed, the exception to this, *P. obliqua,* infected newly formed tissues, and grew well with bacteria in culture. In culture, bacteria stimulated pigmentation by *F. igniarius.* The dark lines associated with *F. igniarius* in the living tree may result from a similar association.

Trees growing on different parent soils could contain different amounts of micro-elements in their wood. This was pointed out by Ellis (1959) for grand fir growing on the western and eastern slopes of the Cascades. The concentration of micro-elements in the medium affected growth and pigmentation of *P. melinii* and *C. decipiens.* Possibly trees growing on different parent soils could be affected differently by these fungi.

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[1] R. W. Brandt conducted these studies while a member of the Northeastern Forest Experiment Station, Forest Service, U. S. Department of Agriculture. Brandt is now Assistant Director of Forest Disease Research, U. S. Forest Service, Washington, D. C.

P. melinii was cultured from discolored tissues of all northern hardwoods, while *C. decipiens* was cultured only from discolored tissues of *A. rubrum*. The selectivity of *C. decipiens* may be due to its exacting requirements for certain nitrogen sources that are available only in *A. rubrum*, and particularly nitrogen sources in those tissues around the pith. *C. decipiens* inhibited the growth of many other organisms in culture. This may explain why it was cultured most frequently from trees with little decay caused by other fungi. The central pink discoloration that yielded *C. decipiens* was common in trees classed as vigorous.

In our studies bacteria and non-hymenomycetes invaded first. When hymenomycetes invaded later they always grew through the discolored tissues. These results indicate that bacteria, non-hymenomycetes, and hymenomycetes must all be considered in the processes that lead to cell destruction in living trees. Discoloration can exist without decay; but decay is always associated with discoloration. Therefore, to understand decay we must also understand discoloration.

Summary

Physiological and ecological studies were conducted in New Hampshire, U. S. A., on factors affecting decay and discoloration associated with logging wounds, branch stubs, and other infection courts in *Acer saccharum*, *A. rubrum*, *Betula alleghaniensis*, *B. papyrifera*, and *Fagus grandifolia*. More than 1,000 trees were examined. Each tree was studied immediately before felling, and after, when it was dissected longitudinally with a chainsaw.

The organisms selected for more intensive study were those cultured most frequently from more than 70,000 isolations: non-hymenomycetes, *Phialophora* spp., *Hypoxylon* spp., *Trichocladium canadense*, and *Cytospora decipiens*; hymenomycetes, *Poria obliqua*, *Polyporus glomeratus*, and *Fomes igniarius*; and bacteria, *Pseudomonas* spp.

Once wood tissues were exposed, a succession of events began that involved abiotic and biotic factors. Bacteria and non-hymenomycetes were associated frequently with discolorations, but all

discolored tissues did not yield organisms. However, some non-discolored tissues yielded organisms. Hymenomycetes invaded only discolored tissues. The rate and extent of decay and discoloration depended primarily on types of infection courts, time, and organisms. Decay and discoloration seldom affected wood tissues that formed after an infection court was created. A common exception to this was caused by *P. obliqua.* Discolorations initiated by wounds were not considered heartwood. Cultural studies indicated that bacteria stimulated pigmentation of some fungi. Bacteria inhibited growth of many hymenomycetes. Pigmentation of some fungi was greatly affected by the concentrations of manganese and calcium in the medium.

Results of these studies indicated that bacteria, non-hymenomycetes, and hymenomycetes must all be considered in the processes that lead to discoloration and decay in living trees.

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