

THE ASSOCIATION BETWEEN RING SHAKE, WETWOOD, AND FIR ENGRAVER BEETLE ATTACK IN WHITE FIR¹

Donald R. Owen

Former Research Assistant²

and

W. Wayne Wilcox

Forest Products Pathologist and Professor of Forestry
University of California, Forest Products Laboratory
47th and Hoffman Blvd., Richmond, CA 94804

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ABSTRACT

Wetwood and a characteristic type of ring shake were found associated with fir engraver beetle scars in discs of white fir. The shakes occurred only in highly discolored areas of wetwood to the pith side of scars and/or traumatic tissue, and were predominantly middle lamella failures that went through the later-formed earlywood of a growth increment. No evidence could be found from either anatomical observations or tension-perpendicular-to-grain tests to support the hypothesis that scar-associated shake might go through bands of traumatic resin canals. It is concluded that the action of microorganisms, most likely wetwood bacteria, was the major factor leading to ring shake. The bacteria are thought to be responsible for the weakening of the middle lamella between cells.

Keywords: Ring shake, fir engraver beetle, wetwood, bacteria.

INTRODUCTION

Ring shake

Ring shake is a "rupture in wood" that occurs "in standing trees in the plane of the growth increment" (Panshin and deZeeuw 1970). Meyer and Leney (1968) described ring shakes from standing conifer trees as compound middle lamella failures, usually in the latewood, with loose fibers and deposits of extraneous material on the shake surface. In contrast, tangential failures that formed as a result of kiln-drying stresses or that were mechanically induced have been characterized by rupture across earlywood cell walls (Meyer 1964). The finding that ring shakes in the standing tree involve between-cell failures has also been reported by other authors (Jorgensen and Lacznar 1964; McGinnes 1968; Kandeel and McGinnes 1970; McGinnes et al. 1971, 1974, 1976, 1977; McGinnes and Wu 1973) who have studied the anatomy of ring shakes in both conifers and hardwoods.

Ring shake in standing trees may be due to any number of factors, but of

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² Presently, graduate student, Department of Entomological Sciences, Berkeley.

interest here is ring shake associated with tree wounding and the presence of microorganisms. Niskala (1960) found that ring shake in Douglas-fir virtually always went through tangential bands of traumatic resin canals. He concluded that such traumatic tissue is a plane of weakness that may lead to the development of ring shake. Similarly, Jorgensen and Lecznar (1964) found that ring shake associated with sapsucker wounding in eastern hemlock occurred between latewood cells of one ring and the earlywood traumatic parenchyma of the next.

The term "compartmentalization" (e.g., Shigo 1975) is used to describe a tree's reaction to wounding in which a "wall" is created around the wood that was formed prior to wounding. This wall may consist of specialized traumatic tissue or apparently normal tissue that is only slightly modified (e.g. chemically). Shigo's findings (1972) were that most wound-related shakes formed between this wall and the wood to the pith side. The shakes usually did not become apparent in the wood until after some drying had taken place. He proposed that the presence of microorganisms, the density and position of wounds, the time of year of wounding, and the action of various stresses may all have an effect on ring shake formation. Kandeel and McGinnes (1970) described the anatomy of severe ring shake in a scarlet oak tree in which traumatic tissue, presumably the result of cambial damage, was found in the same growth ring as the shake. The traumatic tissue occurred on the bark side of the ring shake, and a higher than usual percentage of tension wood fibers occurred on the pith side. McGinnes and Wu (1973), reporting on this same shake, concluded that the traumatic tissue was the structurally weakest zone within the growth ring. The shake went predominantly through the middle lamella and this was attributed to either biological degradation or incomplete polymerization of the lignin due to arrested development following tree injury.

In another study, McGinnes et al. (1971) reported on ring shake in a black walnut tree that had a fire injury at its base and associated heart rot. The ring shake occurred in the same growth increment as was being formed at the time of wounding. A false latewood zone, composed of thin-walled cells, occurred in the ring, and the ring as a whole had a low specific gravity. Extractive and lignin contents were high, as were the contents of certain inorganic chemicals. The shake separation followed the false latewood boundary on its pith side and was predominantly between cells. The authors proposed that microorganism degradation in combination with incomplete cell development were probable causes of the ring shake.

The presence of microorganisms in ring shake zones has been well documented. Ward et al. (1969) were able to isolate bacteria from ring shake zones in northern red oak, black oak, American elm, slippery elm, and cottonwood. A hypothesis (Ward et al. 1972) ". . . is that certain bacteria which can live in the heartwood of living trees will produce enzymes capable of degrading the compound middle lamella of wood cells during the early stages of infection." Given that the middle lamella is weakened in this way, stresses within the tree (e.g. growth, wind, and freezing stresses) could ultimately cause the wood to separate, forming a shake. Kiln-drying of red oak lumber revealed that wood with rancid-smelling heartwood (a sign of bacterial infection) from the butt logs of trees produced the greatest amount of honeycomb and ring failures (Ward et al. 1972). McGinnes et al. (1974)

presented electron micrographs of ring shakes in various hardwoods showing the presence of bacteria and non-hyphomycetous fungi in the shake zones. According to these authors, "Ring shake formation may be attributed to injury, and the extent of subsequent shake formation is related to two factors: 1) the nature of host responses as reflected by the anatomical and chemical structure of the wood following injury; and 2) by the nature and success of microorganism attack."

Wetwood in white fir

Wilcox and Oldham (1971) were consistently able to isolate a gram-variable, facultatively anaerobic, rod-shaped bacterium from a type of discolored wood in white fir known as wetwood (see Hartley et al. 1961). The bacterium was rarely isolated from sapwood. On the basis of the results of another study, Wilcox (1968) concluded that wetwood and heartwood in the white fir trees were essentially the same. The wetwood consisted of a darker, wetter-appearing central column within the trees, being nearly circular in cross section. Irregularities in this nearly circular pattern were associated with *Scolytus ventralis* wounds.

The fir engraver beetle

Scolytus ventralis Lec. is a bark beetle that attacks the main stem of white fir and other true firs in the West. Female beetles initiate the attacks by individually boring through the bark and into the cambial region, where each constructs its own horizontal egg gallery. Typically, a large number of beetles aggregate to mass-attack a single tree. The fir engraver vectors a brown-staining fungus, *Trichosporium symbioticum* Wright (Wright 1935), which infects and kills the tissue of the cambial area in a vertically oriented patch around the egg gallery and the developing larval brood. Many attacks concentrated on a given portion of the stem may girdle the tree and kill it (Struble 1957).

Successful gallery construction and brood development depend in part upon host resistance. It is not uncommon to find living trees showing signs of past unsuccessful attacks. A portion of the cambium may be killed in an individual attack, leaving a scar that eventually is healed over by callus tissue and that becomes embedded in the wood.

The association of fir engraver beetle attack scars with defects in white fir, including ring shake, was reported by Johnson and Shea (1963). However, their work leaves open the questions of how beetle scarring leads to the formation of ring shake, where in relation to the scar the shake forms, and what the anatomical features of the shake are. The purpose of this study was to further elucidate the role of fir engraver beetle attack in the formation of ring shake in white fir trees.

MATERIALS AND METHODS

Ten white fir trees [*Abies concolor* (Gord. & Glend.) Lindl.] were felled for the study. All were taken from a single stand within the Stanislaus National Forest, California. All trees were alive and were of similar height and diameter, ranging from 26.7 to 46.2 cm (10.5–18.2 in.) in diameter at breast height (dbh) and 13.7 to 21.5 m (44.9–70.5 ft) high. Trees were chosen so that the sample included both attacked trees and non-attacked trees. Trees with past attacks were easily iden-

tified because of irregularities in the bark, which indicated that scars were embedded in the wood. For each tree that was felled, cross-sectional discs 7.5 to 10.0 cm (3–4 in.) thick were removed at 1-m (3.28 ft) intervals along the length of the stem up to 15.2-cm (6 in.) diameter outside bark, the first disc being removed at 1 m above the ground.

In the laboratory, one cross-sectional surface of each disc was planed, and then the discs were stored in a cold room at 1–9 C (35–49 F) and 85–90% relative humidity. Gross features of the discs were observed while the discs were green, and material used for microscopic examination came only from fresh, green wood. A number of observations were recorded for each disc: number of beetle scars and ring shakes per cross section, gross anatomical features of each scar, annual ring in which each scar and shake occurred, the tangential length of each scar and shake, and the presence and location of traumatic resin canals. Also, the wetwood zone of each disc was outlined in pencil, and a description of the wetwood pattern was made.

Samples of wood tissue for microscopic viewing were fixed in FAA (Sass 1958) for approximately one week and then transferred to 50% ethanol for storage. A portion of these samples were embedded in celloidin. Sections 2–5 μm thick were obtained from celloidin-embedded material, and sections 8–14 μm thick were obtained from non-embedded material. Brightfield, phase contrast, interference contrast, and polarized light optics were used for viewing the sections on a compound microscope. Sections prepared from ring shake zones and adjacent areas of the wood were inspected for evidence of decay and the presence of other microorganisms.

Tension-perpendicular-to-grain test

This test was designed to reveal whether or not traumatic resin canals represented a tangential zone of weakness within the wood. Discs from seven of the sample trees were used for the test. Four trees were heavily scarred and three had little or no scarring. An average of eight test specimens were taken from each tree at different heights, and were prepared and tested according to ASTM Standard D143-52 (Reapproved 1978). The blocks were prepared from green wood and conditioned to a desired target moisture content of about 14% before testing. All specimens were oriented such that the latewood of either the 1962 or 1963 growth rings went approximately through the middle of the block, with stress being applied perpendicular to this. In effect, the plane of the 1962 or 1963 latewood corresponded to the area of greatest stress concentration when the blocks were tested. The 1962 or 1963 latewood was oriented in the middle of the test blocks for a specific purpose: in trees that were heavily scarred, this area contained a continuous plane of traumatic resin canals, but in trees that were not scarred or only lightly scarred, this area was all "normal" tissue. Thirty-one specimens contained traumatic tissue and twenty-five contained normal tissue.

Each specimen was stressed until failure on a Baldwin testing machine and its tensile strength determined. Gross anatomical observations of the failure were made using either a 3-diopter magnifier or a variable-power dissecting microscope. When it was not possible to determine the exact nature of the failure using these methods, the failure zone was prepared for viewing with the compound microscope using steam sectioning techniques.

Kiln-drying of discs

Four to six discs from each of seven trees (same as for tension perpendicular test) were kiln-dried to determine what effect this might have on shake formation. The discs were taken from different heights within each tree and varied with respect to such factors as diameter, number of beetle scars, presence of traumatic tissue, amount of wetwood, and age. Discs were kiln-dried at constant relative humidity and temperature; the dry bulb temperature was 60 C (140 F) and the wet bulb temperature 52 C (126 F), which gave a wood equilibrium moisture content (EMC) of 10%. It took 207 h of drying to reach this EMC. The average green moisture content for the discs before drying was 132%.

At the end of each day of drying, the discs were temporarily removed from the kiln and the locations of developing ring shakes were marked on the surfaces of the discs using a different color pencil for each day. Thus, shakes could be easily located at the end of drying, and it could be determined on which day they developed. Data included number of shakes per disc, length of individual shakes, location of shakes with respect to scars, wetwood, and growth rings, and on what day during drying each shake became evident. Microscopical observations were made of a representative subset of the ring shakes found. Either non-embedded sections were viewed using brightfield optics or small wood blocks containing shakes were surface polished and viewed using incident illumination under a compound scope.

RESULTS

Each scar represents a patch of cambium that was killed and subsequently overgrown with callus and thus forms a tangential separation of the wood (Figs. 1 and 2). Lengths of scars ranged from less than 10 mm to 157 mm. Only a few of the larger scars were not completely healed. The scar separation is not a ring shake because the wood was never continuous across the scar, and thus the

TABLE 1. *Distribution of beetle scars and traumatic tissue by year for all trees (from cross-sectional discs).*

Total number of scars	Total of scar lengths (mm) in tangential direction	Number of discs with scars	Number of discs with traumatic tissue*	Year
Prior to 1961 scarring was minimal				
12	446	11	0	1961
159	5,762	63	49	1962
95	1,866	33	25	1963
3	18	3	0	1964
2	9	2	0	1965
1	6	1	0	1966
2	13	2	0	1967
37	1,675	9	8	1969
2	61	2	0	1970
14	311	10	5	1971
2	26	2	0	1972
1	6	1	0	1973

* Number of discs with traumatic tissue is those discs with traumatic tissue and scarring comprising greater than half of the circumference of the stated growth ring.



FIG. 1. Exposed tangential surface of embedded fir engraver beetle scar in white fir. Note resin and horizontal egg gallery.



FIG. 2. Cross section of embedded fir engraver beetle scar in white fir.

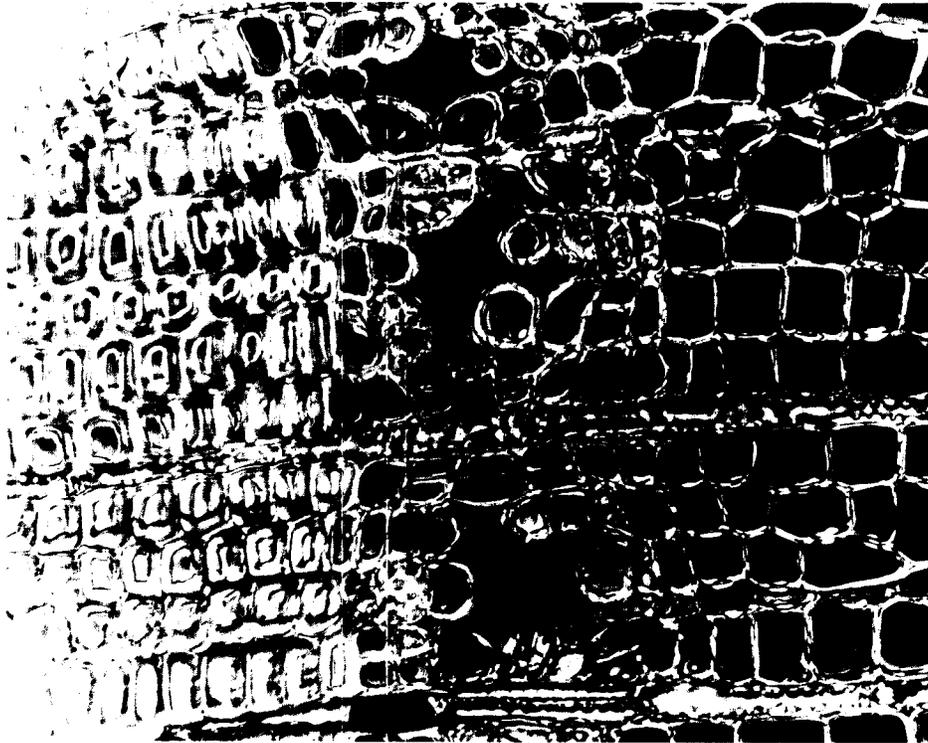


FIG. 3. Traumatic resin canals in a white fir growth ring heavily scarred by fir engraver beetles. (Phase-contrast photomicrograph. Magnification 260 \times).

separation did not result from a rupturing of the wood. Scars were always filled with resin and typically surrounded by traumatic longitudinal resin canals that were continuous with the plane of the scar (Fig. 3). The extent of traumatic tissue formation (i.e., traumatic resin canals) depended upon the degree of scarring. From disc cross sections it was noted that when scars were small and/or isolated from other scars, the traumatic resin canals were restricted to the immediate periphery of the scar. However, when a large number of scars occurred in a given growth ring, a band of traumatic resin canals often extended completely around the growth ring. In such a situation the traumatic tissue and scars formed a continuous cylinder, which appeared as a dark circle on the surface of the disc. In the most heavily scarred tree, this cylinder extended three-fourths of the tree's height. From Table 1 it can be seen that during certain years both a large number of scars and an extensive amount of traumatic tissue were found, especially during 1962 and 1963.

Rarely did scars appear to have decay associated with them. On the other hand, wetwood was always associated with beetle scars (except for some of the smallest scars—e.g. less than 10 mm long). The ray parenchyma cells in wetwood typically lack starch granules and cell nuclei as do those of heartwood. Also, it was assumed that bacteria were present in wetwood zones (Wilcox 1968; Wilcox and Oldham 1971). It was common to see a narrow dry-appearing zone between the sapwood and wetwood on freshly cut discs. In trees that had few or no scars,

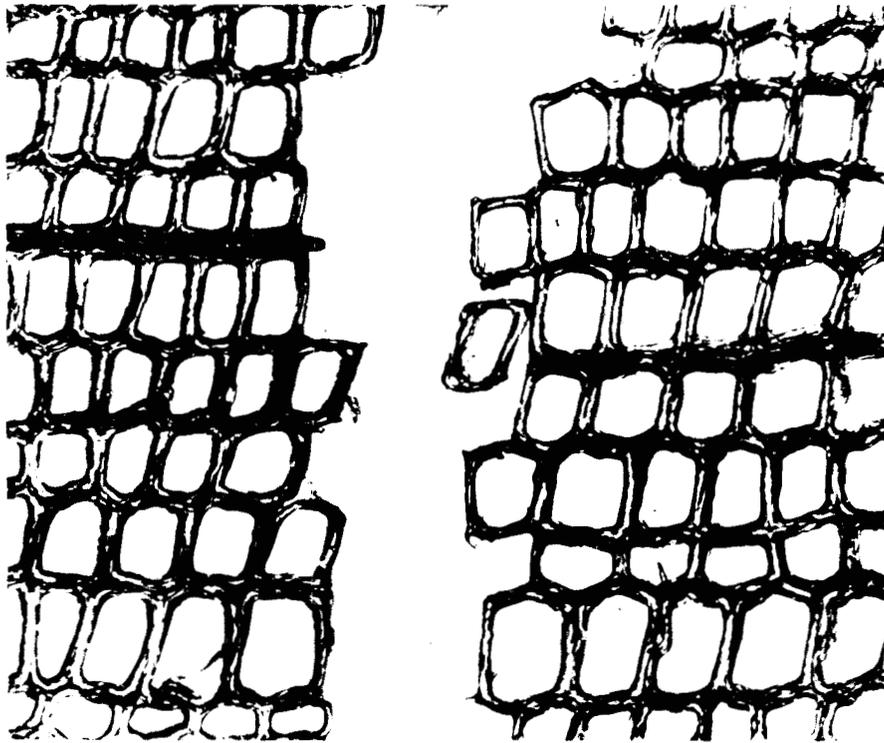


FIG. 4. Middle lamella failure of fir engraver beetle scar-associated ring shake in white fir (Bright-field photomicrograph. Magnification 310 \times .)

the central wetwood column was small and circular, being approximately half or less of the diameter of a cross section and about 25% or less of the total area. In these trees, it was sometimes difficult to separate sapwood and wetwood even on green, freshly cut cross sections. Generally, in trees that were heavily scarred the wetwood was much darker than the sapwood, the wetwood column was irregular in outline (versus uniformly circular), and a large portion of the cross-sectional area consisted of wetwood. For example, in the most heavily scarred tree as much as 67% of a cross section was wetwood.

Although variable, the wetwood outline in cross section was rather predictable in heavily scarred trees because the shape of the wetwood column was directly influenced by scarring. The most common pattern observed involved wetwood directly to the pith side of a scar that was continuous with the central column of wetwood. Occasionally an "island" of wetwood was seen on the pith side of a scar that was not continuous with the central column. In both cases, scarring had apparently induced wetwood formation. Where high scar densities occurred in a given growth ring, nearly all the wood inside the scarred ring consisted of wetwood. In most cases, scars and/or traumatic tissue delineated the furthest outward extent of the wetwood column. The wetwood zone was typically darkest along its outermost boundary, especially adjacent to scars.



FIG. 5. Middle lamella failure of fir engraver beetle scar-associated ring shake in white fir. Birefringence of the intact S_1 layer of the cell wall indicates a middle lamella failure with little or no cell wall tearing. (Interference contrast photomicrograph. Magnification 1,030 \times .)

Ring shake in green discs

Ring shake was found in the green discs of only one tree. This tree had the greatest number of beetle scars and amount of wetwood of all the trees. The 1962 and 1963 growth rings were heavily scarred, and traumatic tissue completely encircled these rings for most of the tree's height. Nine shakes were found—3 shakes each from the 8-, 9-, and 11-meter discs, ranging from 13–85 mm in tangential length and totaling 314 mm. All shakes occurred in wetwood zones proximal to scars in the following growth rings: 1959—two shakes, 1960—one, 1961—five, and 1962—one. These four rings constituted the most highly discolored area of the wetwood zone in the 8-, 9-, and 11-meter discs. When ring shake samples were removed from the discs for microscopic observation, it was found that six of the shakes went completely through the disc. In one disc, two ring shakes became evident only after cutting into the disc, at which time the wood fell apart where these shakes occurred. This indicated that more shakes might be present in the discs than were immediately apparent on a given cross-sectional surface, because perhaps the shakes were closed because of the swollen condition of the green wood. All of the shakes resulted from middle lamella failures (Figs. 4 and 5). Also, all the shakes occurred in the later-formed earlywood of a growth in-

crement, i.e. within the outer half of the growth increment, but not in the latewood. None of the shakes included or originated from either traumatic tissue or scars.

No evidence of decay could be found associated with any of the ring shakes, nor did there appear to be any decay in the tree. Scar size and rate of healing probably affect whether or not decay fungi gain entrance into the wood tissue.

Ring shake in kiln-dried discs

At the end of one day of kiln-drying, discs from the above-mentioned tree (designated A) and a second tree (B) had shakes associated with scars. Both trees A and B had higher scar densities (amount of scarring per unit area), greater amounts of wetwood, and more highly discolored wetwood than the other two beetle scarred trees from which wood was kiln-dried. All eighteen of the shakes that were discovered occurred in the most highly discolored area of the wetwood adjacent to either scars or traumatic tissue. Four shakes each occurred in the 1959 and 1960 growth rings, seven occurred in the 1961 ring, and three in the 1962 ring. Sixteen of the shakes occurred in earlywood in the outer half of the growth increment. All eight shakes from tree A occurred in the disc taken at a height of 10 m, and nine out of the ten shakes from tree B occurred in the discs taken at heights of 10 and 11 m.

Ten of the eighteen shakes in dried discs were sampled for microscopic observation; all were failures through the middle lamella. Of these ten shakes, three went completely through the disc. In short, most of the shakes that opened up by the end of the first day of drying were very similar to the shakes found in the green discs from tree A.

At the end of two days of drying, only two additional shakes were found in tissue proximal to bark beetle scars or traumatic tissue and these were in highly discolored wetwood. These shakes occurred in the 10-m disc of tree A and were located in earlywood in the outer half of the 1960 and 1961 growth increments. The twenty shakes from kiln-dried discs ranged from 7–50 mm in tangential length and totaled 396 mm. No other ring shakes associated with scars developed in the discs during kiln-drying.

Tension-perpendicular-to-grain test

A modified Wilcoxon rank sum test (Lehmann 1975) was used to test the null hypothesis that wood of specimens with traumatic tissue was not different in tensile strength from wood of specimens without traumatic tissue. It was assumed that if traumatic tissue and nontraumatic tissue differed in strength, the traumatic tissue would be weaker, hence a one-sided test was used ($\alpha = 0.05$). However, specimens rarely failed through traumatic tissue, which meant that one was not actually measuring the strength of the traumatic tissue, but rather the strength of some other weaker area of the specimen. Test specimens with traumatic tissue proved not to be significantly different in strength from specimens without traumatic tissue and, thus, the null hypothesis was not rejected.

Anatomically, the failures in test blocks with traumatic tissue were the same as the failures in blocks without traumatic tissue. The presence of traumatic tissue had no effect upon the results. Usually the failure followed a tangential path, but not always, and it often went through more than one growth ring. Typically the

failure would follow a radial path between two adjacent rings and follow a tangential path within a ring. Failures virtually never followed a tangential path through or even next to the traumatic tissue. Failures consistently followed a tangential path through the earlywood of a growth ring, especially the first-formed earlywood of a ring where large-diameter, thin-walled tracheids were present. Also, failures were predominantly across cell walls rather than between cells.

DISCUSSION AND CONCLUSIONS

Traumatic tissue and tension-perpendicular-to-grain test

Prior to this study, it was hypothesized that the production of traumatic tissue in response to bark beetle wounding might be directly related to ring shake formation, since a tangential band of traumatic tissue could form a zone of weakness within the wood along which ring shake would propagate. There are many examples of ring shakes that occurred either through or contiguous with traumatic tissue (e.g. Niskala 1960; Jorgensen and Lecznar 1964; Shigo 1972; Kandeel and McGinnes 1970; McGinnes et al. 1971). In this study, no evidence was found to support the hypothesis of a direct relationship between beetle attack-induced traumatic tissue and ring shake.

The results of the tension-perpendicular-to-grain test support the anatomical observations that no ring shake was found either through or contiguous with traumatic tissue in the discs used in this study. Thus, the plane of wound-initiated traumatic tissue is not necessarily a zone of weakness through which ring shake forms.

The traumatic tissue found within beetle scarred trees usually was located within the sapwood, just beyond the wetwood boundary, and was not older than 15 years. Conceivably, the incorporation of this tissue within the central column of wetwood, through aging, could result in changes that might differentially favor ring shake formation within the traumatic tissue. These changes could be both physiological and microbial.

Ring shake

The only factor that appeared to be directly related to ring shake formation was wetwood. Because wetwood was associated with ring shakes and nearly all scars, it was assumed that bacteria (Wilcox and Oldham 1971) were also present in these zones. It is hypothesized that some action within the wetwood leads to the weakening of the middle lamella, ultimately producing the characteristic type of ring shake that is found associated with beetle scars. On the basis of visual appearance, it is evident that qualitative differences exist within various areas of the wetwood; e.g. some areas are darker than others, especially adjacent to scars. Also, scarring typically causes an increase in the amount of wetwood.

The role of beetle attack in the development of wetwood may be very complex. In the course of scar-induced wetwood formation, at least two kinds of changes may be occurring in the wood: 1) physiological changes, resulting in developmental or chemical effects, may take place in response to wounding and continue to occur as sapwood is converted to wetwood, and 2) microbial activity may increase. Bacteria found in wetwood adjacent to scars could have been vectored by beetles, gained entrance through an open wound, or been indigenous to the

wood (e.g. Knutson 1973; Shortle and Cowling 1978; Wilcox 1968; and Wilcox and Oldham 1971).

Assuming that microorganisms are being introduced from outside the tree by the beetle, the attack density as well as the size of scars will influence the amount of inoculum that the tree receives. Also, the increase in wetwood (or heartwood) production in response to a large proportion of the cambium being killed could favor the growth of indigenous bacterial populations that commonly inhabit wetwood zones. Thus, microorganism populations would be expected to be highest adjacent to areas where the amount of scarring is high. Discoloration, as seen in the areas of ring shake, is a common indicator of microorganism activity in wood.

Two factors, 1) degree of scarring, and 2) subsequent development of wetwood, are obviously related to ring shake formation. A third factor may also be related—drought. Scar-associated shakes were only found in the growth rings produced from 1959 to 1962, and drought occurred in the area from which the samples were collected during the years 1959 to 1961 (Felix et al. 1971). Abnormal wood development and associated ring shake as a result of drought conditions were reported by Barnett (1976) for Monterey pine. No anatomical evidence of incomplete cell-wall development was found associated with the ring shake from white fir discs. This does not mean, however, that drought-induced changes could not have occurred within the wood. Chemical changes, for example, could have occurred and not been evident using standard light microscopy techniques. Even if drought during the years 1959–1961 did have an effect on shake formation, one could not say that drought was a factor predisposing the trees to shake. Within the drought year growth increments, shake was always found in discolored areas of the wetwood. Likewise, attack scars of *Scolytus ventralis* have been found to be positively correlated with drought (Felix et al. 1971; Ferrell 1973). Thus, the possible role of drought in shake formation cannot be separated from the more obvious roles of beetle attack and discolored wetwood.

The following is a hypothetical scenario of the formation of ring shake in white fir associated with fir engraver beetle attack that is consistent with the observations in this study. A tree survives beetle attack, but suffers significant damage. Extensive areas of the cambium are killed and microorganisms may be introduced into the wood. Through time, pathological wetwood formation takes place adjacent to scars. The amount of wetwood produced depends upon the amount of scarring that has occurred and may also be influenced by the introduction of microorganisms. Furthermore, once the wetwood is formed, it apparently provides a more suitable habitat for bacteria than does the sapwood. The end result is that bacterial populations increase in wood adjacent to beetle scars, resulting in highly discolored wetwood. The amount of damage that bacteria inflict upon structural components of the wood depends upon the types of organisms, population size, and conditions for growth as well as the initial condition of the wood. Because of bacterial action, degradation of the compound middle lamella takes place. The weakening of this zone predisposes the wood to ring shake formation. Stresses that are applied to the wood either in the standing tree or during and after felling (e.g. growth stresses, falling shock and drying stresses) are what ultimately cause the shake failure to occur.

REFERENCES

- AMERICAN SOCIETY FOR TESTING AND MATERIALS. 1979. Standard methods of testing small clear specimens of timber. ASTM Designation: D143-52 (1978). Pages 59–116 in 1979 Book of ASTM Standards, Part 22. Philadelphia.
- BARNETT, J. R. 1976. Rings of collapsed cells in *Pinus radiata* stemwood from lysimeter-grown trees subjected to drought. N. Zealand J. For. Sci. 6(3):461–465.
- FELIX, L. S., B. UHRENHOLDT, AND J. R. PARMETER, JR. 1971. Association of *Scolytus ventralis* (Coleoptera: Scolytidae) and *Phoradendron bolleanum* subspecies *pauciflorum* on *Abies concolor*. Can. Ent. 103(12):1697–1703.
- FERRELL, G. T. 1973. Weather, logging and tree growth associated with fir engraver attack scars in white fir. USFS Res. Pap. PSW-92. 11 pp.
- HARTLEY, C., R. W. DAVIDSON, AND B. S. CRANDALL. 1961. Wetwood, bacteria, and increased pH in trees. U.S. Forest Products Lab. Rep. No. 2215, 34 pp.
- JOHNSON, N. E., AND K. R. SHEA. 1963. White fir defects associated with attacks by the fir engraver. Weyerhaeuser Co. For. Res. Center For. Res. Note 54, 8 pp.
- JORGENSEN, R. N. AND S. L. LECZAR. 1964. Anatomy of hemlock ring shake associated with sapsucker injury. USFS Res. Pap. NE-21. 9 pp.
- KANDEEL, S. A., AND E. A. MCGINNES, JR. 1970. Ultrastructure of ring shake in scarlet oak (*Quercus cocunea* Muench.) Wood Sci. 2(3):171–178.
- KNUTSON, D. M. 1973. The bacteria in sapwood, wetwood, and heartwood of trembling aspen (*Populus tremuloides*). Can. J. Bot. 51(2):498–500.
- LEHMANN, E. L. 1975. Nonparametrics: Statistical methods based on ranks. Holden-Day, Inc., San Francisco. 457 pp.
- MCGINNES, E. A., JR. 1968. Extent of shake in black walnut. For. Prod. J. 18(5):80–82.
- , C. I. J. CHANG, AND K. Y.-T. WU. 1971. Ring shake in some hardwood species: the individual tree approach. J. Polymer Sci.: Part C, No. 36:153–176.
- , AND K. Y.-T. WU. 1973. Intra-incremental chemical studies of ring shake in scarlet oak. Wood Sci. 5(4):287–294.
- , J. E. PHELPS, AND J. C. WARD. 1974. Ultrastructure observations of tangential shake formations in hardwoods. Wood Sci. 6(3):206–211.
- , P. J.-Y. LIEU, AND J. E. PHELPS. 1976. Analyses of wood formation associated with tree injury-loose heart in a white oak, and radial seams and cracks in two black oaks. Appl. Polymer Symp. No. 28:1261–1282.
- , J. E. PHELPS, P. S. SZOPA, AND A. L. SHIGO. 1977. Wood anatomy after tree injury—a pictorial study. Univ. of Mo., Columbia College of Agr., Agricultural Exp. Sta. Res. Bull. 1025. 35 pp.
- MEYER, R. W. 1964. The anatomy of shake in three western conifers. M.S. Thesis (Master of Forestry), Univ. of Wash. 89 pp.
- , AND L. LENEY. 1968. Shake in coniferous woods—an anatomical study. For. Prod. J. 18(2):51–56.
- NISKALA, G. S. 1960. Study of the nature and possible cause of ring shake in Douglas-fir. M.S. Thesis in Forestry, Montana State Univ.
- OWEN, D. R. 1980. Ring shake in white fir associated with fir engraver beetle attack scars. M.S. Thesis in Wood Science and Technology, Univ. of Calif., Berkeley.
- PANSHIN, A. J., AND C. L. DEZEEUW. 1970. Textbook of wood technology. 3rd ed. McGraw-Hill Book Co., NY. 705 pp.
- SASS, J. E. 1958. Botanical microtechnique. 3rd ed. The Iowa State College Press, Ames. 228 pp.
- SHIGO, A. L. 1972. Ring and ray shakes associated with wounds in trees. Holzforschung 26(2):60–62.
- . 1975. Compartmentalization of discolored and decayed wood in trees. *From Organismen and Holz, an International Symp., Berlin-Dahlem*. Pub. as a suppl. to Material und Organismen (Beiheft 3):221–226.
- SHORTLE, W. C., AND E. B. COWLING. 1978. Development of discoloration, decay, and microorganisms following wounding of sweetgum and yellow poplar trees. Phytopath. 68(4):609–616.

- STRUBLE, G. R. 1957. The fir engraver, a serious enemy of western true firs. USDA For. Serv. Prod. Res. Rep. No. 11. 17 pp.
- WARD, J. C., R. A. HANN, R. C. BALTES, AND E. H. BULGRIN. 1972. Honeycomb and ring failure in bacterially infected red oak lumber after kiln drying. USDA For. Serv. Res. Pap. No. 165. 36 pp.
- , J. E. KUNTZ, AND E. M. MCCOY. 1969. Bacteria associated with shake in broadleaf trees. *Phytopath.* 59(8):1056.
- WILCOX, W. W. 1968. Some physical and mechanical properties of wetwood in white fir. *For. Prod. J.* 18(12):27-31.
- , AND N. D. OLDHAM. 1971. A bacterium associated with wetwood in white fir. University of California Forest Products Lab., Internal Rep. No. 36.01.81. 12 pp.
- WRIGHT, E. 1935. *Trichosporium symbioticum*, n. sp., a wood staining fungus associated with *Scolytus ventralis*. *J. Agric. Res.* 50:525-538.