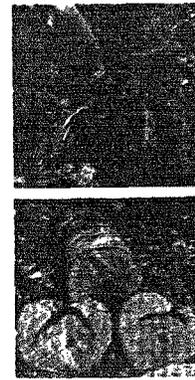


by Alex L. Shigo



**DECAY** *and*  
**DISCOLORATION**  
*following logging wounds*  
*on northern hardwoods*

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**Attention  
to Quality**

**G**ROWING high-quality timber is one purpose of all forest managers. More and more attention has been paid to quality in recent years. And as emphasis on quality has increased, forest managers have felt a need for more information about any management activity that affects the quality of individual trees.

What can happen to a tree that will affect its quality? Logging, for one thing. The trend in logging today is toward bigger machines and fewer men, and toward shorter intervals between timber harvests. This leads to greater productivity, but it brings with it new problems. One is the increase of logging damage to the trees that are left.

This trend toward more serious logging damage was recognized by Fobes (1958), who listed 79 studies on this subject. He considered as logging damage any disturbance by logging that reduced the capacity of the area to produce a desirable future crop. He classed damage as either *primary* — immediately after logging;

or *secondary* — years after logging. Most of the studies that Fobes cited were concerned mainly with machines, methods, and above-ground damage. Olson (1952) pointed out the importance of injury to roots by heavy equipment.

Even though diseases that follow logging injuries are principal causes for low quality among trees, only a few studies have dealt with the pathology of logging wounds. Decay associated with logging wounds has been studied in the West on conifers (Parker and Johnson 1960; Wright *et al.* 1947; Wright and Isaac 1956) and in the Lake States on sugar maple and yellow birch (Hesterberg 1957; Benzie *et al.* 1963). In the South, where fire is the major cause of wounds, decay studies have concentrated on fire scars as infection courts (Hepting 1935 and 1941; Toole 1959). Because decay is the most important defect of trees in the South and West, little attention has been given to other defects — including discolorations.

In northern hardwoods — unlike most other hardwoods — the white wood is usually the most valuable part. For these species — beech, birch, and maple — discolorations are often as degrading as decays. The few studies on logging wounds of these northern hardwoods have dealt primarily with decay and have given only slight attention to discoloration (Hesterberg 1957; Benzie *et al.* 1963). A few studies have been made of the discoloration that follows wounding by increment borers (Hepting *et al.* 1949; Campbell 1939; Lorenz 1944). These studies revealed that discoloration formed much more rapidly in northern hardwoods than in other species studied. Most of the research on discoloration has been done by pathologists studying wood products (Scheffer and Lindgren 1940).

Although the importance of fungi in decay processes cannot be disputed (Boyce 1961), the same cannot be said for discoloration processes in living trees. Thus, while Lorenz (1944) indicated that micro-organisms were not important in discoloring processes, Good and Nelson (1951) stated that most discolorations in maple were caused by fungi. Possibly both views are partially correct, for while beginning stages may not involve organisms, later phases certainly do (Shigo 1965a). The effects on discoloration of

changes in moisture and air following tissue injury have been investigated (Zycha 1948).

In addition to the action of fungi and of changes in air and moisture, other factors, including the action of bacteria, must also be considered (Shigo 1963). Although wood-inhabiting bacteria have been studied in some trees (Hartley *et al.* 1961), their possible role in decay and discoloration processes has been suggested only recently (Shigo 1963). The close association of bacteria, non-Hymenomyces, and Hymenomyces in living trees has been pointed out (Good and Nelson 1962; Shigo 1963).

Because these different organisms are associated commonly in living northern hardwood trees, each must be included in a study of the destructive processes that follow wounding. The purposes of this paper are to report and discuss results of studies on decay and discoloration in northern hardwoods following logging wounds.

## **Materials and Methods**

From 1959 to 1964, 331 northern hardwood trees (sugar maple, *Acer saccharum* Marsh.; red maple, *A. rubrum* L.; yellow birch, *Betula alleghaniensis* Britt.; paper birch, *B. papyrifera* Marsh.; American beech, *Fagus grandifolia* Ehrh.; and white ash, *Fraxinus americana* L.) growing on the White Mountain National Forest in New Hampshire were felled, dissected, and studied. The trees ranged from 6 to 26 inches in diameter at breast height (d.b.h.) and bore logging wounds inflicted 2 to 60 years previously. Logging records and old skid trails and landings aided in locating wounded trees.

Before a tree was cut, the following data were recorded: date; tree number; tree species; location; notes on site; vigor; d.b.h.; crown class; notes on injuries to roots and branches; the number, position, and condition of branch stubs; seams and open cracks; fungi fruiting on the wound surface and elsewhere on the tree; number and position of wounds; greatest length and width of wound; severity of wound (1. bark scraped, 2. wood scraped, 3. wood broken to depth of 0.5 inches, and 4. wood broken to a

depth of over 0.5 inch); healing rate; circumference of tree at wound; percentage of circumference wounded; cause of wound (skidding, felling); and general remarks (insects in tree and in wound face, sapsucker injury, porcupine injury).

The tree was then felled with a chainsaw and dissected longitudinally through the pith as described by Shigo (1964).

Immediately after dissection the following data were recorded: extent of decay and discoloration above and below the wound; volume of decay and discoloration (greatest length, width, and breadth); notes on type of decay and discoloration; age of wound and tree; when present, measurements of the central dark column throughout the tree; merchantable height; notes on branch stubs, other defects, insect injury, and the like.

On some trees, relative moisture content of the clear wood, discolored wood, and decay were taken with a moisture meter (Delmhorst Model RC-1, not accurate above fiber-saturation point). The Truog pH indicator (Hartley *et al.* 1961) was used to measure pH gradients across decayed, discolored, and clear wood.

The wood samples taken for isolation of organisms were approximately 12 x 6 x 4 inches and contained clear wood as well as defects. At least four samples were collected from the immediate wound area and from regions above and below the wound.

In the laboratory, samples were washed in 0.5-percent sodium hypochlorite (Clorox) solutions: 10 minutes in one bucket, and the same time in a second bucket. The samples were then split open with a flamed axe. Small chips of wood were removed aseptically with a gouge from numerous spots on the exposed inner surfaces and placed in an agar medium in petri dishes. A 2-percent agar medium containing 10 g malt extract and 2 g yeast extract per liter of distilled water was used. A total of 34,735 chips were examined.

Assistance in identifying micro-organisms was given by bacteriologists at the University of Connecticut, and by mycologists at the Forest Service Disease Laboratory in Laurel, Md. (Hymenomyces). Species of *Phialophora* were identified by C. J. K. Wang, N. Y. State University College of Forestry at Syracuse; and S. J. Hughes, Department of Agriculture, Ottawa, Canada.

## Results

### Observations in Logged Areas

Observations of areas logged 1 month to 60 years previously indicated that many of the injuries had been apparent at the time of logging but had almost disappeared within a few years.

The shallow and often exposed roots of yellow and paper birch trees were especially vulnerable to injury (fig. 1). The bases of trees bordering bends in trails were injured repeatedly (fig. 2). Trees with such root and basal injuries often died within a few years (fig. 2). Living but weakened trees were attacked by many weakly parasitic organisms and insects, and were thus rendered even more defective. Root and bole injuries, coupled with changes in stand environment resulting from logging, were enough to seriously weaken and sometimes kill trees. This type of after-logging decadence was common (figs. 2 and 3).

The number of injured trees present varied from one logged area to another. Half of one area studied had few injured trees,



Figure 1.—Root and basal injury to a yellow birch tree bordering a skid trail. A common type of logging wound.

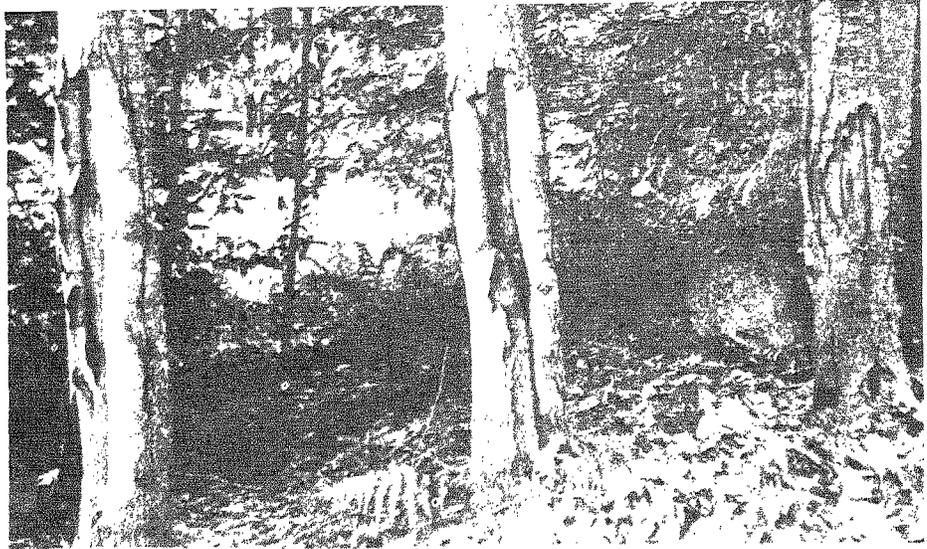


Figure 2.—Injuries on sugar maples bordering a bend on a skid trail. The tree on the right died 8 years after the roots and bole were injured.

Figure 3.—Felling injuries on two yellow birch trees. The tree on the right died and was invaded by decay fungi within 8 years after injury.

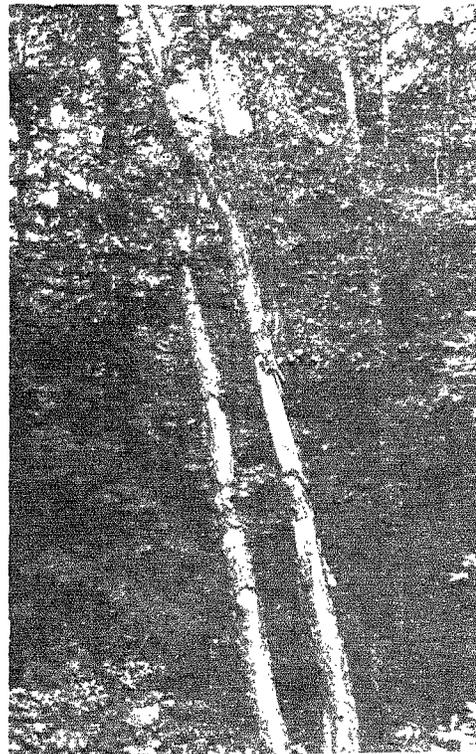


Figure 4.—A 60-year-old wound on a yellow birch tree 160 years old and 26 inches in diameter (d.b.h.). Sporophores of *Fomes ignarius* var. *laevigatus* are on the wound face.

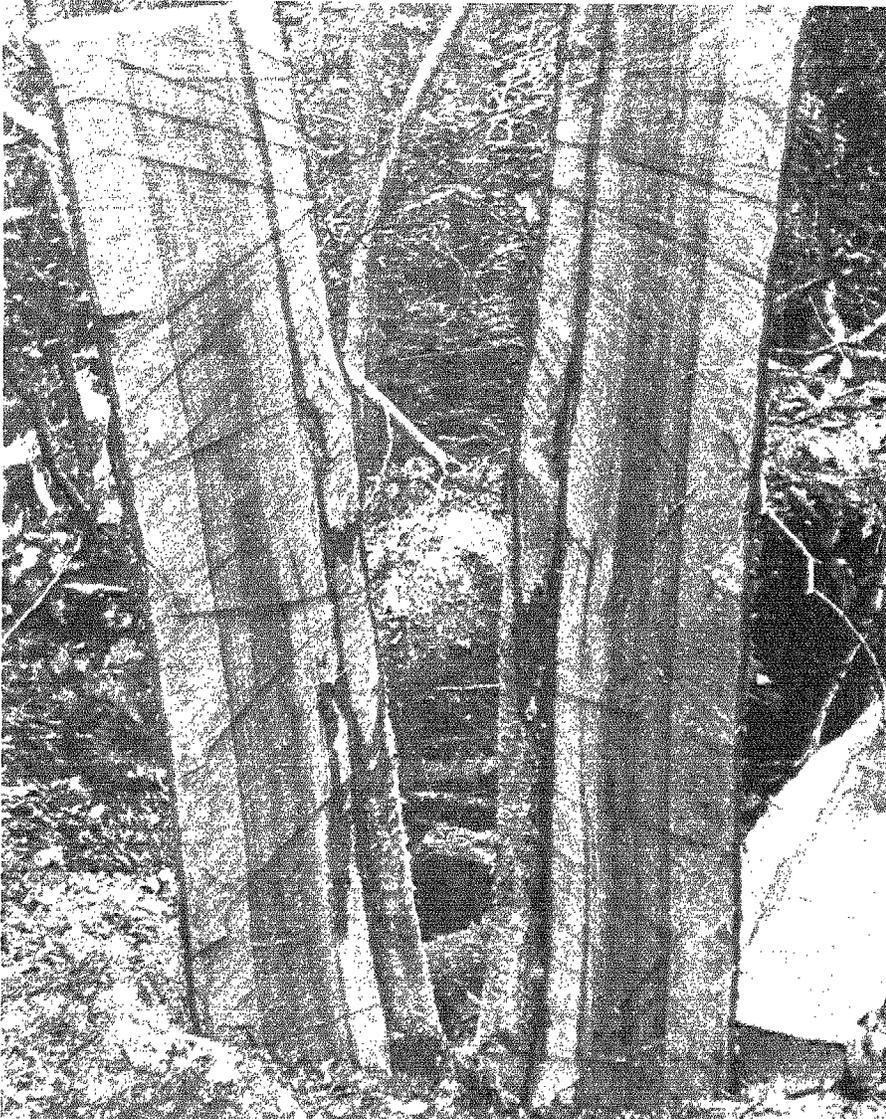


Figure 5.—Dissection of the first 8-foot bolt of the tree shown in figure 4. Decay and discoloration was limited to the wood tissues present when the tree was wounded. More wood formed on the side of the tree opposite the wound. On the wound side, a dark discoloration in the annual ring that formed when the tree was wounded was the boundary between tissues formed before and after wounding. The discoloration extended far above the wound.

while the other half had many, even though topography and stand composition were similar. The local forest ranger said that although logs from both areas were skidded with tractors, two operators were involved and one was more careless than the other.

### **Dissection of Injured Trees**

As the longitudinal dissections (figs. 4 and 5) exposed internal tissues to air, various changes occurred in the wood. The columns of discolored wood enlarged as liquids oozed from cut ends; and the colors of both clear and discolored wood changed, becoming darker in some areas with wetting and lighter in others with drying. In maples, the common black-green discoloration often intensified around the edges. Zone lines, vivid at first, faded upon exposure. In birch, moist dark-pink to tan margins of discoloration surrounding decay dried more slowly than other tissues and often became hard and white. Mottling resulted when moist pockets remained in the discolored zones.

In pH, clear and decayed wood were similar (4.5 to 5.5), while pH of discolored wood varied from 5.0 to 8.5. The highest pH readings were obtained from the narrow zones of moist discoloration immediately surrounding decay. The moisture content of these discolored tissues was higher than that of the clear wood.

### **The Wound**

The appearance of the wound face was the best indicator of the extent of internal defects. Dark wound faces indicated more defect than light ones (figs. 6, 7, 8, and 9). The dark color was due to decaying wood, minute fungus fruiting bodies, dark mycelium and spores, and bits of soil and debris. Dark faces usually occurred on wounds that had deep cuts (figs. 6 and 7) and on wounds that had been shaded from the sun.

Dry, white-faced wounds indicated little decay and discoloration, even if large and old (figs. 8 and 9). Such wound faces usually formed when wounds were exposed to sunlight or did not penetrate the wood deeply. In one location (logged 13 years previously), several red maple trees had white-faced wounds. The callus tissue around the wounds of some of these supported perithecia of *Nectria galligena* Bres. Dull tan-colored stains occurred

Figure 6.—An 8-year-old wound on yellow birch 106Y. The wound face was dark and had deep cuts in it. Sporophores of *Polyporus versicolor* were abundant on the wound.



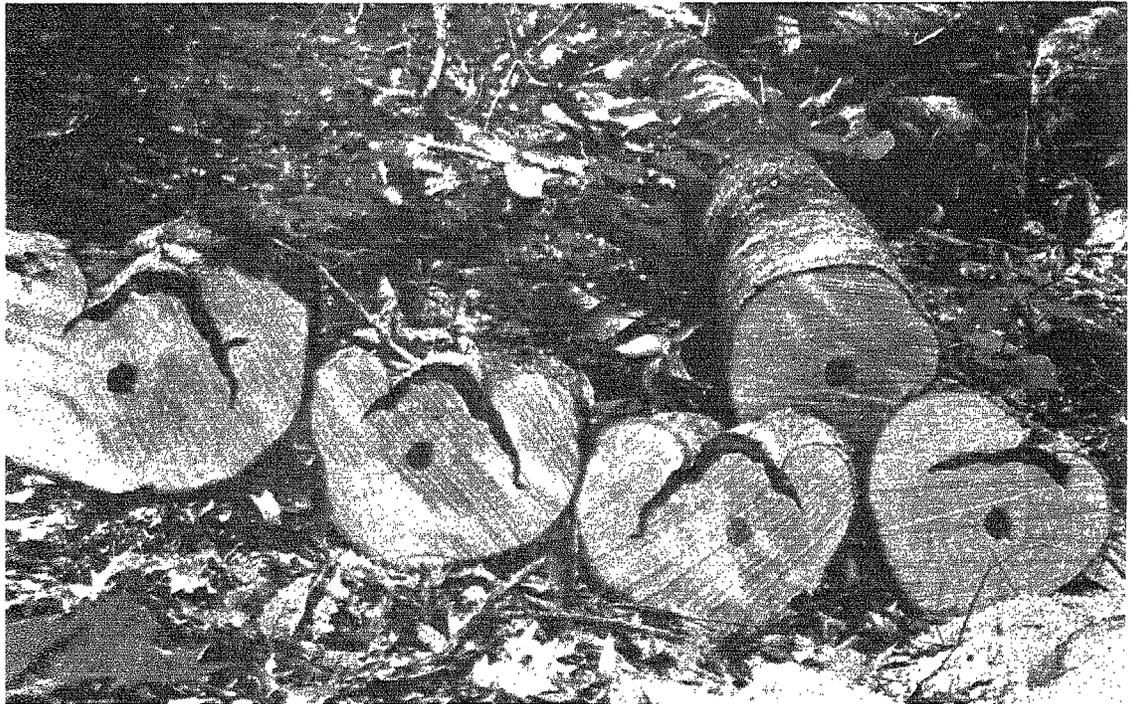
Figure 7.—Dissection of yellow birch 106Y. Decay and discoloration from the wound and from branch stubs joined. The dark core in the upper bolt was limited to tissues formed when the branches died.





Figure 8.—A white-faced wound on a sugar maple. Dark tan stains are on the wound face.

Figure 9.—Dissection of the tree shown in figure 8. Very little decay and discoloration was associated with the wound.



on many white-faced wounds (fig. 8). Other factors, including insects, affected the decay and discoloration that developed behind wounds.

When insects bored in wounds, the discoloration or decay advanced at least to the depth of the holes. Insects commonly infested new wounds within a year, and attack continued until hundreds of holes were bored in some wounds. Ants commonly infested wounds on beech, but usually confined their activities to areas already discolored or decayed.

Birches particularly were infested by ambrosia beetles after the trees had been weakened by severe wounding. Insect attacks resulted in several different internal patterns. A U-shaped pattern revealed that some beetles attacked trees and then left them within a short period during the year of wounding (fig. 10). When the trees were attacked a year or more after wounding, the ambrosia



Figure 10.—Cross-sections of a yellow birch at 4 and 16 feet above the basal wound. The U-shaped discolorations were caused by insects that attacked the tree after it was wounded. All the tissues present when the tree was wounded by thousands of insects all around the bole were discolored slightly pink, but no organisms were associated with the slight discoloration. The wedge-shaped column of discoloration and decay advancing from the logging wound joined the central column of discoloration. Organisms were associated with these defects.

beetles bored approximately  $\frac{1}{4}$  to 1 inch straight into the trees. These holes resembled many minute increment-borer wounds. The discoloration patterns around holes were similar to those around increment-borer wounds (Hepting *et al.* 1949). Small discrete areas of discoloration often coalesced to form larger ones, with ends pointed outward toward the cambium (fig. 11).

Several sugar maple trees had been attacked by the sugar maple borer, *Glycobius speciosus* (Say), the same year they were wounded during logging (figs. 12 and 13). This may have been an indirect effect of logging rather than wounding, because these beetles often attack trees in opened stands.



Figure 11.—Ambrosia beetles attacked this paper birch after it was wounded at the base. The tissues formed after the insects attacked were not discolored. The discolorations from the insect wounds coalesced with each other and with the central discolored column in the tree. Organisms were associated with the discolorations.

Figure 13.—Dissection of the tree shown in figure 12. The sugar maple borer attacked the same year the tree was wounded. Tissues formed after both wounds were inflicted remained clear. Discolored wood that yielded bacteria and non-Hymenomyces surrounded the decay column.

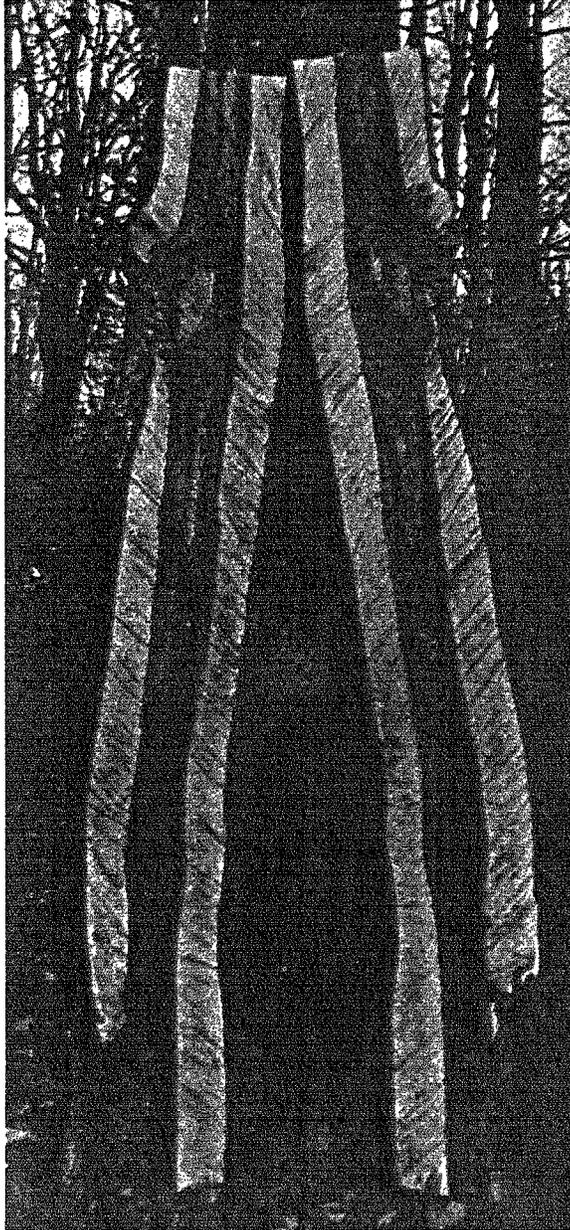


Figure 12.—The basal wound on this sugar maple bears a sporophore of *Fomes connatus*. The large wound above was caused by a sugar maple borer.



Cracks formed on some trees above and below logging wounds. This was most noticeable on paper birch trees because such cracks and wounds turned rough and dark in contrast to the thin white bark (fig. 14). These cracks increased greatly the defects associated with wounds. Callus tissue that developed around such cracks and wounds was less extensive in beech than in other species.

In beech, several factors influenced the effects of wounds. One was the beech bark disease. The beech scale, *Cryptococcus fagi* (Baer.), infested wound callus tissues and *Nectria* spp., infected through the insect wounds. To complicate this further, another scale insect, tentatively identified as *Xylococcus betulae* (Perg.) Morrison, often attacked callus tissues too. These organisms made it difficult to assess the severity of the original wound.

Beech differed from other species in that its root collar was highly resistant to decay. Internal defects usually were constricted

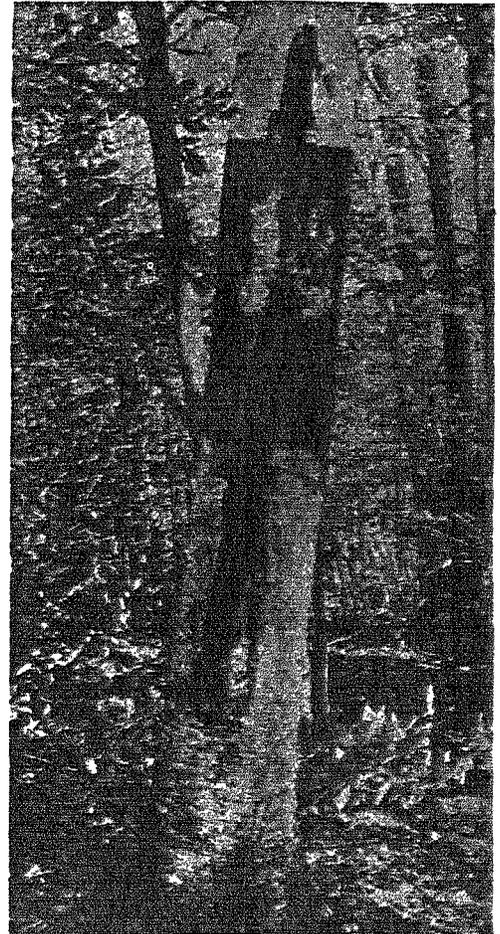


Figure 14.—Cracks formed above and below the wound on this paper birch. The bark became rough and dark around the cracks. This was not the result of mechanical bark stripping that is common along roadsides.



Figure 15.—The column of defect in this beech tree narrowed abruptly as it approached the base, but the column was large above the wound as it joined the central column formed after branches died.

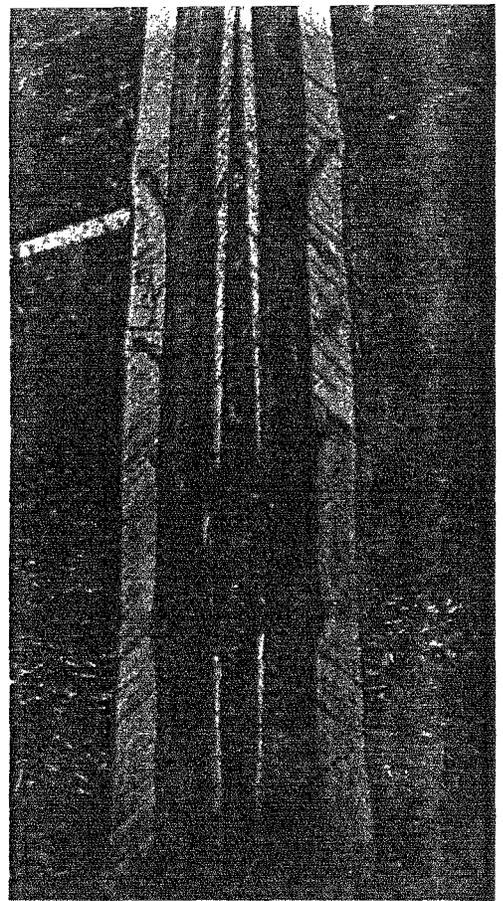
abruptly near the root collar (fig. 15). Two common exceptions were basal wounds infected by *Fomes applanatus* (Pers. ex Wallr.) Gill. and *Polyporus versicolor* L. ex Fr. These fungi were aggressive invaders of butts and roots.

The sides of trees above and below old wounds usually were flattened. The extent of these areas depended on the size, age, and severity of the wounds. Internal defects associated with wounds usually were confined to the wounded sides of trees (fig. 16).

#### **Patterns of Decay and Discoloration**

The amounts and types of decay and discoloration within nearby trees of the same species having similar wounds often differed markedly (figs. 17 and 18). Extensive decay and discoloration was associated with wounds on trees that already had defective

Figure 16.—This yellow birch was wounded 3 feet above the base, and the discoloration that followed was wedge-shaped and confined to the side of the tree that was wounded. Organisms were associated with the discoloration.



centers, and especially when such previously formed defects were associated with branch stubs. On the other hand, little additional defect developed if the wounded trees had but little previous defect (fig. 18). Decay and discoloration initiated at logging wounds appeared to spread toward similar defects already present in the trees. Thus the presence of prior defects apparently influenced the rate of formation of additional defects from logging wounds.

It was often difficult to separate the effects of logging wounds from those of branch stubs when both injuries occurred on the same tree (fig. 7). This was true especially of older wounds on older trees. Because decay followed discoloration and advanced more slowly, separate decay columns that once were isolated did not coalesce as readily as did separate discoloration columns.

With few exceptions, *tissues formed in the years after trees were wounded did not become discolored or decayed* (figs. 5, 13, and 19). While this means that the maximum diameter of discolored cores was limited by the diameter of the tree when its branches died or when wounds were inflicted, it does not mean that *all* tissues present when wounds were inflicted ultimately would be discolored or decayed. On the contrary, the extent to which such tissues were affected was determined principally by wound age, severity, and size.

For example, the presence of several large, severe wounds about the base of a tree usually indicated the presence of circular central cores of defect (figs. 5, 13, and 19). Yet, if these were large white-faced wounds, little defect was associated with them and no circular defect core developed (fig. 9). But upon close examination of even these wounds with relatively little associated defect, a faint discoloration column was noticeable for several feet above and below the wound in all wood tissues present when the wounds were inflicted. These tissues yielded no organisms. In birches and maples a slight pink discoloration was common that faded quickly after dissection and was difficult to see a few hours later. The annual ring formed the year of wounding became darkened, and this served to indicate the date of wounding (fig. 5).

In radial sections the most common shape of discoloration was a wedge with its point near the pith (fig. 10). This configuration, common in wounded trees that had little or no other previous internal defects, affected more tissues than did the thin bands associated with white-faced wounds (fig. 9), and less tissues than did the continuous central columns associated with severe wounds (fig. 19). But, if internal defects were present when trees were wounded, shapes of defect columns varied. For example, thin bands of discoloration behind white-faced wounds often joined the other defects to form jagged patterns, and wedge-shaped defects formed blunt-shaped defects as they joined central columns (fig. 10).

The upper ends of most decay columns in all species examined ended abruptly. Even extensive columns often had rounded tops (fig. 18). A few short sections of hollowed centers were seen in trees wounded severely on opposite sides (fig. 19).

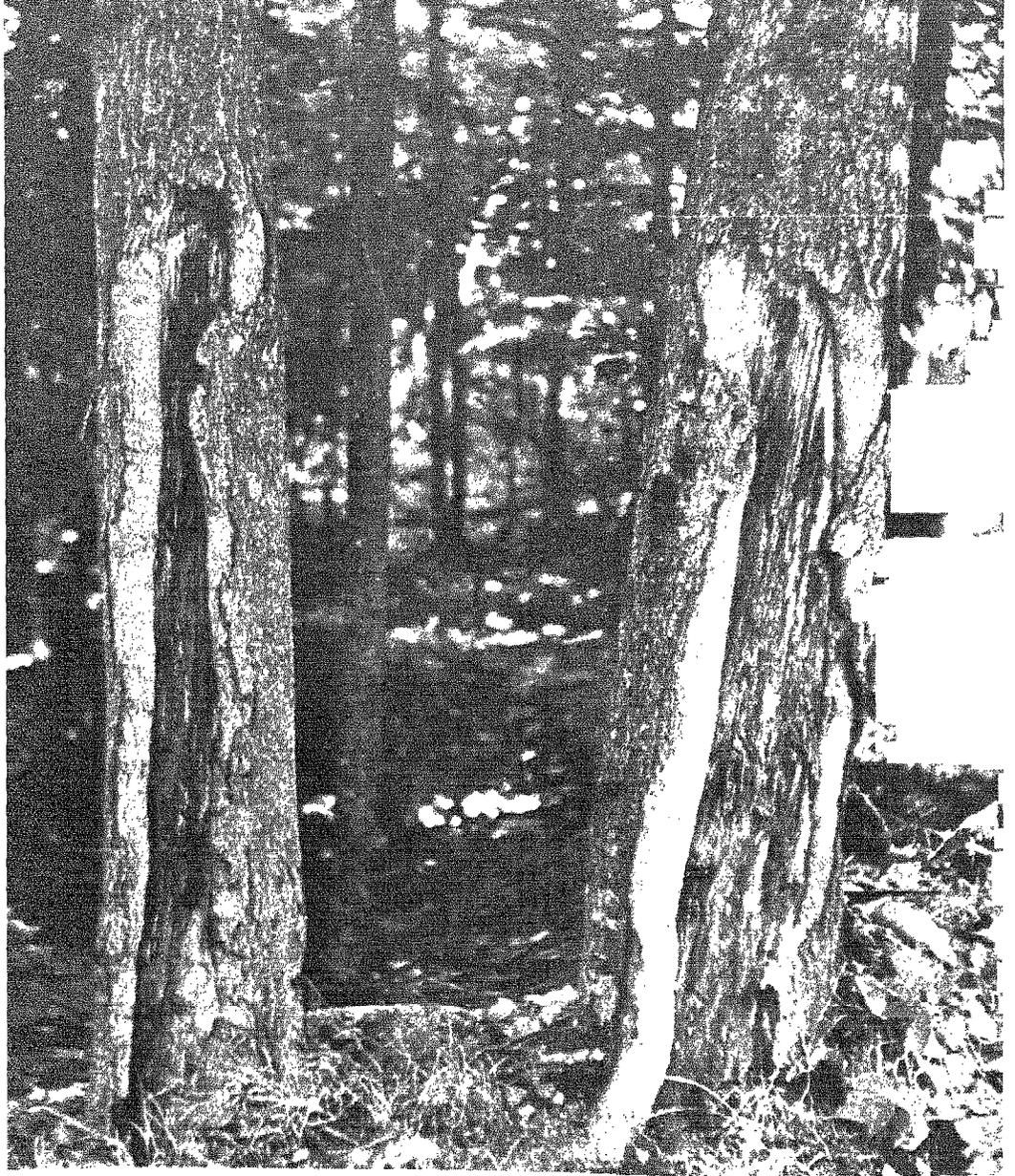


Figure 17.—Two sugar maple trees approximately the same size and age, both with similar 8-year-old wounds.

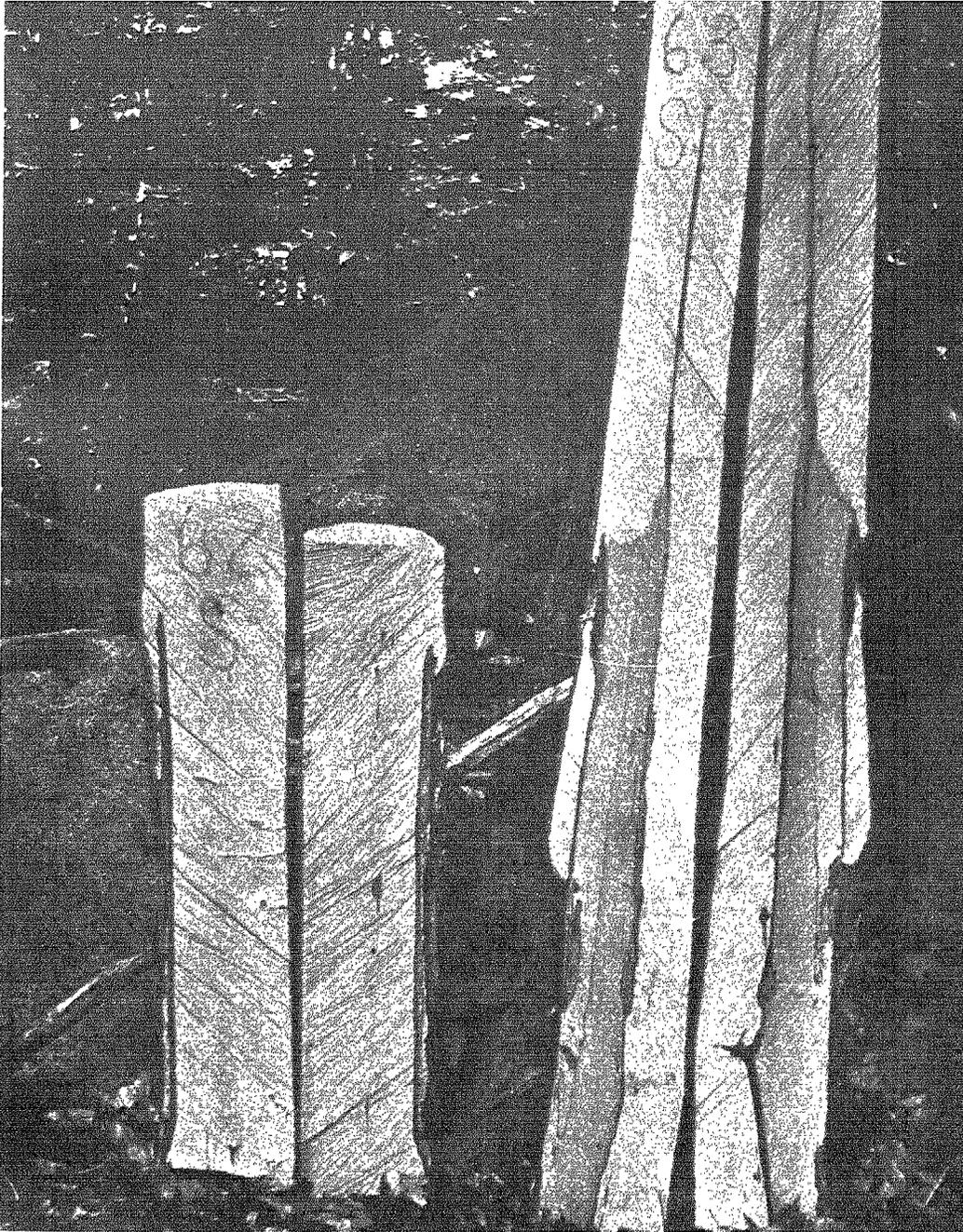


Figure 18.—Dissection of trees shown in figure 17. The tree on the left had very little defect associated with the wound, while the other tree had extensive decay. Tree 62S had few defects in it when it was wounded, while 63S had defects in it from a low branch stub. The decay ended abruptly above the wound in 63S.

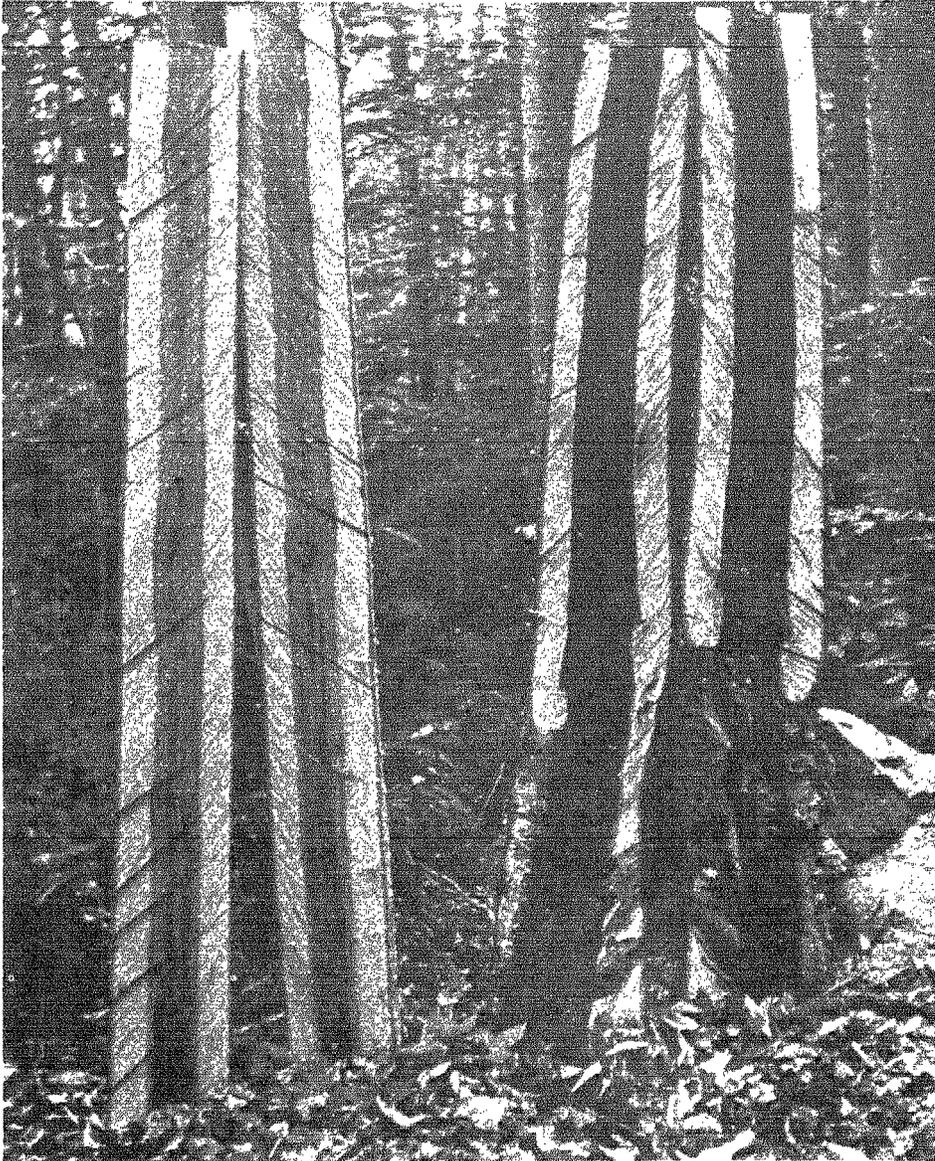


Figure 19.—Two 50-year-old wounds on opposite sides of the base on a 100-year-old paper birch. The tissues present when the wounds were inflicted were digested completely in the first 8-foot section. The decay advanced through the discoloration and the discoloration was limited to those tissues formed when the tree was wounded.

Most defects already present had advanced from branch stubs (fig. 7). Dark discolored cores in many trees were caused by processes initiated when branches died (fig. 7). Discolored cores in northern hardwoods did not form independent of branch stubs or other wounds, and unwounded trees that bore no large branch stubs had white wood throughout (fig. 18).

When wounds occurred or when branches died at about the same time, the resultant discolored core was contained within the tissues bordered by the same growth ring (figs. 5 and 13). But when such events occurred at different times, discoloration and decay from different defects coalesced to form defect columns with uneven margins.

Several decay fungi disrupted the usual pattern of decay and discoloration. Once established in birches, *Poria obliqua* (Pers.) Bres. became weakly parasitic and invaded tissues that formed around the infection court. *Fomes igniarius* (L. ex Fries) Kickx sometimes invaded similar tissues on beech and sometimes on maples. Fungi growing into roots from basal wounds also disrupted the usual defect pattern in the stem.

#### **Organisms Associated with Decay and Discoloration**

Fruiting bodies of fungi, especially non-Hymenomycetes, were common on wound faces. The most common fungus to fruit on wound faces 3 years old or older was *Hypoxylon rubiginosum* Pers. ex Fries (fig. 20). The *Acrostaphylus* imperfect stages of five *Hypoxylon* spp. were isolated from discoloration and decay associated with wounds. Again the most common species was *H. rubiginosum*. It was isolated from tissues discolored red-brown and from white pockets of decay in all species. Stromata were often near fruiting bodies of other fungi on wound faces, especially those of *Stereum complicatum* (Fr.) Fr. and *Polyporus versicolor*. These Basidiomycetes formed fruiting bodies readily on wounds that were less than 10 years old (fig. 6). *H. rubiginosum* frequently was isolated together with bacteria, but this association was not so common with *H. rubiginosum* as it was with some other non-Hymenomycetes. Many stromata were scraped and scratched as if insects had attempted to eat them.

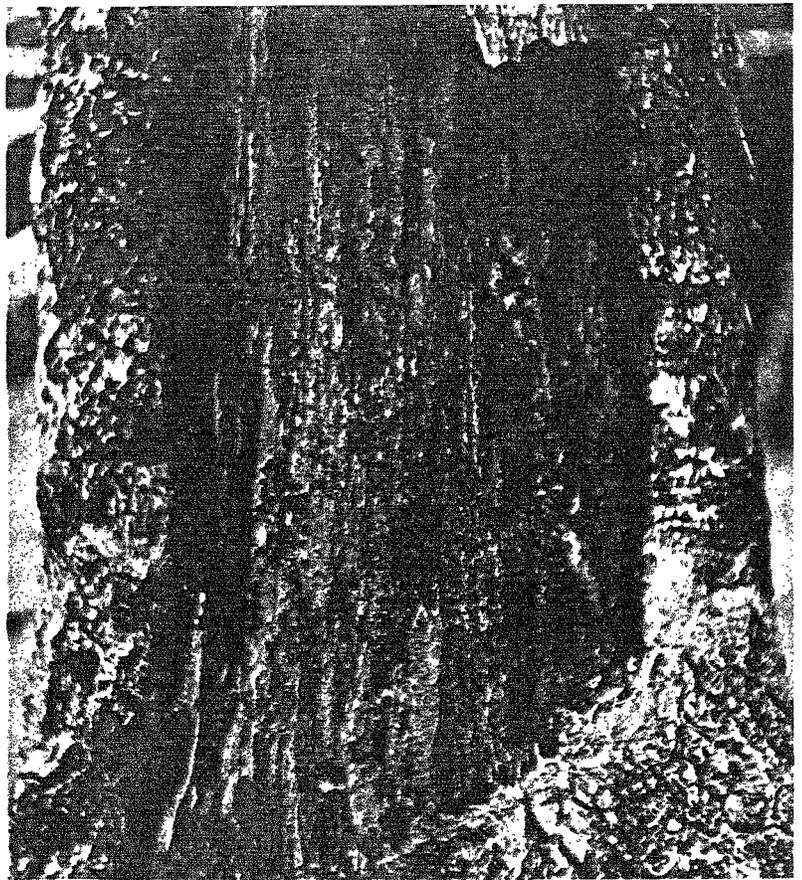


Figure 20.—Stromata of *Hypoxylon rubiginosum* on a basal wound on a beech tree. Both globose and effused forms are present.

Another member of the Xylariaceae, *Daldinia concentrica* (Bolt. ex Fr.) Ces. and deN., formed stromata on wound faces and frequently in crevices formed in the callus tissues around the edges of wounds. Decay and discoloration caused by this fungus were similar to those caused by *H. rubiginosum*. Stromata formed most frequently on sugar maple and yellow birch wounds that were over 4 years old. It was an aggressive early invader of wounds and of dead stems and branches, especially those of yellow birch. In the laboratory, stromata formed on debarked, unautoclaved small stems of red maple in jars. No perithecia formed, but the imperfect *Acrostaphylus* stage produced an abundance of spores on the wood.

Stromata of *Hypoxylon deustum* (Hoffm. ex Fr.) Grev. (*Ustilina vulgaris* Tul.) seldom were seen on basal wounds, and the fungus was cultured but rarely from wounds on sugar maple. The fungus caused a decay similar to that caused by *Daldinia* and other species of *Hypoxylon*.

*Phialophora* spp. were not found fruiting on the wound faces, yet these fungi were the principal ones isolated from discolorations in all species (table 1). The fungi were isolated commonly from discolored tissues that usually were very moist, ranged in color from light tan to black-green, and had a pH as high as 8.5. *Phialophora* spp. were cultured frequently from the pith and from discolored tissues surrounding the pith, and they produced spores in pith cells and in vessels of discolored wood in living trees (fig. 21). Although these fungi were some of the first to invade the wounds, they also were isolated frequently from discolorations surrounding decay that had advanced from wounds inflicted over 50 years ago.

The principal *Phialophora* was *P. melinii* (Nannfeldt) Conant. This species closely resembles *P. fastigiata* (Lagerberg and Melin) Conant (van Beyma 1943). Frequently the fungus was associated intimately with bacteria in the wood, and in culture these organisms grew well together.

*Phialophora lignicola* (Nannfeldt) Goidanich was not isolated as frequently as *P. melinii*, but it also was associated intimately with bacteria.

Other unidentified species of *Phialophora* were isolated, but they were not so abundant as the above-mentioned species. Fungi identified as *Margarinomyces* are probably species of *Phialophora*.

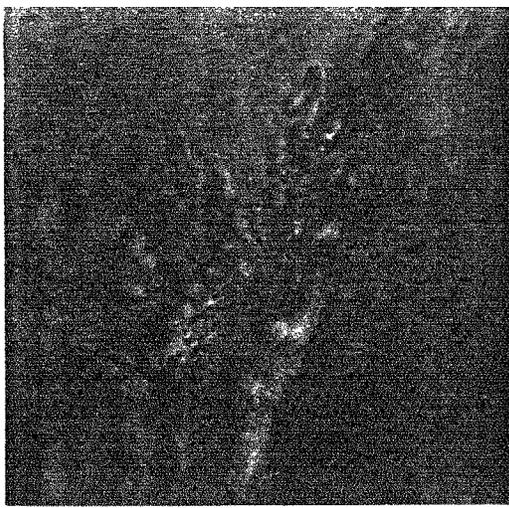
At least two species of *Phialocephala* were isolated: *P. bactrospora* Kendrick and a species close to *P. dimorphospora* Kendrick (Kendrick 1961). Most of these fungi were isolated from discolorations associated with wounds on yellow birch.

*Trichocladium canadense* Hughes (Hughes 1959) was the fungus isolated most frequently from the light tan to deep brown discoloration in maples and beech, and especially the red-brown discoloration in birches, and from moist tissues with a high pH (table 1). The fungus was isolated frequently along with bacteria.

Table 1.—Numbers of trees yielding organisms

Trees	Beech	Sugar maple	Red maple	Paper birch	Yellow birch	White ash
Total trees	82	48	29	46	116	10
Bacteria	53	33	23	40	97	8
Non-Hymenomycetes	72	45	29	41	115	8
<i>Phialophora</i> spp.	52	29	21	27	68	6
<i>Trichocladium canadense</i>	38	12	13	32	77	1
<i>Hypoxyton</i> spp.	34	13	9	7	33	7
<i>Libertella</i> sp.	4	5	3	4	9	0
<i>Nectria</i> spp.	12	8	5	5	17	0
<i>Daldinia concentrica</i>	1	4	0	1	7	0
<i>Coryne</i> sp.	4	2	1	2	7	0
<i>Graphium</i> sp.	3	2	1	2	7	0
<i>Cytospora decipiens</i>	0	0	6	0	0	0
<i>Mucor</i> spp.	6	1	0	0	2	0
<i>Cladosporium</i> sp.	0	1	0	0	0	0
<i>Cephalosporium</i> sp.	1	3	1	0	1	0
<i>Verticillium</i> sp.	0	1	1	0	0	0
<i>Ceratocystis</i> sp.	1	1	0	0	2	0
Hymenomycetes	62	32	20	32	98	8
<i>Pholiota squarrosa-adiposa</i>	5	0	0	8	20	0
<i>Poria obliqua</i>	0	0	0	8	8	0
<i>Stereum pupureum</i>	0	0	0	1	5	0
<i>Tricholoma unifactum</i>	1	0	0	1	3	0
<i>Polyporus versicolor</i>	1	2	0	0	7	1
<i>Fomes ignarius</i>	4	0	2	0	1	0
<i>Fomes connatus</i>	0	4	2	0	0	0
<i>Fomes applanatus</i>	3	0	0	0	0	0
<i>Trechispora raduloides</i>	2	0	0	0	1	0
<i>Hericium</i> sp.	6	0	0	0	0	0
<i>Corticium velleum</i>	1	1	1	0	0	0
<i>Armillaria mellea</i>	2	1	0	0	1	0
<i>Polyporus tulipifera</i>	1	2	0	0	4	0
<i>Polyporus adustus</i>	0	1	0	1	0	0
<i>Polyporus ostreatus</i>	1	0	0	0	0	0
<i>Polyporus glomeratus</i>	0	0	1	0	0	0
<i>Stereum murrayi</i>	0	0	0	1	1	0
<i>Poria cocos</i>	0	0	0	0	1	0
<i>Lenzites betulinus</i>	0	1	0	0	0	0
Unidentified Basidiomycetes	25	15	13	1	22	7

Figure 21.—Phialophores of *Phialophora* sp. producing spores in a vessel in discolored wood in a living tree.



These organisms grew very slowly together in culture. Faster-growing fungi often overgrew *T. canadense*, but its presence could be detected by the black mycelium that grew to the bottom of the petri dish.

Many other fungi were isolated from discolorations (table 1), but none so frequently as those mentioned above. *Nectria* spp. were isolated occasionally from beech and yellow birch, but not consistently even from wounds bearing *Nectria* perithecia on in-rolled callus. Therefore, they may have been more abundant than indicated by isolations. A species of *Libertella*, isolated occasionally from all species, resembled the imperfect stage of the well-known canker fungus *Eutypella parasitica* Davidson and Lorenz. Fungi not listed in table 1, but which were isolated a few times, were members of the following genera: *Gliocladium*, *Fusarium*, *Phomopsis*, *Penicillium*, *Sphaeropsis*, *Sporotrichum*, *Leptographium*, *Chaetomium*, *Chloridium*, *Mortierella*, *Streptomyces*, and *Trichoderma*.

As with the non-Hymenomycetes, many species of decay fungi were isolated, but relatively few were isolated frequently. Many fungi, comprising a large share of the isolations, were isolated only a few times and were not identified.

*Pholiota squarrosa-adiposa* Lang<sup>1</sup> was the principal fungus isolated from decay in birches and beech. In culture small fruiting

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<sup>1</sup> Identified by Dr. Orson K. Miller, Jr., U.S. Forest Service Forest Disease Laboratory, Laurel, Maryland.

bodies that produced spores often formed after 3 weeks. Ephemeral sporophores formed on trees in early fall.

*Poria obliqua* was isolated from paper birch as frequently as *Pholiota squarrosa-adiposa* (table 1). The large, black, sterile masses of fungus material were found on many old wounds from which a brown liquid oozed. Decay in such trees was moist and had a foul odor, and the discoloration around it abounded with bacteria.

*Fomes applanatus* caused decay in bases and roots of beech. *Hericiium* spp. were isolated only from beech and sporophores formed on old wounds. Other decay fungi isolated from wounds are listed in table 1.

Bacteria were isolated frequently from decayed and discolored tissues. Isolation results revealed that although bacteria were the first organisms to infect new wounds, they were present also in the oldest wounds. They grew alone and in close association with fungi. In culture they grew rapidly and sometimes retarded the growth of the fungi. In many such instances the only indications that fungi were present were small tufts of mycelium growing from tops of isolation chips. Possibly bacteria may have inhibited completely the growth of some fungi.

To determine the identity of the principal bacteria associated with decay and discoloration in northern hardwoods, a cooperative study was initiated with the University of Connecticut.<sup>2</sup> Bacteria isolated from some 6,000 chips from decayed and discolored zones in 68 trees were included in the preliminary study. Isolations from non-discolored wood yielded only a few bacteria (mainly from beech) and fungi.

Many species of bacteria were isolated, but only a few species were isolated frequently from all trees. The principal bacteria were slime-producing, gram-negative, short rods with perichrichic flagellation. They were similar in morphology and physiology to members of the genus *Pseudomonas*. Other groups commonly isolated were identified tentatively as members of *Xanthomonas* and *Bacillus*.

Microscopic examinations revealed bacteria in vessels of dis-

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<sup>2</sup>Taxonomic studies conducted by Dr. Benjamin Cosenza and Miss Mathilda McCreary, Department of Bacteriology, University of Connecticut

colored wood in living trees, and they were often in intimate contact with fungi. Bacteria were isolated most frequently from moist tissues having a high pH.

Nematodes were obtained occasionally from advanced decay, and they suppressed the growth of mycelium in culture.

### **Successions of Organisms in Wounds**

Bacteria and non-Hymenomycetes such as *Hypoxylon* spp., *Phialophora melinii*, and *Trichocladium canadense* were the first organisms to infect logging wounds. These were the organisms isolated most frequently from wounds less than 10 years old. Occasionally a decay fungus such as *Polyporus versicolor* infected wounds less than 10 years old. Usually, however, extensive decay columns were not associated with wounds less than 30 years old.

When decay fungi infected, they usually followed bacteria and non-Hymenomycetes and grew longitudinally through — but never beyond — the discolored tissues. While decay was occurring, the surrounding tissues continued to support bacteria and non-Hymenomycetes. Occasionally, when the decay process ceased radially, a hard rim developed around the hollowed column and



Figure 22—Inhibition of *Fomes igniarius* by a bacterium isolated from the edge of a decay column that yielded the fungus.

the usual bacterium-fungus complex was absent. In these trees, the hard rim was contiguous with white uninfected wood (fig. 19).

Sometimes organisms were not obtained from the leading edges of discolorations advancing from recent wounds. Likewise, not all points along discolored columns yielded organisms. In such cases, however, organisms usually were obtained from areas behind the leading edges. In radial sections, organisms were obtained from bands of discolored wood adjacent to clear wood. Extensive isolation trials indicated that while organisms were present, they were not always distributed uniformly. Thus an organism isolated from one point might be absent from a point only an inch away.

Preliminary experiments indicated that while many non-Hymenomycetes grew well in culture with bacteria, most decay fungi were inhibited by them. A bacterium isolated commonly from edges of decay columns yielding *Fomes igniarius* not only inhibited growth of *F. igniarius* in culture, but the agar darkened where the two organisms grew near to each other. In culture, inhibition was related directly to the distance between the two organisms (fig. 22).

#### **Preliminary Experiments on the Discoloration Process**

Stem sections of vigorously growing young hardwoods were cut, debarked, and surface sterilized in 0.5-percent sodium hypochlorite (Clorox). Pieces approximately 1 inch in diameter and 4 inches long were placed upright in pint jars that had been autoclaved with 10 ml of water in them. Agar blocks supporting mycelium of the principal fungi isolated from discolorations were then placed on the pith of the stems in the jars. At least 25 stems were observed for each fungus. After 6 weeks, dark discolorations had developed in stems inoculated with *Phialophora* spp. and *T. canadense*, and tan discolorations developed in stems inoculated with *Hypoxylon* spp. No discolorations developed in stems autoclaved before inoculation or in the uninoculated controls.

**Statistical Analyses of the Data  
on Yellow Birch, Sugar Maple and Beech**

A total of 23 measurements and attributes by classes were recorded for all trees in this study (table 2). Only the data for yellow birch, sugar maple, and beech were subjected to analysis;<sup>3</sup> the other species had too few representatives to contribute an adequate sample. Since we wished to determine what factors affected the amount of decay and discoloration, the latter two (variables 18 and 19) were taken as the dependent variables. Pertinent tree, wound, and organism variables (1-11 inclusive) were included

<sup>3</sup> Analysis conducted by Dr. W. E. Waters, Assistant Director, Forest Insect and Disease Research, and Dr. R. W. Wilson and R. C. Peters, Biometrics Unit, Northeastern Forest Experiment Station, New Haven, Connecticut. Facilities of the Yale University Computer Center were used for the calculations.

Table 2.—Data recorded on all trees

Variable number	Description of variable
1	Age of tree when wounded.
2	Relative size of wound (percentage of circumference wounded).
3	Years since wounding.
4	Tree diameter at breast height.
5	Proximity to other entry point for decay and discoloration.
6	Type of wound (bark scrape; wood injury).
7	Index of wound size (greatest length x greatest width).
8	Occurrence of <i>Hypoxylon spp. stromata</i> .
9	Location of wound (feet from base).
10	Causes of wounds (skidding; felling).
11	Degree of healing (callus formation) 1 to 4.
12	Merchantable height of tree.
13	Gross cubic-foot volume.
14	Distance of decay above wound.
15	Distance of decay below wound.
16	Distance of discoloration above wound.
17	Distance of discoloration below wound.
18	Cubic-foot volume of decay.
19	Cubic-foot volume of discoloration (including decay when present).
20	Height of first branch stub above wound.
21	Circumference of tree.
22	Tree age.
23	Seams on tree.

as the independent variables. The remaining measured values or classified attributes were not pertinent or did not lend themselves to analysis in the form recorded.

The first analysis was a "full screen" of the associations between the respective dependent variables and the independent variables and of the intercorrelations among the latter. This technique involves the computation of all possible regressions of the dependent variable and the independent variables, taking the latter individually and in all combinations (Furnival 1965). For the present analysis, three variables judged most important in the relationships concerned were "fixed" in the full screen computations; i.e. they were included in all the regressions. These were: age of tree when wounded (variable 1), relative size of wound (variable 2), and years since wounding (variable 3).

The proportions of the total variation in amounts of decay and discoloration in the sample trees accounted for by the respective independent variables are shown in tables 3, 4, and 5. Several interesting points emerge. In yellow birch, there is a marked difference in the degree of association of variables 1-11 with decay (11.3 percent) and with discoloration (46.7 percent), while in sugar maple and beech there is no significant difference in this regard. In yellow birch, the three fixed variables accounted for most of the variation in both decay and discoloration. In sugar

Table 3.—Significant statistical data for yellow birch

Independent variables	Volume of decay,	Volume of discoloration
	cubic feet	(including decay when present), cubic feet
	<i>R</i> <sup>2</sup>	<i>R</i> <sup>2</sup>
1 (Age of tree when wounded)	0.016	0.045
2 (Relative size of wound)	.006	.018
3 (Years since wounding)	.025	.400
1, 2, 3	.033	.416
All; 1 - 11	.113	.467

Regression equation:  $Y = 0.031 + 0.284X$ , Where Y = volume of discoloration and X = years since wounding.

Table 4.—*Significant statistical data for sugar maple*

Independent variables	Volume of decay,	Volume of discoloration
	cubic feet	(including decay when present), cubic feet
	<i>R</i> <sup>2</sup>	<i>R</i> <sup>2</sup>
3 (Year since wounding)	0.261	0.281
3, 5 (5, Proximity to other entry points for decay and discoloration)	.344	.361
3, 5, 3 x 5	.462	.406
3, 5, 7, 3 x 5 (7, Index of wound size)	.563	.456
All; 1 - 11	.600	.550

Regression equations

$$Y_1 = -.653 + .0493 X_1 + .0015 X_2 + .0257 X_3 - .0022 X_4$$

$$Y_2 = -.927 + .0915 X_1 + .0025 X_2 + .0184 X_3 - .0030 X_4$$

Where  $Y_1$  = Volume of decay, cubic feet;  $Y_2$  = Volume of discoloration, cubic feet;  $X_1$  = Years since wounding;  $X_2$  = Proximity to other entry points for decay and discoloration;  $X_3$  = Index of wound size (greatest length x greatest width); and  $X_4$  = Interaction of years since wounding and proximity to other entry points for decay and discoloration.

Table 5.—*Significant statistical data for beech*

Independent variables	Volume of decay,	Volume of discoloration
	cubic feet	(including decay when present), cubic feet
	<i>R</i> <sup>2</sup>	<i>R</i> <sup>2</sup>
7 (Index of wound size)	0.300	0.292
4 (Tree diameter at breast height)	.100	.108
3 (Years since wounding)	.085	.105
11 (Degree of healing)	.094	.098
3, 7	.345	.352
All; 1 x 11	.480	.540

Regression equations:

$$Y_1 = 0.0199 + 0.0070 X_1$$

$$Y_2 = 0.4110 + 0.0128 X_2$$

$$Y_1 = 0.6080 + 0.0066 X_1 + 0.0268 X_2$$

$$Y_2 = 0.9390 + 0.0119 X_1 + 0.0576 X_2$$

Where  $Y_1$  = Volume of decay, cubic feet;  $Y_2$  = Volume of discoloration, cubic feet;  $X_1$  = Index of wound size;  $X_2$  = Years since wounding.

maple, proximity to other entry points (variable 5), the interaction between years since wounding and other entry point proximity (variable 3 x variable 5), and index of wound size (variable 7) were significantly associated with the amounts of decay and discoloration, in addition to the mixed variables. In beech, index of wound size (variable 7), tree diameter at breast height (variable 4), and degree of healing (variable 11) appeared related to the dependent variables, in addition to the fixed variables.

Stepwise multiple regressions were then run for each tree species, using the indicated significant independent variables in turn. These analyses revealed that for yellow birch, years since wounding (variable 3) was the primary variable of importance. With sugar maple, years since wounding (variable 3) was the single most important variable; but proximity to other points of entry (variable 5), the interaction of these two variables, and index of wound size (variable 7) also were consistently associated with variation in the amounts of decay and discoloration. In beech, the age of the wound and index of wound size (variables 3 and 7) were shown to be most important. The pertinent regression equations are given in tables 3, 4, and 5.

## Discussion and Conclusions

Decay and discoloration in living trees are the results of dynamic processes that involve interactions of organisms that in turn are affected by environmental factors, including the actions of man. When a dissected tree is examined, the decay and discoloration processes are observed as of that moment. And immediately thereafter other processes also begin to function.

The statistical analyses indicated that in yellow birch and to a lesser extent in beech the variables measured had more influence upon discoloration than upon decay. A similar situation was reported by Hepting *et al.* (1949), who stated that while discoloration about increment borer holes within a given species was very consistent, the occurrence of decay varied from tree to tree. In other increment-borer studies little or no discoloration or decay was associated with the injuries in balsam fir, spruce, pines, hemlock, hickory, oaks, white ash, and black cherry, while considerable discolorations and localized decay were found in beech, paper birch, yellow birch, and sugar maple (Campbell 1939). Northern hardwoods appear to differ greatly from other species in their susceptibility to decay and discoloration.

The events that begin when a tree is wounded and continue until the wood is destroyed all depend greatly on one factor: time. It takes time for changes in moisture and air to affect cellular processes, and for organisms to infect and invade tissues. Of all the independent variables tested, time was the most important. Similarly, time was important statistically in the development of decay of Appalachian oaks (Hepting 1941) and of softwoods in the Northwest (Wright and Isaac 1956).

The indication that size of wound was the most important independent variable tested for beech is very interesting. Insects (especially ants) that attacked the wounds, and the beech bark disease, may have been factors contributing to this. The unknown factors that appeared to have restricted the advancement of decay and discoloration in other species may have been disrupted in beech by the insect attacks. The callus around the wounds were attacked frequently by both species of scale insects and *Nectria* spp., and

such wounds were invaded frequently by *H. rubiginosum*. As wound size increased, greater numbers of these organisms infested and infected the callus tissue.

Also, we must account for the extremely small correlation (11 percent) between the independent variables and decay in yellow birch. Yellow birch had many white-faced wounds, which were associated with very little decay and discoloration; it had wounds infected by *P. obliqua*, a fungus that invaded tissues that formed after the tree was wounded; and it had wounds invaded by *P. squarrosa-adiposa*, an aggressive invader of tissues present when wounds were inflicted. Also, discoloration advanced rapidly in yellow birch; and when decay followed, the decay columns were not discrete and they were difficult to measure. These could have been some of the reasons for the low correlation.

On the other hand, decay and discoloration advanced slowly in sugar maple. These discrete columns could be measured easily.

The statistical analyses indicated that the data collected accounted for but little of the decay associated with wounds in yellow birch and therefore were not useful for prediction purposes. Approximately half of the variation in the amount of discoloration in the birch and of both decay and discoloration in sugar maple and beech was associated with the independent variables taken, and the regression equations derived will provide estimates of relatively low precision. Thus the statistical analyses show clearly that factors other than those recorded in this study must be considered. These analyses give greater emphasis to the importance of organisms and intrinsic factors in the decay-and-discoloration processes in living trees. The biochemical and physiological interactions of organisms and the tree tissues are undoubtedly part of the unknown revealed by the analyses. Decay and discoloration following logging wounds in northern hardwoods definitely cannot be explained or predicted on the basis of external characters or features alone.

Yet reliable predictive curves for decay following logging wounds have been plotted for other tree species (Wright and Isaac 1956) and for decays following fire wounds (Hepting 1935; Toole 1959; Hepting 1941).

The difference between the decay results obtained by Wright and Isaac (1956) and in this study may be attributed to differences in the trees studied, and to the fact that one fungus, *Fomes annosus* (Fr.) Cke., dominated the decays in the softwood study (63 percent of the rots on the Coastal Range). The uniformity brought about by the dominance of *F. annosus* rendered the data more suitable for analysis. By contrast there were so many organisms causing decays in northern hardwoods that no consistent relationship could be shown.

In studies of fire wounds on hardwoods in the South, Toole (1959) isolated 30 species of fungi but only 5 were responsible for 50 percent of the decay. Hepting (1935) also isolated many fungi but cited two, (*Lentinus tigrinus* Bull. ex Fr. and *Polyporus lucidus* Fr.) as most important in trees wounded by fire on the Mississippi Delta.

Another important difference between logging wounds and fire wounds lies in the nature of the wounds. No two logging wounds are alike; and even though they occur in one logging area, they may have been inflicted at different times. On the other hand, fire wounds all have somewhat similar patterns; and in a given area they often were inflicted at the same time. Fire wounds are at the base, and decay develops upward. The width of fire wounds 12 inches above ground were used consistently as the width of the wounds (Hepting 1941). These considerations are mentioned here only to indicate some of the differences between studies that at the outset appeared similar.

One of the most difficult problems encountered in this study was to measure columns of decay and discoloration that joined other columns advancing from other infection courts. Many measurements had to be discarded because it was impossible to distinguish the columns from different infection courts. The longitudinal dissections were necessary to get proper results. With cross sections alone it is hardly possible to assess the contributions to the major defect column of organisms from other infection courts. Also, cross-section measurements at intervals up a log are by themselves inaccurate because of the abrupt ending of defect columns in northern hardwoods. Defect within a log may be

missed entirely if the ends appear sound, or may be exaggerated when different defects, but similar in appearance, exist on the ends of the log.

The other principal infection court that complicated the measurement of logging-wound defects was the branch stub. Longitudinal dissections exposed many healed stubs, and revealed their influence on the internal defect column. Defects advancing from wounds often joined those already present that were associated with branch stubs. This explained to a great extent why some wounds had little defect associated with them, while similar wounds had extensive defect.

Cracks sometimes formed above and below logging wounds. Vasiloff and Basham (1963) pointed out that careful examination revealed that what seemed at first to be frost cracks often were cracks that formed above and below wounds. Nordin (1954) stated that frost cracks were the most important courts of entry for decay fungi in sugar maple in the area studied. My observations and those of Vasiloff and Basham (1963) suggest that mechanical wounds may initiate some of the cracks.

Trees with small cores of discoloration usually had little defect associated with logging wounds, compared to trees with large cores of discoloration. Because some mature trees had little or no discolored cores, the nature of this discoloration had to be determined. If these central discolored columns were "normal" and actually "heartwood" as they are called frequently (Bromley 1941), then the advancement of defects from logging wounds into this central discoloration would have to be treated as a normal phenomenon of wounded trees. Because the discolored cores were not uniform in size and shape in trees of the same size and age, and because the pattern of defects advancing from logging wounds into these columns was equally erratic, the columns were considered not to result from normal tissue changes. This was pointed out by Good *et al.* (1955) for sugar maple. Much confusion still exists over factors affecting true heartwood formation.

Jorgensen (1962) stated that, according to available information, heartwood is formed in live sapwood by changes in metabolism of dying cells exposed to aeration and/or desiccation. Chat-

taway (1952) discussed a transition zone that formed between heartwood and sapwood. In this study the dark central cores of the northern hardwoods studied were not considered to be true heartwood, but rather were considered to be wound-initiated discoloration (Shigo 1965b).

The nature of this central discoloration was investigated further because of its effect on the advancement of defects from logging wounds. Detailed accounts of this appear elsewhere (Shigo 1965a and 1965b). In northern hardwoods, the tissues formed subsequent to wounding (dead branches are considered wounds because they provide openings into trees) usually are not infected by organisms or affected by other processes that result in discolorations and decay. A similar statement was made by Nylander (1955) for tissues formed after live branches were pruned from oaks. All trees lose some branches at different times, and wounds are formed. The extent of discoloration is affected by many factors, abiotic and biotic. As trees are wounded at different points over the years, discoloration columns form. These columns usually advance fastest near the pith, suggesting a reason for the central location of most columns. If a tree containing a large core of discoloration from prior wounds is again injured severely during logging, new infections advance into the central column. Larger wounds, or several wounds around the tree, sometimes initiate the processes that form new limits for columns of defect.

The advancement of decay and discoloration toward the pith suggests that aeration may be a factor affecting the process. Thacker and Good (1952) concluded that aeration was probably not important in decay of sugar maple, but, as pointed out by Zycha (1948) for European beech, aeration may be important in certain discoloring processes that do not involve organisms. Since organisms were not isolated consistently from discoloration around recent wounds in northern hardwoods, the first phase of the discoloration process may be the reactions occurring between wood tissues and air entering via the wounds. Many softrot fungi grow better than Basidiomycetes in wood with a high moisture content (Duncan 1960), and these fungi have a superior tolerance of poor aeration (Duncan 1961). Possibly excess aeration first stimulates

advancement of the discoloration, and then the organisms that follow bring about conditions of high moisture and low aeration. Bacteria and non-Hymenomyces, but not Basidiomyces, could thrive in such an environment and enhance the discoloration processes.

The specific factors accounting for the pattern of decay and discoloration in living trees are not known, but the frequency of isolation of bacteria suggests that bacteria are important in these processes. The deterioration of pine logs in storage by bacteria has been demonstrated (Knuth and McCoy 1962). Yet, except for studies of elm and poplar (Hartley *et al.* 1961), the role of bacteria in living forest trees has received little attention. The fact that most of the bacteria isolated in this study were motile suggests that they are not dependent entirely upon the translocation stream of the tree for their movement between cells.

The association of many species of non-Hymenomyces with discolorations in northern hardwoods has been recognized (Nordlin 1954; Lorenz 1944), but no detailed study has been made of these organisms. They often are isolated but not identified. Non-Hymenomyces were often referred to as "contaminants" in investigations on other trees (Hepting 1935; Eslyn 1962). Eslyn (1962) stated that a number of "contaminants" were natural inhabitants of soft maple wood.

To my knowledge, *P. melinii* has not been reported previously from northern hardwoods. Species of *Phialophora* are common inhabitants of pulp and paper (Wang 1961; Melin and Nannfeldt 1934) and they have been isolated from timber showing soft rot (Savory 1954; Duncan 1960). The abundance of these fungi in living trees and their ability to persist in woodpulp makes them economically important.

*Trichocladium canadense* was called *Torula ligniperda* (Willk.) Sacc. (Hughes 1959)<sup>4</sup> by earlier investigators. The fungus has been recognized for a long time as a wood-inhabiting Hyphomycete (Siggers 1922) and as being associated with red-heart in birch (Fritz 1931; Campbell and Davidson 1941). Its intimate

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Personal communication from R. W. Davidson, Colorado State University.

association with bacteria was pointed out by Campbell and Davidson (1941).

*Phialophora* spp. and *T. canadense* are similar in several respects. They are dark, are associated with bacteria, are isolated from moist tissues having a high pH, and produce phialophores. Such conidiophores are well adapted to spore production in confined areas. Phialophores producing spores of *Phialophora* sp. were observed in cells of discolored tissues in living trees. How long these spores remain viable, and whether or not they move through some of the tissues, are questions that need answers. Possibly spores produced in abundance are stimulated to germinate and develop by changes in tissues induced by wounding.

Chlamydo-spores of *Torula ligniperda* (*Trichocladium canadense*) also have been observed in wood (Siggers 1922; Fritz 1931). Such spores may be able to live under conditions not suitable for mycelium.

*Hypoxylon* spp. were the principal pioneer fungi that infect wounds. The primary species isolated from wounds on northern hardwoods was *H. rubiginosum*. Miller (1961) stated that in the herbaria of the world, forms of *H. rubiginosum* have been given almost every other *Hypoxylon* name possible. Yet, many *Hypoxylon* species are probably either missed, not identified, or mistaken for a Hymenomycete because of their erratic fruiting habits in culture. In an otherwise excellent account of the species of *Hypoxylon*, Miller (1961) makes little or no mention of the imperfect stages encountered in culture. A study of the cultural characteristics of the species is needed. Fungi in the Xylariaceae are often cited as examples of non-Hymenomycetes that decay wood (Merrill *et al.* 1964). Apparently these fungi compete successfully with all other invading fungi. They were cited as some of the first fungi to invade fire wounds (Hepting 1941). On northern hardwoods, fruiting bodies of *Hypoxylon* spp. and the Basidiomycete *Stereum complicatum* commonly occurred on the same wound. Toole (1959) stated that *S. complicatum* was also a pioneer on fire wounds.

*Hypoxylon* spp. were the principal fungi isolated from wood of oak trees that had been girdled as part of the control for oak wilt

in West Virginia (Shigo 1958). These fungi seem to be aggressive wound-invading organisms.

The importance of *Pholiota squarrosa-adiposa* as an aggressive decay fungus that invades logging wounds was pointed out. With this fungus the value of isolating rather than relying upon observation in the forest is demonstrated, for it produces a sporophore that persists for but a short time. For this reason, assessment of fruiting in the forest would not adequately reveal its importance.

The close association of bacteria, non-Hymenomyces, and Hymenomyces in living trees suggests that all are important in the processes that result in decay and discoloration (Shigo 1964). The results of this study emphasize the need for greater understanding of the many factors that affect processes resulting in decay and discoloration in living trees.

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