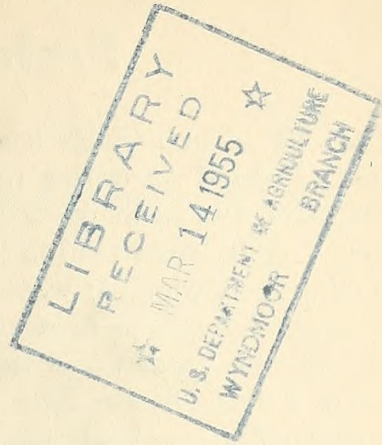


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RED ROT of Ponderosa Pine



Agriculture Monograph No. 23

Forest Service
U. S. Department of Agriculture

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Preface

A NUMBER of individuals have contributed to a better understanding of red rot during the past 40 years. The late W. H. Long, who was in charge of the Division of Forest Pathology at Albuquerque, N. Mex., from 1913 to 1937, devoted many years to studies of the rot in the Southwest. It would have been impossible to prepare this publication without frequent references to his work. Recent studies dating from 1935 were made under the direction of Lake S. Gill, Chief of the Division of Forest Disease Research, Rocky Mountain Forest and Range Experiment Station with headquarters at Colorado A & M College, Fort Collins, Colo., who assisted in all phases of the work, including the preparation of this manuscript. Carl Hartley, in charge of the Laboratory of Forest Disease Research at Beltsville, Md., made numerous valuable suggestions throughout the same period.

Of the many former members of the Division who participated in the field and office work and laboratory studies the following made special contributions: T. R. Moberg, R. E. Millenbaugh, and Bessie E. Etter. Thomas Hinds, Forestry Aid in the Forest Insect and Disease Laboratory at Albuquerque, provided material assistance in laboratory investigations and in the preparation of the illustrations. Administrative personnel of the Forest Service in the Central Rocky Mountain and Southwestern Regions cooperated in much of the fieldwork. Finally, thanks are expressed to E. C. Stakman, Frank H. Kaufert, Clyde M. Christensen, and Ralph L. Hossfeld, members of the faculty of the University of Minnesota in 1953 when an unabridged version of this manuscript was submitted to the Graduate School of that institution in partial fulfillment of the requirements for the degree of doctor of philosophy.

This publication does not mark the culmination of research on red rot. Instead it presents the best available answers to many perplexing questions and carries strong implications for continued study of the rot problem. Because of the differences between virgin and second-growth forests, basic studies must be continued for many years before the importance of red rot can be accurately evaluated for managed stands.

Red Rot of Ponderosa Pine

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Red Rot of Ponderosa Pine

INTRODUCTION

the Southwest (Arizona and New Mexico) and the Black Hills of South Dakota ponderosa pine (*Pinus ponderosa* Laws.) is the dominant commercial species, providing 90 to 95 percent of the annual production (16, 23).¹ In these two regions, gross wood volumes markedly reduced by red rot² caused by the fungus *Polyporus anceps* Pk. (*P. ellisianus* (Murr.) Sacc. & Syd. (1911)). In the past this rot was often confused with white rot caused by *Fomes pini* (Fr.) Karst., which primarily attacks ponderosa pine in the Southwest and Black Hills.

It has been estimated that at least 15 to 25 percent of the gross sawtimber volume of virgin stands in the Southwest is lost because of red rot (23) and probably the same amount is lost in the Black Hills. Old timberland areas, which are often littered with the remains of trees and logs (fig. 1), provide dramatic reminders of the losses. Although a large amount of this defective timber is usually disposed of in first cuttings, until the bulk of the overmature timber has been liquidated, there is a possibility that red rot will continue to reduce by significant amounts the gross volumes removed. Furthermore, even after conversion to second-growth stands has been completed, rot losses will not recede to the present level proposed as one objective of intensive management (39) unless indirect control measures are put into general practice and trees harvested when they are 120 years old.

Although losses were probably less impressive 40 years ago, when virgin stands afforded a seemingly inexhaustible supply of timber, decay in mature and overmature trees has been considered a serious problem since the start of commercial logging in the Southwest during the 1880's. After 1905, when the Forest Service assumed administration of the National Forests (renamed National Forests in 1907), timber records apparently substantiated general impressions of excessive cull and indicated the need for defectives, particularly in the Southwest. Early in the history of studies started in 1913 red rot was found to be the principal decay of ponderosa pine; it has received more or less continuous attention up to the present time. A limited part of the results of these studies has been published.

The purpose of this publication is to summarize existing information on red rot. Preparation involved reevaluation of the early work by W. H. Long and

others, as well as a reexamination of the data from more recent studies, parts of which have been published. In addition, hitherto unpublished results of new investigations have been included. The latter are concerned chiefly with the red rot fungus, but they will assist in developing control policies and methods for second-growth stands.

HISTORY OF PATHOLOGICAL STUDIES

Von Schrenk (45) was the first to recognize red rot as a disease of living trees. In 1903 he stated that, in addition to a common sap rot of insect-killed timber in the Black Hills, he had found logs with decay at the center that must have developed when the trees were still alive. This statement was supported by a photograph of red rot showing at the end of a cross-tie. Twelve years later Long (24) in reporting his slash decay studies in the Southwest noted that what he then called the "yellow-pine *Poria*" not only was the main agent in rotting cull logs and large branches of ponderosa pine slash but also was the cause of a serious and widely distributed heart rot of this species in Arizona and New Mexico. The following year he added that one form of the newly observed fungus closely resembled *Polyporus ellisianus*, and he used the common name "western red rot" for the first time (25).

Long (25, 26) intensified his attack on the red rot problem in 1914. The results of his work, mainly on timber-sale areas in the Santa Fe National Forest of New Mexico, seemed to indicate that the decay was of minor consequence in blackjacks. In 1935 Pearson and Marsh (40) pointed out that the high percentage of cull from rot in ponderosa pine could be attributed to the general overmaturity of the forests, and that in future generations the percentage of heart rot should decrease because few trees would attain an age of more than 200 years before cutting. At the same time, however, these authors cautioned that second-growth stands might be more subject to attack by decay fungi than old growth because of their more limby character.

Recognition of a potential heart rot problem in second-growth sawtimber was the outcome of an extensive survey of red rot in young stands that was made during 1933 and 1934. In summarizing the findings of this survey Long³ said that red rot was established in the butt logs of an alarmingly high proportion of the trees examined, in contrast to its infrequent occurrence in merchantable-sized blackjacks that he had studied earlier in virgin stands.

¹ Cyclic numbers in parentheses refer to the Literature Cited.

² This common name is preferred to Long's (25) "western red rot" and Hubert's (19) "red-ray rot." Otherwise, the common names of rots are in agreement with the latter author. The scientific names of rot fungi are in accordance with the International Rules of Botanical Nomenclature.

³ LONG, W. H. WESTERN RED ROT IN PONDEROSA PINE. Region 3, U. S. Forest Service. 6 pp. January 1934. [Typewritten report to the Investigative Committee; on file at Forest Insect and Disease Laboratory, Albuquerque, N. Mex.]



F-475709

Figure 1.—Old timber-sale area littered with the remains of cull trees and logs. Jarita Mesa, Carson National Forest, New Mexico. (Photo courtesy of J. L. Mielke.)

Long's report led to additional surveys, not only in the Southwest, but also in the Black Hills, and on two national forests in the northern Rocky Mountain area (the Salmon in Idaho and the Bitterroot in Montana). These surveys were planned to supplement the extensive observations of 1933-34, and, by improved sampling methods, to provide an immediate appraisal of the importance of decay in second-growth ponderosa pine. The ultimate objective was to develop a control program that could be undertaken, when required, during and with the least modification of routine stand-improvement operations.

Between 1930 and 1940 several studies, in which red rot was separated from other defect, were made by the Forest Service in connection with first and second cuttings of ponderosa pine. The most important of these was on the Wing Mountain Unit of the Fort Valley Experimental Forest at Flagstaff, Ariz. (11).

Pathological field studies since 1947 have been limited to the Southwest and have dealt with the relationship of red rot to pruning (2) and, to a lesser extent, to proposed thinning operations in immature stands.

THE RED ROT FUNGUS

Host Range and Geographic Distribution

The red rot fungus occurs throughout North America (although unreported it is presumed to be present in the pine forests of Mexico) and probably Europe⁴ and may be worldwide in distribution. Under the names *Polyporus anceps*, *P. ellisianus*, *P. stipticus* Fr., and *P. albidus* Fr. (the last 2 being European species names that were used for a few collections made after the 2 American species had been described), the fungus has been reported on 31 species of 7 coniferous

⁴ Based largely on collection records from herbariums maintained by the Branch of Forest Pathology, Division of Forest Biology, Science Service, Dept. of Agriculture, Ottawa, Canada; Division of Forest Disease Research, U. S. Forest Service (at Albuquerque, N. Mex., Asheville, N. C., Beltsville, Md., Madison, Wis., New Haven, Conn., Portland, Oreg., and San Francisco, Calif.); Horticultural Crops Branch, Agricultural Research Service, Beltsville, Md.; and the New York Botanical Garden, New York, N. Y. In addition, collection records from the personal herbariums of J. S. Boyce and J. R. Hansbrough of New Haven, Conn., were also used.

genera in 16 Eastern and 11 Western States, in Alaska, and in 7 Provinces and the Northwest Territory of Canada.

Numerous collections of the fungus on dead wood were made in this country before systematic observations were started in the Southwest. Consequently, Long's early reports (24, 25, 26) on the importance of the rot in Arizona and New Mexico must have alerted pathologists in other western regions to the potentialities of what had been considered strictly a slash decay fungus. It is probably significant, therefore, that there were no immediate reports of a similar rot problem elsewhere. In 1923 Boyce (9) noted that red rot was the most common decay in the sapwood of ponderosa pine felled on insect control projects in the Pacific Northwest. Later, Hubert (18) indicated that the rot appeared to be well distributed throughout the ponderosa pine regions and was of prime importance commercially, but it is apparent that his statement regarding its importance was based largely on Long's findings in the Southwest.

Red rot has been found in the heartwood of living ponderosa pine not only in Arizona, New Mexico, and the Black Hills, but also in California, Idaho, Montana, and Utah. It has not yet been collected in Wyoming. Heart rot is of negligible importance in California but causes significant losses in some localities of Colorado, Idaho, and Montana. There is no indication as to its importance in Utah, except that it has been reported only once. As a sap rot of dead ponderosa pine material, red rot has been found in all of the above States, except Utah and Wyoming where it is presumed to be present but not common. In addition, it has been collected in Nebraska, Oregon, Washington, and British Columbia.

Recently red rot has been identified as one of several heart rots in lodgepole pine (*Pinus contorta* Dougl.) in the Rocky Mountain region of Canada (36). Otherwise, information on the importance of the rot in other living conifers is incomplete, and is based largely on casual examination of fruiting bodies and decayed wood rather than cultural methods. In addition to ponderosa pine Hubert (18) lists red rot on the following species but does not distinguish between heart rot and sap rot: Jack pine (*Pinus banksiana* Lamb.), lodgepole pine, Englemann spruce (*Picea engelmannii* Parry), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) grand fir (*A. grandis* (Dougl.) Lindl.), western redcedar (*Thuja plicata* Donn), and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco). Boyce (10) omits the two species of true firs in his list of hosts. In the Southwest, Long (24) reported it in the heartwood of living limber pine (*Pinus flexilis* James) and as a sap rot in a cull log of Mexican white pine (*P. flexilis* var. *reflexa* Engelm.), and in a fallen Chihuahua pine (*P. leiophylla* var. *chihuahuana* (Engelm.) Shaw). He reported that the rot had not been found on Douglas-fir, white fir (*Abies concolor* (Gord. & Glend.) Lindl.), or Englemann spruce (24).

In view of the widespread occurrence of red rot as a sap rot of other conifers, virtual limitation of the heart rot to ponderosa pine in the Southwest and Black Hills has led to considerable speculation. This situation

may be explained in part by environmental conditions in the two regions that are more favorable to the development and spread of the causal fungus than other rot fungi. It may also result from the susceptibility of the host; this is suggested by the infrequent occurrence of red rot in associated species. Finally, it is possible that the fungus has several distinct varieties or physiological races. From an economic standpoint alone, the importance of red rot may be explained by the fact that it is the only heart rot of consequence in the dominant commercial species of the two regions.

Taxonomy

Following Long's report in 1916 (25) that red rot was caused by a fungus resembling *Polyporus ellisianus* (44), this technical name became generally accepted for the fungus in the Southwest. For many years it was believed that Long had no doubt as to its validity and there is considerable evidence in the Herbarium of the Forest Insect and Disease Laboratory at Albuquerque, N. Mex., that he considered *P. ellisianus* more or less specific to ponderosa pine. Most other mycologists (8, 46) and forest pathologists (10, 18) have tended to consider it the same as *P. anceps* (42), which was known to have a wide host range. *P. ellisianus* had been described in 1907 from material collected by J. B. Ellis on pine (*Pinus* sp.) in New Jersey. *P. anceps* had been described in 1895 from material collected by E. A. Burt on eastern hemlock (*Tsuga canadensis* (L.) Carr.) in Massachusetts. Murrill's descriptions for the two species, however, were sufficiently alike to lead to some confusion (33).

One objective of recent laboratory studies of the red rot fungus has been to determine if there is any valid reason for continuing to use the name *Polyporus ellisianus*. From a practical standpoint, retention of this name would eliminate much of the present confusion concerning the heart rot in living trees and the sap rot of dead wood. Another objective of the studies was to reveal aspects in the behavior of the fungus that would explain the importance of red rot in ponderosa pine, or its susceptibility to control.

The first southwestern collections of the red rot fungus were made by G. G. Hedgcock and Long between 1909 and 1911 and placed in the Herbarium of the Division of Forest Pathology in Washington, D. C. The fungus was not identified nor its pathological importance recognized at the time, and shortly afterwards Hedgcock (15) stated that in northern Arizona ponderosa pine was diseased more often by *Fomes laricus* (Jacq.) Murr. than by any other fungus.

Although Long did not repeat Hedgcock's error, for a brief period after he began his independent observations in the Southwest in 1913, he followed local practice and referred to the cause of red rot as *Trametes* (*Fomes*) *pini* (fig. 2). After about a year and a half of study, during which he (24) referred to the red rot fungus as "the yellow-pine poria," Long (25) reported that the fungus was similar, if not the same as *Polyporus ellisianus*. This name was selected with the concurrence of Murrill and E. A. Burt to whom he had sent portions of several collections.

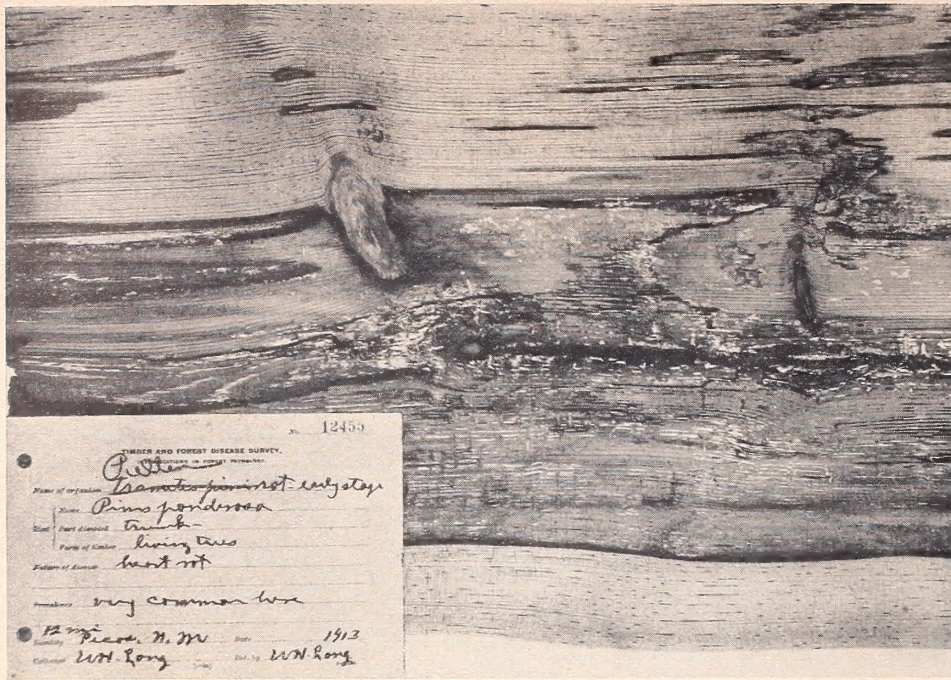


Figure 2.—Red rot in the heartwood of a 1-inch thick board typifying Long's early collections. Santa Fe (Pecos) National Forest. 1913.

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TREE AND FOREST DISEASE SURVEY
 (Continued on reverse)

Name of organism *Polyporus aniceps*

Host *Pinus ponderosa*

Part of host trunk

Part of lesion heart rot

Remarks very common here

Locality Pecos N. M. 1913

Collector W. H. Long Det. by W. H. Long

F-475691

Because of the morphological similarities of *Polyporus aniceps* and *P. ellisianus*, Long (26) added in 1917 that while the red rot fungus resembled *P. ellisianus*, he hesitated to use the name until he had completed certain laboratory investigations that were in progress. Records of these investigations indicate that in comparing cultures of *P. aniceps* from western redcedar and *P. ellisianus* from ponderosa pine he had noted some microscopic differences. A later reference to the red rot fungus as one that had previously been called *P. ellisianus* suggests, however, that the cultural differences had not proved significant (27). In 1923, Long wrote J. R. Weir that he had never been able to separate *P. ellisianus* from *P. aniceps* with certainty and felt that they were probably the same fungus. In spite of this, the tendency to consider them distinct species continued in the Southwest.

In 1924, Hubert (17) reported that he had evidence from laboratory decay tests with *Polyporus aniceps*, *P. ellisianus*, and a collection labeled "*Polyporus stipticus*" that *P. aniceps* was probably identical with *P. ellisianus* as used by Long. It is likely that the *P. stipticus* collection mentioned by Hubert and other collections of the species in this country were named by Weir, and according to Overholts (37) properly belong under the name *P. aniceps*. Weir also applied the name *P. albidus* to a few specimens that he admitted resembled the red rot fungus. More recently, Lowe (28) placed *P. albidus* under *P. immitis* Pk., but Weir's determinations coincide with *P. aniceps*.

So far as can be determined Kauffman (21) was the only mycologist who questioned the identity of Weir's western collections of *Polyporus aniceps*. In 1926 he pointed out that Weir had referred a western plant growing on *Larix* and *Pinus* to *P. aniceps* but that this

western polypore tended to become reddish or sordid stained in age, whereas the true *P. aniceps* remained white. Although at first Overholts (37) also stressed the unchanging color of *P. aniceps*, his later description (38) indicates that he was of the opinion that discoloration of sporophores had no taxonomic significance.

Shope (46) published the first diagnosis of *Polyporus aniceps* in which *P. ellisianus* was reduced to synonymy. This synonymy is not indicated in Lowe's (28) description of *P. aniceps*, primarily because he had no record of the occurrence of *P. ellisianus* in New York State. From Overholts' description (38) it is evident that after examining a number of collections from the Western as well as the Eastern United States he concluded that *P. aniceps* and *P. ellisianus* were morphologically identical. Overholts' opinion has been generally accepted in this country and Canada during the past 15 years.

As a result of cultural study of collections labeled both *Polyporus aniceps* and *P. ellisianus* from widely separated localities in the United States and Alaska, Baxter and Mannis (8) concluded that numerous cultural variations point to the fact that different races or strains exist and that the morphological distinctions largely in habit of growth are not great enough to consider *P. aniceps* and *P. ellisianus* as separate species.

Studies described on the following pages have confirmed the opinion that *Polyporus aniceps* and *P. ellisianus* are identical, and have also provided additional evidence of the existence of several varieties or strains of *P. aniceps*. On the basis of priority, *P. aniceps* must be accepted as the name of the red rot fungus, whether it is associated with heart rot or sap rot, although the original and subsequent descriptions of this species fail to indicate variations in western collections of the fungus.

Fruiting Bodies

Macroscopic Characters

According to Overholts (38) the macroscopic characters of the *Polyporus anceps* fruiting body or sporophore are as follows:

Sporophore sessile and often somewhat imbricate or more often effused-reflexed or entirely resupinate, watery-tough to corky when fresh, compact and rigid when dry, reviving; pileus 0-2 x 1-7 x 0.5-2 cm., white, concolorous on drying or becoming pale tan or brownish discolored, glabrous or very finely velvety-tomentose, rarely with a slight evidence of a thin cuticle on drying, azonate; context white, tough when fresh, firm and hard on drying, 4-10 mm. thick, bitter; pore surface white, or drying gray or yellowish, the tubes 2-7 mm. long, the mouths angular, rather thin-walled but entire, averaging 4-5 per mm.

In the Southwest and Black Hills, the effused or resupinate form is most common. The reflexed condition generally does not develop until sporophores begin to dry, and is rarely evident in those that age naturally because they are usually damaged by insects before they have dried to any extent. Connate,

imbricate, and unguulate sporophores sometimes form on the sides or exposed ends of cull logs, and on cull trees or leaning dead trees.

Sporophores vary from fleshy and watery-tough to subcorky when fresh. Some become firm or remain subcorky after drying and are not severely attacked by beetles. Others become friable and, in many cases, are riddled by insects. When moistened for hand sectioning, the context of friable sporophores has a cheesy texture, whereas that of the firm sporophores remains unchanged and can be readily cut.

Kauffman (21) correctly noted that some *Polyporus anceps* fruit bodies cover much more of the vertical surface of the substratum than did the type specimens. In the Southwest and Black Hills it is not uncommon to find sporophores extending along the undersides of cull logs for nearly the entire length of the logs and covering laterally the lower one-third of the circumference (fig. 3). Sporophores of this size often cover areas of 15 to 20 square feet. Smaller sporophores occur on small pieces of slash or on dead branches of living trees.



F-475706

Figure 3.—Scattered large fruiting bodies (sporophores) on the lower side of a cull log. The log was rotated about 90 degrees to expose the fruiting surfaces. Old timber-sale area. Pine Flat, Kaibab National Forest, Ariz.

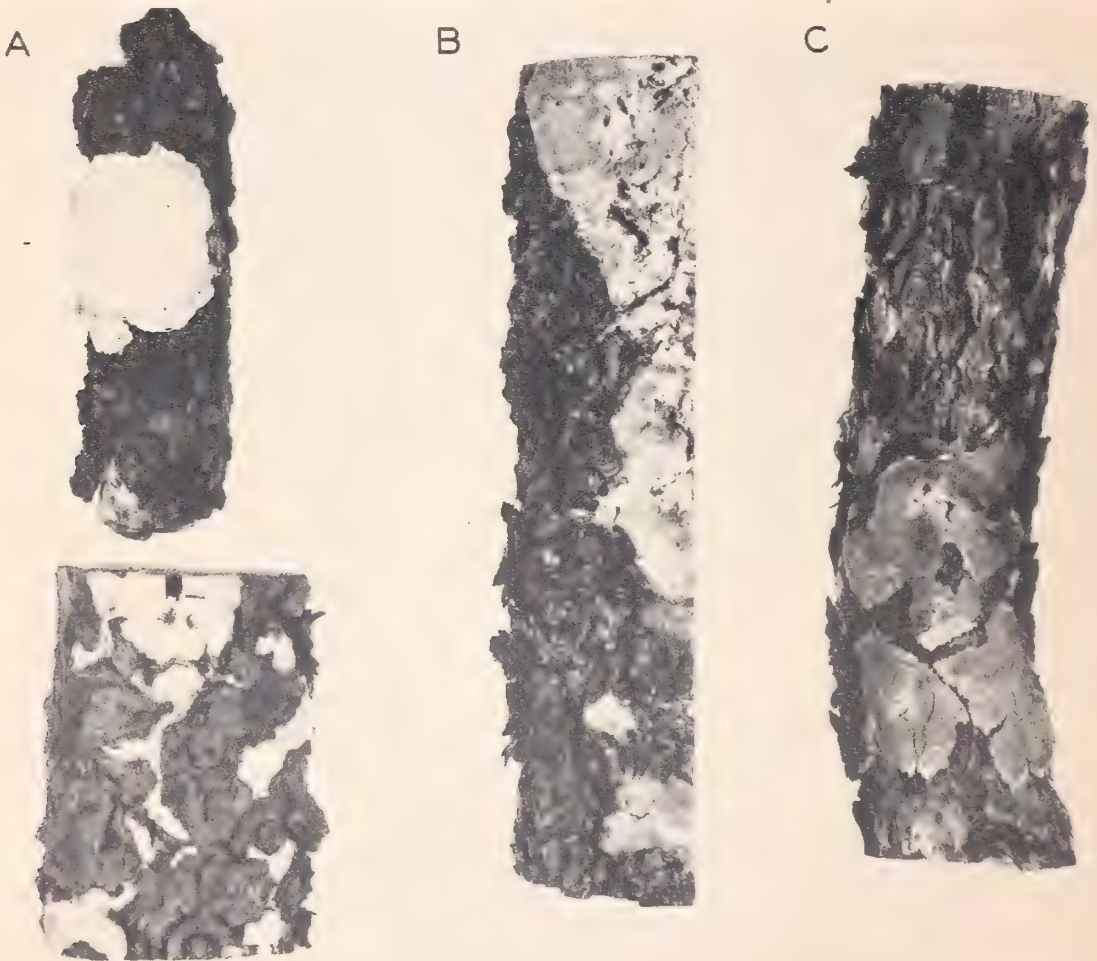
The upper surface of sporophores is highly variable. Resupinate forms are firmly attached to the substrate and the upper surfaces have none of the characteristics of exposed pilei. The appearance of upper surfaces is, therefore, of dubious diagnostic value. The margin is highly variable being either obtuse or acute, and either fertile or lacking in pores.

In the fresh condition *Polyporus anceps* fruiting bodies are white except where they have been damaged. In the dried condition there is considerable variation in color. In view of Kauffman's (27) conception of *P. anceps* as a species that remains white or whitish on drying, a request for information on the color of the fruiting or hymenial surface was included in a questionnaire sent to a number of herbariums⁵ during 1951. Data on color were procured for about 180 sporophore collections in addition to approximately 80 specimens in the Albuquerque Herbarium. Dark sporophores (matching or darker than b tones, mainly in Plates XIV, XV, and XXIX of Ridgway's Color

Standards and Nomenclature (43)) were much more common in western than in eastern collections (30 as compared to 10 percent). Furthermore, a much larger proportion (38 percent) of the sporophores from ponderosa pine had dark hymenial surfaces than was the case for other species of pine (19 percent) or for other coniferous genera (0-20 percent). Of the ponderosa pine collections from Arizona and New Mexico, 53 percent were classified as dark, in contrast to 40 percent of those from Colorado and the Black Hills, and none at all from other ponderosa pine regions. Examples of light and dark sporophores are shown in figure 4. Contrary to Overholts' (38) opinion, these differences in color are not the result of bruising and do not appear to be associated with maturity nor to the rapidity of drying after collection.

Of the 47 ponderosa pine collections in the Albuquerque Herbarium in which the hymenial surfaces could be studied in detail, 27 had thin and acute dissepiments (tissues separating the pores) the edges of which were often dentate or even lacerate. This percentage probably would have been higher if con-

⁵ See footnote 4, p. 2.



F-475692

Figure 4.—Examples of light and dark sporophores formed by *Polyporus anceps* on decayed dead branches. **A**, Light sporophores on detached dead branches from the Sitgreaves and Santa Fe National Forests. **B**, Dark sporophore on dead branch of living tree from the Coconino National Forest. **C**, Dark sporophore on dead branch of living tree from the Prescott National Forest.

clusive examinations could have been made of insect-damaged collections. In some sporophores the dissepiments varied from obtuse to acute, and this character may be dependent partly on the maturity and rate of development of the hymenial surface.

Friability, color, and thickness of dissepiments appear to be related and may have some genetic significance. To determine this, comparisons must be made between the cultural appearance and behavior of a large number of isolates from sporophore tissue. The present stock culture collection in the Albuquerque laboratory contains very few such isolates, and additional collections must be procured for further study.

Microscopic Characters

The microscopic characters of *Polyporus anceps* (fig. 5) have been described most completely by Nobles (35). Although her observations were made on sporophores that developed in culture, as Mounce (32) has pointed out, microscopic characters are generally the same in sporophores produced artificially and under natural conditions. According to Nobles (35), fruit bodies have nodose-septate hyphae (clamp connections at the septa), fiber hyphae, and well organized hymenia with basidia 5–7.5 μ in diameter bearing four spores that are hyaline, even, cylindric, 7.5–10.0 \times 2.2–3.0 μ . She does not mention hyphal pegs, which Mounce (32) considers to have taxonomic significance, and reports dendritically branched hyphae in only one of six *P. anceps* cultures upon which her description is based. Overholts states (37) that the demonstration of dendritically branched hyphae of the tube walls and context of fruiting bodies, as well as in the hyphae of cultures, is the only safe criterion for *P. anceps*. Allowing for differences in terminology, the extent to which mycologists have reported dendritically branched hyphae, fiber hyphae, and hyphal pegs in *P. anceps* sporophores is as follows:

Microscopic character:	Reported as—		Not mentioned
	Present	Absent	
Dendritically branched hyphae.	Lowe (28), Mounce (32), Overholts (38), Shope (46).	Nobles (35) ¹	Kauffman (27).
Fiber hyphae.....	Lowe, Nobles, Overholts, Shope.	Kauffman, Mounce.
Hyphal pegs.....	Lowe, ² Mounce, Overholts. ³	Shope.	Kauffman, Nobles.

¹ Reported in only 1 of 6 isolates studied.

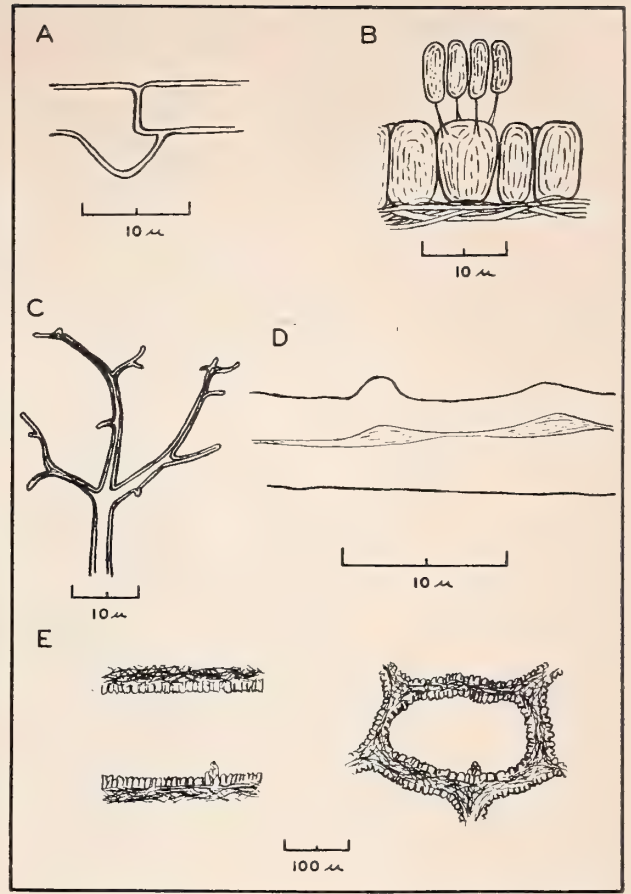
² Credits Mounce (36).

³ Reported short-conoidal hyphal pegs as occasional.

The lack of agreement on the occurrence of these characters suggests that careful study often is necessary to distinguish the species on a morphological basis alone.

Type collections of *Polyporus anceps* and *P. ellisianus* from the New York Botanical Garden have been carefully examined. Sporophores comprising both types are subcorky and not friable, although the *P. ellisianus* material is definitely darker than that of *P. anceps*.

Red Rot of Ponderosa Pine



F-475705

Figure 5.—Some microscopic characters of *Polyporus anceps* sporophores. A, Clamp connection (nodose-septate hypha). B, Longitudinal section of hymenium showing basidium bearing four basidiospores. C, Dendritically branched hypha. D, Fiber hypha. E, Longitudinal and transverse sections of a tube showing hyphal pegs projecting above the level of the hymenium.

Both types are characterized by fiber hyphae, dendritically branched hyphae, and hyphal pegs. The basidiospores seen in both collections were cylindric, hyaline, smooth, and, in some cases, very slightly curved, measuring 1.5–3.2 \times 6–7.2 μ in water. It is obvious that there is no microscopic morphological basis for considering the two collections as separate species. Microscopic examination of other light and dark sporophores indicated that the two types are identical with respect to microscopic characters.

Behavior in Culture

Origin of Cultures

Cultural studies of the red rot fungus were made with 33 mass isolates referred to either *Polyporus anceps* or *P. ellisianus*. For the eastern region the number of isolates studied per host were as follows: *Pinus banksiana* Lamb., 1; *P. resinosa* Ait., 1; *Picea* sp., 3; *P. glauca* (Moench) Voss, 2; *P. mariana* (Mill.) B. S. P., 1; for

the western region: *Pinus ponderosa* Laws., 21; and *Pseudotsuga menziesii* (Mirb.) Franco, 4. Fifteen of the isolates were selected from the stock culture collection maintained in the Forest Insect and Disease Laboratory at Albuquerque, N. Mex., and were from specimens collected in 10 national forests of Arizona and New Mexico, in the Black Hills of South Dakota, and in 1 forest in Utah. The remaining isolates were transfers from stock cultures in a number of other laboratories in this country and Canada,⁶ and were from specimens collected in at least 7 widely separated localities of the United States, and in 7 localities of Canada.

Variations in Appearance and Growth Rate

Nobles (35) and Baxter (6) have described the cultural appearance of *Polyporus anceps* in detail. According to Nobles (35), her isolates had the following appearance when incubated in the dark at room temperature:

"Mat white, newest growth raised cottony becoming appressed and felty in part with more or less extensive fruiting surfaces formed after two to six weeks consisting of small compact pored areas or broad zones covered with irregular pores or teeth. Reverse unchanged. Odor none."

Baxter (6) has suggested that *P. anceps* may be somewhat variable in appearance when incubated at 35° C., viz:

"3. Cultures not appearing watersoaked or arachnoid at 35° C., i. e., agar not visible from beneath the snow-white mycelium, or, if arachnoid in spots, the mycelium growing at such a rapid rate that it extends out between the lid and the dish . . ."

The watersoaked or arachnoid appearance is evident in 2 of the 3 cultures shown in Baxter's Plate II (6). The third is similar to the isolate illustrating Nobles' (35) cultures of *P. anceps*. Hereafter the watersoaked or arachnoid mats will be referred to as nonuniform types, in contrast to the more or less homogeneous felty mats which will be called uniform types.

According to Baxter (6), at 30° C. the mycelium of *P. anceps* appears distinctly flaky, i. e., does not exhibit a uniform growth, and develops so luxuriantly that it grows out of the petri dishes. Such lush development of aerial mycelium is almost entirely lacking at Albuquerque where relative humidities are exceptionally low during most of the year. The resulting loss of moisture from the atmosphere of petri dishes leads not only to a rapid decrease in the water content of solid media, but also to a desiccation of exposed hyphae, and a resulting reduction in aerial growth. Striking differences in the volume of aerial hyphae were noted in a number of the same isolates that were grown at both St. Paul, Minn., and Albuquerque.

To facilitate comparison with the results obtained by Nobles (35), the isolates studied at Albuquerque were grown under approximately the same conditions: in petri dishes of 1.5 percent malt for a period of 3 weeks in the dark at a room temperature of 22° C.

⁶ Mass isolates were furnished by Division of Forest Disease Research at Beltsville, Md.; New Haven, Conn.; and San Francisco, Calif.; and by the Division of Botany and Plant Pathology, Science Service, Dept. of Agriculture, Ottawa, Canada.

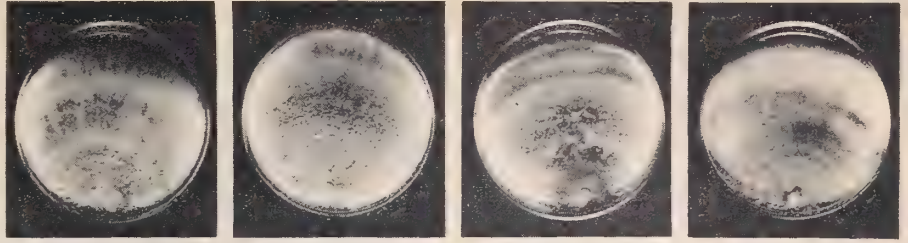
(20°–24° C.). Duplicate cultures were grown on 2.0 percent malt agar to observe the effect, if any, of this higher malt concentration, which was used for other cultural studies of the red rot fungus at Albuquerque. At the end of 3 weeks there were no important differences in the isolates on the two concentrations of malt agar with respect to growth rate or gross cultural characteristics. It was concluded, therefore, that results obtained with the 2.0 percent concentration were also comparable in other respects to those reported by Nobles (35).

Although grown at a lower temperature than that used by Baxter (6), 24 of the isolates (23 western and 1 eastern) had essentially nonuniform mats. In the older portions of the cultures the mycelium was water-soaked, appressed, or downy with scattered tufts of cottony aerial mycelium; in the younger portions there was a substantial, if not profuse, development of loose cottony aerial mycelium. The remaining isolates (7 eastern and 2 western) formed rather homogeneous cottony-felty mats with slightly fimbriate margins and, in most cases, distinct zonate-radiate markings. Limited watersoaked areas and the occurrence of vague zonate or radiate markings in some nonuniform mats suggested some overlapping of the two types. Examples of the uniform and nonuniform mats are shown in figure 6.

Baxter and Mannis (8) reported that *Polyporus anceps* (including isolates referred to *P. ellisianus*) was among the most rapid-growing forms of approximately 140 species in their laboratory. Nobles (35) also classified *P. anceps* as a fast-growing species. Both Baxter, in other studies (6), and Nobles (35) based rate of growth on the length of time in total darkness required for isolates to cover the surface of 1.5 percent malt agar in standard petri dishes. The former inoculated dishes at the center and incubated his isolates at 30° and 35° C. The latter inoculated dishes at the edge and incubated her isolates at laboratory temperatures. Inasmuch as both reported petri dishes covered in 2 weeks, it is natural to conclude that growth was more rapid at the presumably lower temperatures prevailing during Nobles' tests (35) than at 30° and 35° used by Baxter (6), and that *P. anceps* has a relatively low optimum temperature.

Tests were made to determine the number of days required for the isolates studied at Albuquerque, N. Mex., to cover the surface of 2 percent malt agar in 90 mm. petri dishes at room temperatures of 22° and 29.5° C. in diffuse light with a relative humidity of about 26 percent. Inocula from vigorous-growing stock cultures were planted at the centers of the dishes. Number of days was calculated from the date of transfers. At 22°, 14 (13 from ponderosa pine) of the 25 western isolates tested required only 7 days to cover the dishes, whereas none of the 8 eastern isolates covered the dishes in this length of time and most of them required 9 or 10 days. Of 6 isolates from ponderosa pine grown at 22° at both St. Paul, Minn., and Albuquerque, 4 grew more rapidly at the latter location, 1 at the same rate, and 1 more slowly. At 29.5° all but 2 isolates (both eastern) covered the plates in 6 days in the Albuquerque tests. These results sug-

EASTERN ISOLATES



WESTERN ISOLATES

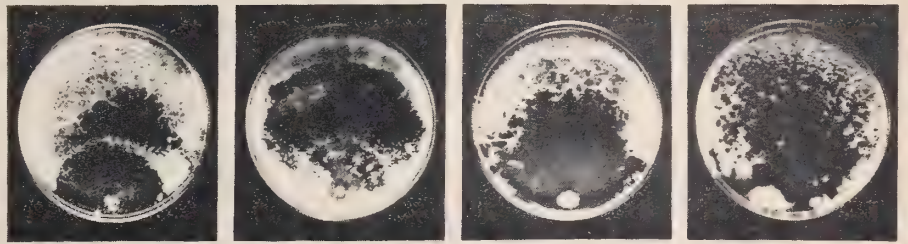


Figure 6.—Petri dish cultures of representative eastern and western isolates included in studies of the red rot fungus. Cultures on 2 percent malt agar after 7 days' growth in darkness at 22° C.

F-475703

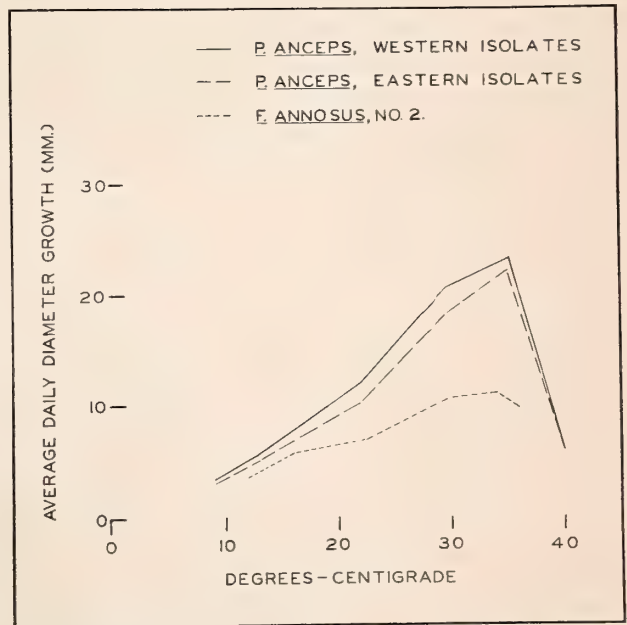
gested that *Polyporus anceps* had a high rather than a low optimum temperature, and that growth was more rapid at Albuquerque than had been observed elsewhere. The only exceptions to this generalization were transfers of 5 isolates from eastern Canada which grew somewhat more slowly at 22° than reported by Nobles (35) for her laboratory temperature.

Differences between eastern and western isolates suggested by these tests were verified by a comparative study of growth over a wide range of temperatures. All isolates were grown on 2 percent malt agar on 4 or more occasions in darkness at 9°, 13°, 22°, 29.5°, and 35.5° C. Some of them were also grown at 40°. Two transfers of uniform size (5 mm.) from week-old cultures of each isolate were placed opposite each other near the edge of a single petri dish. The petri dishes were not placed in temperature chambers nor growth measurements started until the isolates had become established in the agar of the dishes; this usually required 1 day; and the colony size at the end of that time was outlined with wax crayon. Diameter growth was determined from the marked outline.

Figure 7 gives the average daily diameter growth for the isolates studied. Although the western isolates had a greater mean growth at all temperatures except 40° C., the unsmoothed curves show that the two groups of isolates have similar temperature requirements.

Statistics on growth are given in table 1. Differences between western and eastern isolates appeared to be pronounced and relatively consistent at 22°, 29.5°, and 35.5° C. Diameter growth of the western isolates was more rapid than that of the eastern isolates

at all three temperatures: tests of significance of the differences in means indicated $P < 0.01$. However, the differences between the means of the four western



F-475704

Figure 7.—Average daily diameter growth (mm.) for 25 western and 8 eastern isolates when grown on 2 percent malt agar in darkness at 6 different temperatures as compared to *Fomes annosus* No. 2 (20).

isolates from hosts other than ponderosa pine and the eastern isolates were not significant at any of the temperatures analyzed. There were no significant differences in growth of western and eastern isolates or between ponderosa pine and eastern isolates at 9°, 13°, and 40°.

It is apparent from these studies that conditions at Albuquerque are conducive to rapid growth of *Polyporus anceps*, especially of the western isolates; that *P. anceps* is a very fast-growing fungus within a wide range of temperatures, inasmuch as the growth of eastern as well as western isolates exceeded that reported for the fast-growing *Fomes annosus* (Fr.) Cooke (20), particularly around 22°, 29.5°, and 35.5° C.; and that *P. anceps* is a high temperature fungus, all but three isolates having made most rapid growth at 35.5°.

Limited comparisons indicate that most of the *Polyporus anceps* isolates make more rapid growth on malt agar than other branch decay fungi found on ponderosa pine with the exception of some strains of *Stereum pini* (Fr.) Fr. As would be expected from the preceding discussion, this advantage in favor of the red rot fungus becomes more marked as temperatures rise.

TABLE 1.—Summary of average daily diameter growth of *Polyporus anceps* mass isolates grown on 2 percent malt agar at three temperatures

Temperature and isolates ¹	Growth		
	Mean	Range	Standard deviation
22° C.:	mm.	mm.	mm.
Ponderosa pine only.	12.2	10.6–13.4	±0.7
Western.....	11.9	8.5–13.4	±1.2
Eastern.....	9.5	8.0–10.6	±.8
29.5° C.:			
Ponderosa pine only.	20.5	18.0–23.7	±1.2
Western.....	20.4	18.0–23.7	±1.5
Eastern.....	17.9	16.7–19.2	±.9
35.5° C.:			
Ponderosa pine only.	23.3	20.0–27.3	±1.8
Western.....	23.4	20.0–27.3	±1.7
Eastern.....	21.9	19.5–24.1	±1.6

¹ Number of isolates tested; Ponderosa pine only, 20 at 22° C. and 21 each at 29.5° and 35.5°; Western, 24 at 22° and 25 at 29.5° and 35.5°; Eastern, 8 each at all 3 temperatures.

Reaction on Malt Agar Containing Gallic Acid or Wood Extractives

It has been reported that the reactions and rates of growth of wood decay fungi on gallic and tannic acid media are generally characteristic for a particular species (12). Early during the course of laboratory studies of the red rot fungus it was considered possible that the behavior of the different isolates on these media might provide evidence of the existence of more than one species. Although this did not prove to be the case, tests were continued on the assumption

that they might afford an acceptable method for distinguishing varieties or physiologic races.

The oxidase reaction of *Polyporus anceps* has been tested by workers in this country and Canada (12, 35). On gallic acid medium the reaction is very strong and growth varies from 0 to a trace;⁷ on tannic acid medium the reaction is strong but growth varies from a trace to 25 mm., or there may be no growth, in which case the reaction may be either positive or negative. Presumably most, if not all, of the isolates tested were from decay in the sapwood or from associated sporophores that had been collected from a number of hosts in widely scattered regions. Similar tests had never been made with cultures from the common heart rot of the Southwest, although some of the isolates used by Davidson, et al. (12) were from ponderosa pine in Colorado and South Dakota where decay in living trees is common.

In the Albuquerque tests, most of the isolates used in the other laboratory studies were grown on both gallic and tannic acid media on two occasions: during October and November 1949 and in December 1950.

Both reaction and growth were very erratic on tannic acid (reaction varied from weak to strong while growth varied from a trace to 68 mm.), and it was apparent that this medium could not be used to differentiate forms of the red rot fungus.

On gallic acid medium the reactions were uniformly very strong. On the other hand, growth was variable and in some cases it was appreciably greater than reported for *Polyporus anceps* (12, 35). Of the 13 isolates previously studied at other laboratories only 4 made less growth at Albuquerque. Of the 4, 2 had exceeded the upper limits of growth for *P. anceps* to such an extent in the earlier tests as to raise some doubt concerning the significance of the results.

Apparently variations in the composition of the media and difference in temperature can lead to unusual growth rates. In general, however, growth on the gallic acid medium was more rapid at Albuquerque than at Washington, D. C. (12), or Ottawa, Canada (35). Twenty isolates grew onto the gallic acid medium for varying distances, 13 growing 10 mm. or less, 7 growing more than 10 mm. Thirteen isolates either did not grow at all or showed only a trace of growth. Of the 21 isolates from ponderosa pine, only 5 or 24 percent remained within the *P. anceps* limits, and 6 or 29 percent grew more than 10 mm. onto the acid medium; the other 10 were intermediate. Of the 12 isolates from other species, 8 or 67 percent remained within the *P. anceps* limits, and only 1 or 8 percent grew more than 10 mm. onto the acid medium; the remaining 3 made intermediate growth. Seven of the 8 eastern isolates fell within the *P. anceps* limits, whereas this was the case for only 6 of the 25 western isolates. The rapid growth of isolates from ponderosa pine and of the western isolates in general agrees with the results of other cultural studies.

⁷ Davidson, et al. (12) define trace as growth limited to the agar transfer disk. In a memorandum dated January 15, 1951, however, Davidson indicates that growth less than 10 mm. in diameter probably was also considered a trace during the reported tests of *P. anceps*.

The reactions and rates of growth of a few typical eastern and western isolates of *Polyporus anceps*, as well as a number of other decay fungi that commonly attack ponderosa pine dead branches, were also compared on malt agar to which had been added extractives from the knots of this species. The purpose of the tests was to provide some explanation of the apparently unique ability of *P. anceps* to progress through the pitch infiltrated wood of knots. It was assumed that the fungus forms metabolic products that dissolve resins and related substances in the knots, which seem to inhibit all other decay fungi that commonly attack the outer parts of dead branches.

Some results of the tests are given in table 2. Although the extractives exerted an inhibitory effect on the western as well as on the eastern isolates of *Polyporus anceps*, the former made somewhat better growth in the higher concentrations of hot water and alcohol-benzene soluble extractives. These differences in growth probably are large enough to be in agreement with other cultural differences that have been discussed.

Quite unexpectedly, the other decay fungi, with the exception of *Fomes tenuis* Karst., were less affected (in terms of relative growth rates) than the *Polyporus anceps* isolates by the alcohol-benzene extractive. While the results were erratic because of the limited scope of the tests, there is an indication that the water-soluble extractives may be the controlling factor in growth of the other fungi. Failure of *F. tenuis* to survive in any of the plates containing extractive material is of interest because of its recognized inability to penetrate knots despite its abundance in dead branches.

Several noteworthy phenomena were observed during the tests. Zones of decoloration or discoloration

developed in all of the extractive media in advance of the expanding colonies of white-rot fungi. The appearance of the zones was similar to that associated with the oxidase reaction on gallic and tannic acid media (12). According to Southam and Ehrlich (48) similar rings of decoloration occurred when certain wood-decaying fungi were grown on malt agar containing the hot water soluble extractives of western redcedar heartwood. These authors suggested that the zones resulted from the leaching of metabolic products from the fungus into the surrounding medium.

About one month after the tests were started examination of the dried plates revealed that the surface layers of the alcohol-benzene extractive had lost their gummy consistency in all plates containing *Polyporus anceps*. Superficial study suggested that the fungus had induced a chemical as well as a physical change in the extractive, and this possibility is being investigated further.

The inconclusive results thus far obtained with extractives may be explained by the limited number of isolates included in the tests. It is also likely that higher concentrations of the extractives should have been used. Considerable improvement might have been obtained by homogenization of the alcohol-benzene extractive agar.

Compatibility of Eastern and Western Isolates

Inasmuch as Mounce (32) had found that *Polyporus anceps* as it occurred on ponderosa pine in British Columbia was heterothallic and bisexual, it seemed likely that the specific relationship of eastern and western types might be revealed by the method

TABLE 2.—Average ¹ daily diameter growth of eastern and western isolates of *Polyporus anceps* and other branch decay fungi on 2 percent malt agar to which extractives from ponderosa pine knots had been added

Fungus	Isolates	Growth on 2 percent malt agar—check on hot and cold water extractives		Growth on 2 percent malt agar plus ether ² —check on alcohol-benzene extractives		Percentage of growth on checks for—					
						Cold water extractive ³		Hot water extractive ³		Alcohol-benzene extractive ³	
		1	2	1	2	1	2	1	2	1	2
<i>Polyporus anceps</i> Pk.:	No.	mm.	mm.	Pct.	Pct.	Pct.	Pct.	Pct.	Pct.	Pct.	Pct.
Eastern	2	12	14	75	67	58	42	27	7		
Western	3	15	15	67	53	60	53	27	14		
<i>Fomes tenuis</i> Karst.	1	11	8	0	0	0	0	0	0		
<i>Lenzites saepiaria</i> Fr.	1	9	8	(4)	0	11	0	44	11		
<i>Polyporus abietinus</i> Fr.	1	8	8	25	12	12	50	75	75		
<i>Stereum pini</i> (Fr.) Fr.	1	4	5	(4)	(4)	75	75	100	75		
<i>Fomes pini</i> (Fr.) Karst. ⁵	1	2	1	(4)	100	50	0	100	50		

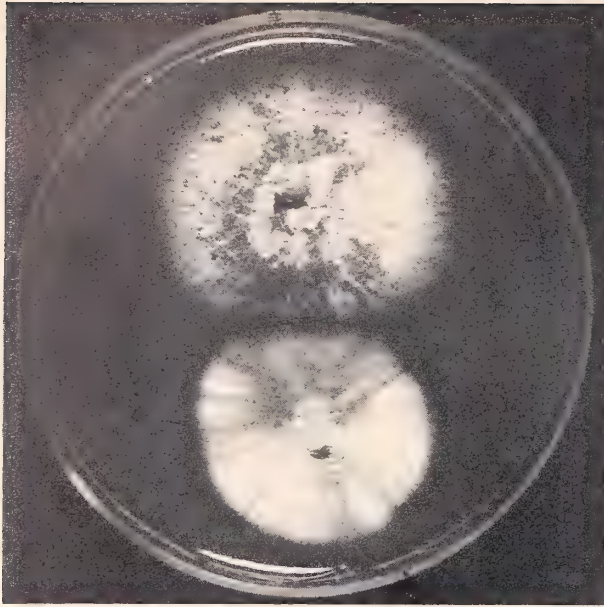
¹ Based on about 7 days' growth.

² Volume of ether used to introduce the extractive.

³ Concentration 1 was approximately 16 gm. of alcohol-benzene extractive, and 4 gm. each of cold and hot water extractives per liter of medium. Concentration 2 was approximately 32 gm. of alcohol-benzene extractive, and 8 gm. each of cold and hot water extractives.

⁴ Trace.

⁵ Rare in ponderosa pine but included because of its common occurrence in other conifers.



F-475695

Figure 8.—Petri dish containing 3-day-old transfers of monosporous mycelia of isolates from decay in the heartwood of a young ponderosa pine on the Kaibab National Forest in Arizona and from sap rot of dead white spruce at Madison, Wis.

Nobles (34) has termed the “interfertility” phenomenon. She states:

This method depends on the demonstration . . . that every monosporous mycelium obtained from one fruit body of a given species will pair with every monosporous mycelium from another fruit body of the same species from a different source, in such a way as to produce mycelium bearing clamp connections. This complete interfertility between monosporous mycelia is accepted as proof that the fruit bodies belong to the same species . . . Conversely, complete lack of fertility between monosporous mycelia from different fruit bodies indicates that the fruit bodies are of different species, although certain exceptions to this have been recorded. . . .

All of the mass isolates studied at Albuquerque formed clamp connections and presumably were dicaryons. Many, but not all, of them readily formed hymenial surfaces in both test-tube and petri dish cultures. Monosporous cultures were procured from 15 of the 33 isolates by a modification of the method used by Mounce (30). Eight such cultures obtained from an isolate from decay in the heartwood of a young ponderosa pine on the Kaibab National Forest in Arizona were matched in all possible combinations. Results of the test indicated that the isolate was heterothallic and bisexual.

An isolate from sap rot of dead white spruce (*Picea glauca* (Moench) Voss) at Madison, Wis., was similarly tested and found to be heterothallic and bisexual also. The appearance of typical monosporous colonies of these two isolates is shown in figure 8, and it can be seen that they represent fairly well the eastern and western types in culture. Four monosporous cultures from each mass isolate were paired in all combinations. Microscopic examination of mycelium after 2 weeks' incubation indicated that conspicuous clamp connections were present in all 16 pairings.

This test between single-spore cultures of typical eastern and western isolates provided additional evidence that the rapid-growing nonuniform types and the slow-growing uniform types belong to the same species. Further studies must be made to determine whether there are distinct varietal or racial differences between isolates and to what extent they are associated with host substrate, sporophore color, and cultural behavior. It is, of course, possible that the behavior of *Polyporus anceps* in ponderosa pine is more closely associated with host susceptibility and environmental factors than with differences in the fungus.

APPEARANCE OF RED ROT IN PONDEROSA PINE

The red rot fungus causes a typical white pocket rot in ponderosa pine (10). Fungi associated with rots of this type first decompose the pentosans and lignin, then the cellulose, and ultimately reduce the wood to a brittle residue (50). Like other wood decays, red rot may be considered as having two distinct stages; the incipient stage, and the advanced stage.

The incipient stage is characterized by a reddish-brown discoloration of the infected wood unaccompanied by any obvious changes in structure or strength. This stage is not preceded by an “invisible” attack, according to Hubert (18) who did not find cultural or microscopic evidence of the fungus in unstained wood in advance of the discoloration. The intensity of the color is usually low in dead sapwood and is recognizable only when it can be compared with adjoining uninfected wood. It is more pronounced in heartwood, which is naturally darker, and is most striking in the pitchy wood of knots where it may be dark brown to black.

The advanced stage is characterized by small white pockets in the stained wood accompanied by progressive changes in structure and a resulting reduction in strength. In radial or tangential view the pockets are of variable sizes and shapes with their long axes parallel to the grain, and they appear to be filled with a lintlike (cellulosic) substance. Sometimes they contain small black spots. At first only a few scattered white pockets are present. As decay continues, they become more and more numerous until they merge with one another and give the affected wood the appearance of a fibrous white mass. Finally, the white lintlike material disappears leaving the bleached grayish-brown decayed wood in either a stringy or a somewhat amorphous condition.

Although the appearance of affected dead sapwood and heartwood is about the same in both stages of decay, the manner in which infections originate results in differences in the overall aspect of red rot in the two types of wood.

As a Sap Rot

Dead sapwood is invaded radially by a generalized infection from a fungous pad beneath the bark that often covers a sizeable part of the surface of even large

cull logs. Once inside the wood, decay spreads rapidly in a longitudinal as well as in radial and tangential directions. As a result, practically all of the wood underlying the pad will show either incipient or advanced decay, but rarely a combination of the two stages in isolated streaks or spots. Sap rot is illustrated in figure 9, which shows both the incipient and the advanced stages in a section of a dead branch. This type of decay occurs in the sapwood of dead branches of living trees, standing or fallen dead trees, cut stumps, cull logs and tops, other logging debris, and occasionally in unpeeled round products in storage or in use.

As a Heart Rot

Heartwood is invaded longitudinally by a localized infection in the form of a decay column from a knot. Radial and tangential spread is initially slow in contrast to longitudinal development. As a result, the wood appears to be decayed in irregular streaks or pockets. Decay entering through knots is concentrated in the pith cavity or in limited parts of one or more annual rings and it tends to follow a similar path in the heartwood of the trunk. This type of rot occurs in the heartwood of living trees and large living branches. It can of course be found in heartwood of

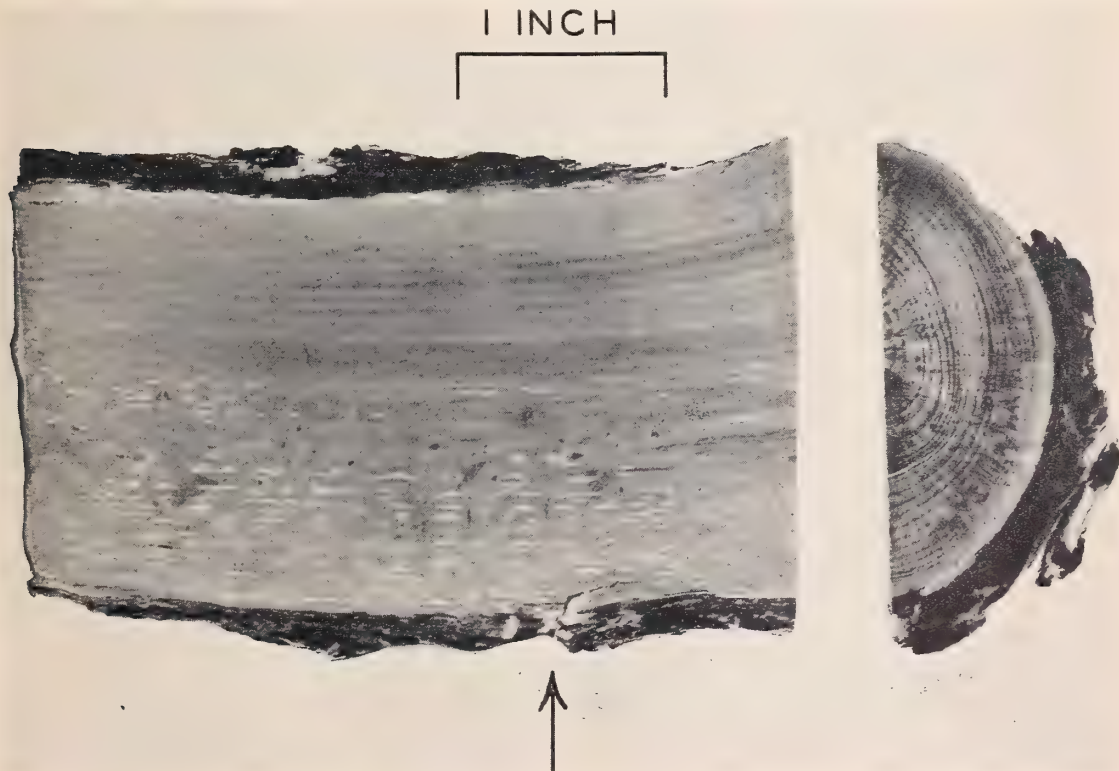
dead material, but usually the rot developed before death and is no longer active, although Hubert (78) has suggested that it invades the sapwood of cull logs. Red rot in knots looks very much like heart rot except that the pockets are smaller and more sharply delimited, probably because the high density and extractive content of the knots inhibits radial spread.

Long (26) recognized three stages of red rot in the ends of freshly cut logs. His description has been paraphrased to conform with the generally accepted concept of two stages of wood decay.

Incipient stage. The heartwood is firm but shows reddish to dark brown discolored areas. These areas are often fan shaped and radiate outward from the center of the log like spokes from the hub of a wagon wheel, or they may be isolated and occur anywhere in the heartwood (fig. 10, A).

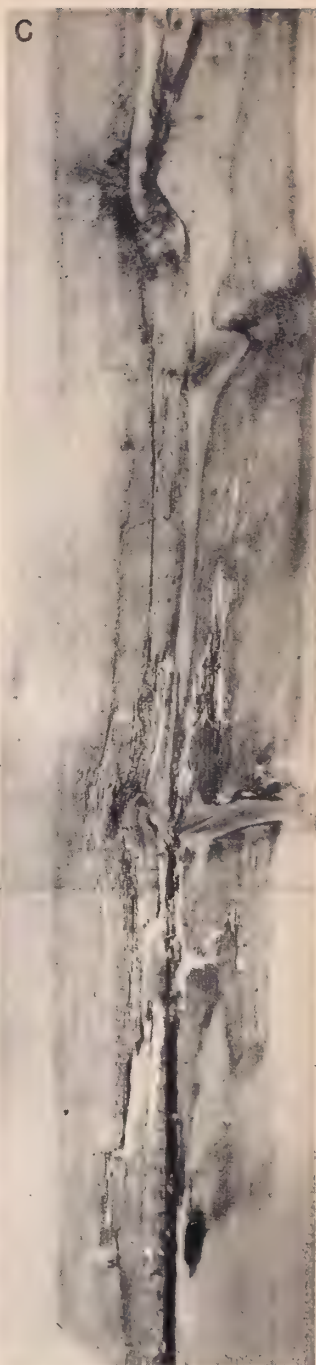
Advanced stage. The affected heartwood is whitish or grayish in color and is so disintegrated that small pieces can be pulled out. The rotted wood consists of soft white strands of cellulose intermixed with less rotted wood particles. The rotten wood in this stage is often so wet and soggy that water can be wrung out of it. This stage is usually in the center of the log and is often surrounded by the brownish fanlike areas of the incipient stage. Weathering results in disappearance of the cellulose strands, leaving straw-colored to dark brown wood elements reduced to a stringy or amorphous mass that ultimately falls away creating a cavity (fig. 10, B).

In longitudinal section, as on the surface of sawed lumber, incipient decay often appears as several



F-475697

Figure 9.—Sap rot in longitudinal and cross sections of a dead branch about 2 years after it was inoculated with the red rot fungus at a point indicated by the arrow. The incipient stage in the upper half of the longitudinal section is revealed only by a slight discoloration of the wood. The advanced stage in the lower half is characterized by small white pockets running parallel to the grain. The irregular white line between the bark and the wood on the upper side of the section is the edge of the fungus pad. The cross sectional view illustrates rapid radial invasion from the pad.



F-475964

Figure 10.—Appearance of red rot in the heartwood: *A*, Incipient decay showing at the end of a sawlog; *B*, advanced decay showing at the end of a sawlog. *C*, advanced decay bordered by incipient decay in the heartwood of a board from a cull log. The centrally located area of disintegration probably indicates that rot entered the trunk at this height.

apparently separate discolored areas, their long dimensions parallel to the grain of the wood. The discontinuous appearance results largely from the fact that the sawcut exposes only portions of one or more decay columns that tend to follow the spiral grain of the wood. In the same view advanced decay is more likely to appear continuous having spread enough radially to be present in several planes. The latter stage is characterized by the somewhat indefinite small white pockets that tend to run together. Finally, the white fibers disappear from the pockets, exposing the residual structure of the wood (suggestive of wood decayed by *Polyporus abietinus*).

Both stages of red rot are usually visible in a board or timber sawed from a decayed tree (fig. 10, C). At the point where rot started in the trunk heartwood, advanced decay often has resulted in a cavity around the knot. Extending in both directions from this point are more or less continuous columns of advanced decay bordered by incipient decay. The incipient stage extends longitudinally for some distance beyond the advanced decay. If rot entered the trunk through several knots, there usually are corresponding points of intense decay even if the columns have lost their individual identities.

THE ROT IN LIVING TREES

Sources of Infection

Presumably most, if not all, of the decay in living trees develops from spores released by fruiting bodies (sporophores) associated with the sap rot of dead material (18, 24).

Long (24) reported that fruiting bodies are produced most abundantly on cull logs (fig. 3) and large branches (4 inches or more in diameter) that are in direct contact with the ground, although they also occur on windthrown trees, stumps, and occasionally on dead branches of living trees. He believed that the red rot fungus rarely fruits on dead material that is a foot or more above the ground, although decay may be present.

Observations in a variety of blackjack and yellow pine stands since 1935 have confirmed this description of the fruiting habits of the fungus with a few exceptions. It is now known that fruiting occurs regardless of the size or location of dead material, provided decay has reached the advanced stage and moisture and temperature conditions are at an optimum. In warm moist situations, or in normally dry locations during and after heavy rains, fruiting bodies are common, if not abundant, on decayed branches less than 2 inches in diameter which are on the ground or attached to living trees, and on the latter they may be 5 feet or higher above ground. Fruiting at the same or greater heights occurs on cull tops and on the trunks of erect or leaning snags.

Fruiting of consequence probably does not occur until the fourth or fifth year after cutting or death, when rot in the underlying sapwood has reached the advanced stage, and it may be resumed periodically during the following 3 or 4 years. According to

Long (24) cull logs in warm situations may show early stages of rot during the third year following cutting and fruiting bodies appear shortly thereafter. In small branches, however, they may appear sooner, as rot is often pronounced during the second year, although it may have been present before the branches became detached from the trees.

Of 19 sporophore collections from timber-sale areas in Arizona and New Mexico, none was found on material that had been cut for less than 3 years, whereas 18 had developed on cull logs or other debris that had been on the ground 4 to 9 years. Fruiting bodies appear earlier on thinning slash in blackjack stands: they have been observed on stumps and trees cut only 16 months. This is probably explained by the favorable moisture and temperature conditions of dense young stands in contrast to parklike old growth, the high susceptibility of the slash which is mainly sapwood, and to the presence of slash in many dead branches before cutting.

Inasmuch as fruiting is common on naturally occurring debris as well as on that resulting from logging, thinning, and other woods operations, sources of infection are more or less widespread in virgin as well as in recently cut-over areas. The greatest number of fruiting bodies develop during the summer rainy season in Arizona and New Mexico, when the total precipitation for the 3-months' period, July to September, inclusive, amounts to about 8 inches and high temperatures prevail. Fruiting probably starts earlier in the Black Hills as a result of greater rainfall during May and June.

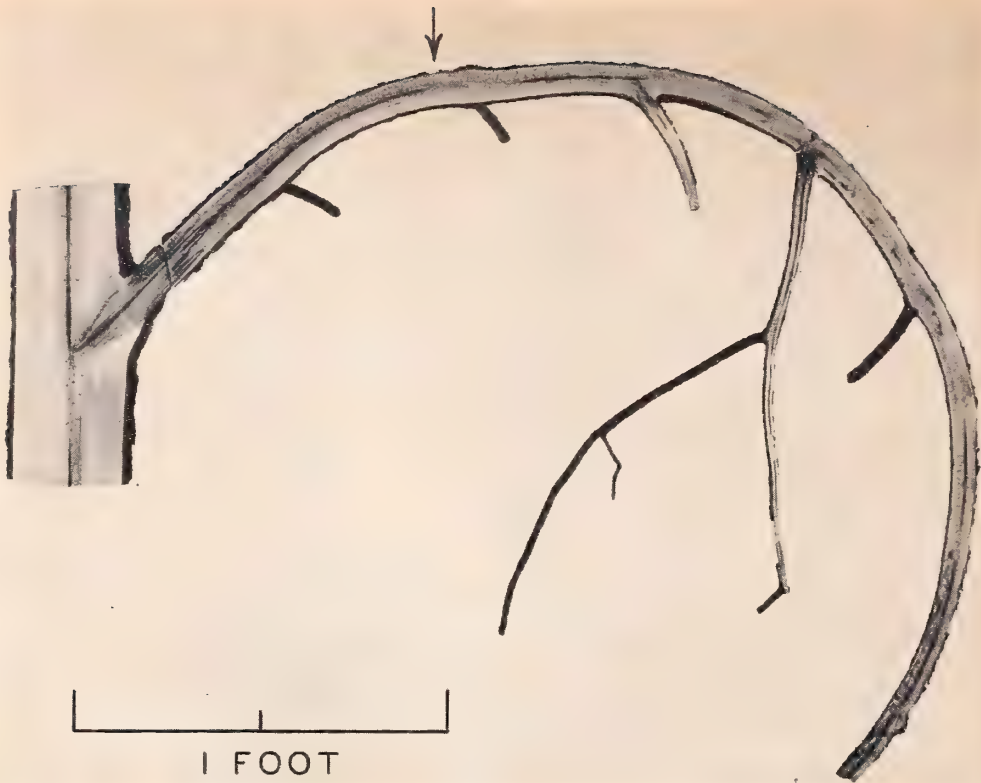
Means of Spread

Most infection is spread by airborne spores from the fruiting bodies rather than by some vegetative means. A number of beetles, mainly of the family *Tenebrionidae*, attack fruiting bodies and no doubt are covered with spores in the process, but they probably do not attack dead branches. On the other hand, some infection may originate from fragments of the fungus carried from decayed branches or down material to recently dead branches by species of *Ips*, *Pityogenes*, *Pityophthorus*, and related genera. Tunnels formed by these insects often appear to be the centers of typical fungus pads between the bark and wood. Considerable experimental work is needed before the methods of dissemination will be thoroughly understood.

Processes of Infection

Establishment of the Red Rot Fungus in Dead Branches

In 1915 Long (24) noted that the red rot fungus infected living trees through their dead branches. He did not show an infection entering the trunk through an unbroken dead branch (fig. 11), and for many years other pathologists with less familiarity with the fungus in the Southwest and the Black Hills, reported that it attacked trees through dead branch



F-475693

Figure 11.—Longitudinal section through a bark-covered dead branch and adjacent part of the trunk of a small blackjack exposing red rot that apparently originated at about the point marked by arrow. Decay had extended as far as the pitchy base of the branch where it had concentrated into slender, highly pigmented columns.

stubs and dead tops (7, 18). This misconception probably indicated a tendency to consider the behavior of many heart rot fungi similar to that of *Fomes pini* which Hartig (14) first reported infecting living trees through “branch-wounds” or stubs. The few pathologists who observed red rot in the Southwest apparently saw only old infections in which the decayed branches had been broken. Other pathologists who had not seen the rot in the field must have assumed that Long referred to branch stubs, or they did not appreciate that stubs rarely retain enough moisture to meet the requirements of the red rot fungus.

There is no experimental evidence that the fungus cannot establish itself in broken branches, but repeated examinations suggest that infection rarely, if ever, occurs in this way. Although branch stubs containing red rot are common on young ponderosa pine, in practically all cases they develop when the decayed and weakened branches break with their own weight or from the exertion of some external force.

The exposed surfaces of knots left after pruning are probably even less likely places for red rot to develop than branch stubs. Inasmuch as red heart caused by *Stereum sanguinolentum* (Fr.) Fr. had been reported to enter through the cut surfaces left after pruning large branches of eastern white pine (*Pinus strobus* L.) (47), approximately 1,500 knots of 8- to 13-year-old

pruning cuts were dissected and examined on 9 widely separated areas in Arizona in 1947 (2). In none of them was any indication found that red rot had originated in the exposed wood left after pruning.

The conditions necessary for infection of living trees were briefly summarized in an earlier publication (5). It was emphasized that the fungus establishes itself only in recently dead, bark-covered branches. Shrinkage cracks and a moderate number of insect tunnels probably do not preclude decay, but when appreciable areas of bark slough off, the wood becomes too dry for development of the fungus. The summary also stressed the fact that dead branches (exclusive of the buried parts or knots) did not have to contain heartwood in order to serve as infection courts.

Germinating spores or possibly vegetative fragments of the fungus become established in small cracks in the bark or in insect tunnels where moisture conditions are favorable. Optimum conditions for establishment are usually present when fruit-body production is at a maximum during the summer rainy season. Subsequent decay development in dead branches is the same as that described by Long (24) for slash and cull logs: the fungus begins its growth as a cottony layer between the bark and wood; this cottony layer grows into a firm, white pad that attaches the bark firmly to the wood; the wood itself is then invaded from the pad (fig. 9).

The significance of the pad to infection has not been discussed in previous publications (2, 4, 5, 24, 25, 26). In the first place, by attaching the bark firmly to the wood, it reduces loss of bark to a minimum and thus tends to maintain the moisture (including metabolic moisture produced by the fungus) content of the branch at a constant and near-optimum level for decay despite fluctuations in the relative humidity on the outside. In the second place, the fungus makes more rapid progress toward the base of the branch in the form of a pad than it does through the wood. Since wood is readily invaded from all parts of the pad including the advancing front, decay often appears in close proximity to the trunk although the fungus may have become established at a distant point. This process often leads to penetration of the trunk by the fungus shortly after the death of a branch.

It was first supposed that only dead branches with a basal diameter greater than 2 inches served as entrance points for the red rot fungus. This was the natural outcome of Long's (24, 25) early observations in virgin stands in which no systematic examination was made of small dead branches on the lower trunk because they were often buried in the wood of yellow pines or seemingly uninfected in blackjacks. He revised his original concept of the relationship of susceptibility to size after making observations in dense second-growth stands in which most of the small lower branches were examined⁸ regardless of size or appearance.

The relationship of branch decay to size of dead branches is given separately for the Southwest and the Black Hills in table 3. The table is based on data from plots in unthinned stands only in which practically all of the dead branches studied presumably had passed through the period of susceptibility to rot. It provides a good indication of the incidence of decay in large and small branches under natural conditions, and shows that the liability of an individual branch to attack is directly proportional to its size. Incidence of decay in small dead branches was much higher in Arizona and New Mexico than in the Black Hills. This may be explained by more favorable environmental conditions in the Southwest, which probably keep even small dead branches from drying out during periods when the fungus is most likely to become established. Similar rates of decay in large dead branches in the two regions probably resulted from the fact that the moisture content of the wood is not seriously affected by external changes.

It is generally believed that branches can be attacked by the red rot fungus as soon as any part of them dies, and that they remain susceptible to attack as long as they are covered by bark and are able to absorb and retain moisture during the summer rains. Broken branches or branches that have lost appreciable amounts of bark probably are no longer liable to attack, regardless of how long they have been dead.

The period of susceptibility cannot be determined accurately from natural branch decay. The volume of infectious material varies considerably in some

TABLE 3.—*Relationship of branch decay (red rot) to size of dead branches*¹

Basal d. i. b. (inches)	Southwest ²			Black Hills ³		
	Total branches examined	Decayed		Total branches examined	Decayed	
	No.	No.	Pct.	No.	No.	Pct.
Small, 0.6–1.5.	13, 671	487	3. 6	13, 046	129	1. 0
Large, 1.6+ . .	436	93	21. 3	924	201	21. 8
Total, or av- erage.	14, 107	580	4. 1	13, 970	330	2. 4

¹ Based on examination of pruned dead branches that occurred below a height of 17 feet.

² From 1,136 trees on 15 survey plots in unthinned 61- to 100-year-old stands.

³ From 574 trees on 8 survey plots in unthinned 91- to 110-year-old stands.

⁴ Infection in 0.6- to 1.0-inch class was 2.4 percent and in 1.1- to 1.5-inch class, 10.8 percent.

areas, depending upon the quantity of actively decaying material on the ground, and many branches presumably pass through the susceptible period without being exposed to attack. For example, advanced reproduction on a large sale area may be too young to be infected during the period of maximum decay activity in the logging slash and cull logs, whereas it may be highly susceptible 10 to 15 years later when activity of the red rot fungus has subsided. Observations on susceptibility are also complicated by the fact that decay in some branches may not develop enough to be recognized before the fungus dies, because of unfavorable environmental or biotic factors. Controlled experiments are needed to obtain reliable information on branch susceptibility.

Analyses of data on all dead branches (buried stubs or knots where the outer parts of branches had been shed) that were present on 206 trees dissected on 34 survey plots in the Black Hills suggest that the general trend of branch decay has been upward since 1796. Most of the branches that had died prior to 1896 occurred on a few plots in old-growth stands where the incidence of decay may have been determined by local conditions, and also in which many infected trees probably had already dropped out of the original stands. Consequently, table 4 presents the data for branches that died between 1896 and 1935 only. Information for this period was collected from a large number of plots that were widely distributed throughout the Black Hills, and should, therefore, reflect average rather than local conditions.

The table indicates that the highest incidence of red rot in the Black Hills was found in branches that had been dead 11 to 20 years. This is true for each of the three basal diameter classes that were used in the table to eliminate any effect of variations in branch size during the 10-year periods. The ascending trend of branch decay during the first 30 years (1896–1925) of the time covered by the table suggests that sources of infection were increasing, and may have been more

⁸ See footnote 3, p. 1.

TABLE 4.—Relationship between branch decay (red rot) and the length of time branches had been dead, in the Black Hills¹

Period during which branches died	Length of time branches had been dead as of 1936 ²	Basal-d. i. b. (inches)					
		0.6–1.0		1.1–1.5		1.6+	
		Total branches	Decayed	Total branches	Decayed	Total branches	Decayed
	(Yrs.)	No.	Pct.	No.	Pct.	No.	Pct.
1896–1905.	31–40.....	502	1	141	6	34	15
1906–1915.	21–31.....	702	3	233	10	72	24
1916–1925.	11–20.....	581	4	227	16	59	32
1926–1935.	1–10.....	234	1	87	9	46	15

¹ Data from 206 trees dissected during the intensive survey.
² As determined by the "callus-count" method (3).

abundant between 1926 and 1935 than in the preceding period even though rot incidence was lower. If this assumption is correct, it appears that branches which have been dead 11 to 20 years may be somewhat more susceptible to attack by the red rot fungus than those which have been dead 1 to 10 years. On the other hand, if the low rate of infection in the latter class is indicative of a period during which sources for infection were scarce, it is possible that such branches are equally if not somewhat more susceptible to attack than those that have been dead for 11 to 20 years. Inasmuch as bark was removed and the outer parts of all recently dead branches carefully examined for mycelial pads, it is doubtful that an appreciable number of cases of early decay were missed in branches that had died between 1926 and 1935.

Some rot becomes established in branches before they are entirely dead. This is possible because death associated with the suppression of primary branches is characterized by the progressive death of their twigs, lateral branches, and parts of the primary branches themselves during a period of gradual decline. Any of the dead, bark-covered woody parts may be attacked by the red rot fungus. Although branch decay of this type occurs in dense young stands, its existence does not seriously affect the generalization that tree infection occurs through dead branches. Such early decay does not precede the overall death of branches of moderate size by an appreciable period, and the fungus usually becomes established in primary branches themselves before any decay columns in laterals or twigs have extended to the trunk. On the other hand, infections often enter the upper trunks of mature and overmature trees through the heartwood in large living branches from decay that developed in dead secondaries. Living branches that contain little or no heartwood occasionally are infected from decayed secondary branches. In these infections the red rot fungus apparently is able to attack living, if somewhat devitalized, sapwood (fig. 12).



F-475698

Figure 12.—Red rot infection in the sapwood of a large living branch that developed from a decayed dead secondary branch.

Penetration of the Knot

Probably the most critical stage in the development of red rot occurs when the fungus is progressing through the knot into the heartwood of the trunk. Fortuitous circumstances, which will be discussed later in this section, may suddenly lead to inactivation or death of the fungus during this stage.

The knots of dead branches of ponderosa pine are heavily infiltrated with resin. According to limited laboratory tests for substances soluble in an alcohol-benzene mixture, about 25 percent of the oven-dry weight of knot wood is made up of resins and gums, as compared to about 18 percent for trunk heartwood and only 5 percent for sapwood. This high resin content is readily apparent from the dark appearance of the knot shown in figure 13 in contrast to the surrounding sapwood. Heavy deposits of resin in knots are generally considered to be an effective barrier against most decay fungi (29). Such a condition, as it occurs in Scotch pine (*Pinus sylvestris* L.) and other conifers in Europe, has been termed the protective wood zone by Liese (22) who pointed out that its formation was a dynamic process.

The deposition of resin apparently does not extend into any heartwood that may be present in the knot prior to death. In branches that do not contain heartwood, however, the entire knot, with the exception of the pith, is infiltrated with resin. Mayer-Wegelin (29) believes that this infiltration of resin extends outwardly and impedes decay even before it reaches the knot. Limited extractive tests (table 2) suggest that in addition to the physical barrier afforded by pitch, the water-soluble extractives may

be of considerable importance in inhibiting the development of other branch decay fungi in knots.

Like a number of other heart rots, red rot readily gains entrance to the trunk when the heartwood in a decayed branch and knot is continuous with that of the trunk. If it were the only avenue for infection, red rot would be relatively unimportant in dense young second-growth stands, because heartwood rarely develops in the small lower branches of immature trees.

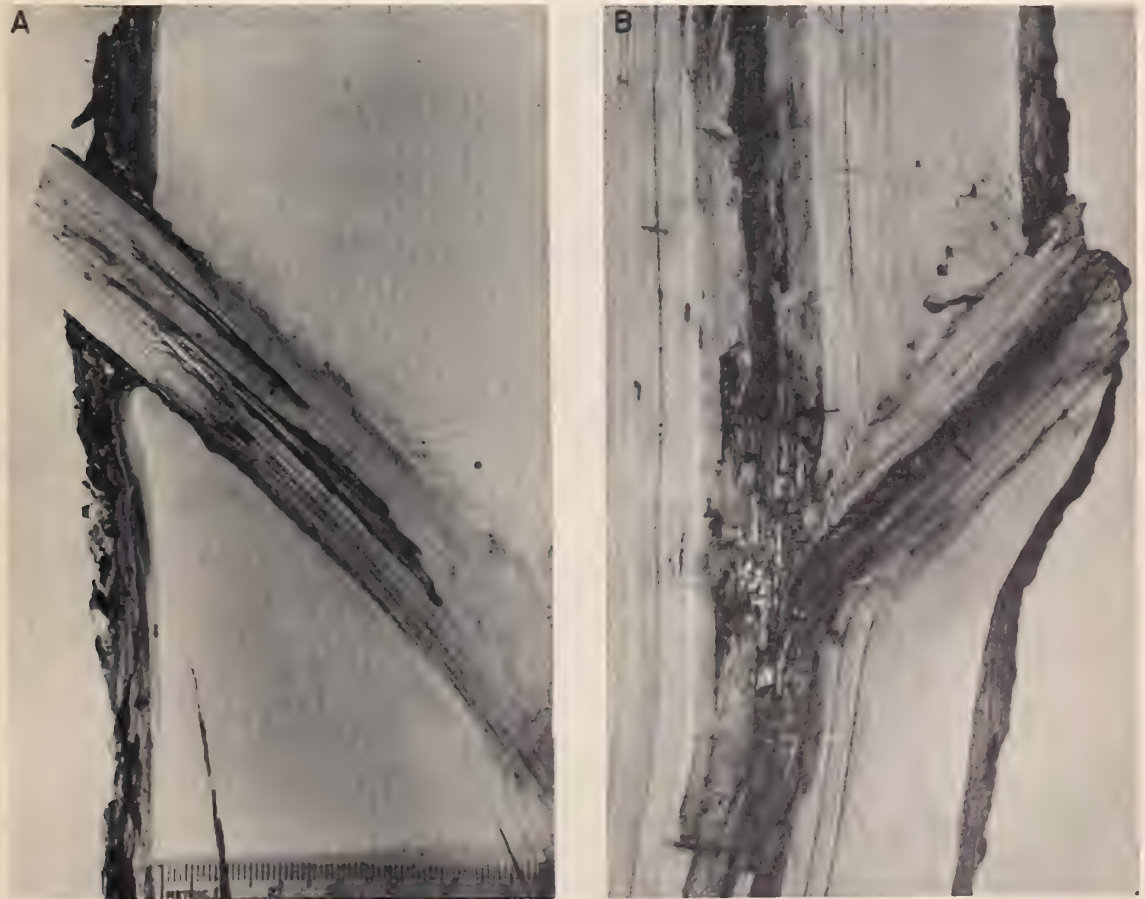
The importance of red rot in young stands, therefore, is explained by the fact that the fungus readily penetrates the knots and thereby reaches the trunk heartwood. In some cases it attacks the knot wood only, in other cases it travels through the pith cavity, and in still other cases it may be active in both wood and pith (fig. 13).

Haddow (13) found that *Fomes pini* can infect young eastern white pine (*Pinus strobus*) through very small "branch stubs" before any heartwood has formed. He indicated, however, that little is known yet of the nature of these courts and the manner in which infection takes place. This was true because in most of the stubs he examined, decay had reached the advanced stage and "punk knots" had formed. Until

the method of knot penetration has been observed in early *F. pini* infections, the red rot fungus must be considered unique among heart-rotting fungi because of its known ability to breach the protective zone. Nevertheless, recent observations and study of intensive survey (5) records suggest that the activity of the fungus in knot wood has been overemphasized. Actually, a majority of heart-rot infections enter through the pith cavities while decay columns in the adjoining wood often seem to remain behind in the knot (fig. 13, A).

Although the pith cavity offers little or no resistance to the fungus, it does not provide any nourishment. This may be of minor consequence if the fungus is still obtaining food from the undecayed parts of the outer branch. If the branch is broken off, the fungus may survive provided it has invaded wood adjacent to the pith to some extent, as was the case in the decay columns shown in figure 13. This invasion, which often occurs through needle-bundle traces, enables the fungus to fulfill its nutritional requirements from the knot wood.

Unpublished notes on 37 heart-rot infections found in the Cibola National Forest of New Mexico and the Prescott National Forest of Arizona during the in-



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Figure 13.—Radial-longitudinal sections of the trunks of infected blackjacks. A, Red rot extending about 0.2 foot into the knot. The central position of the longest column indicates that the red rot fungus made more rapid progress through the pith cavity than in the wood. B, Red rot infection that reached the trunk heartwood through the pith cavity of the knot.

Signs of Decay

Red rot is difficult to detect in living trees because fruiting bodies are rarely formed on them and then only on dead branches (10, 18, 26). Even if this type of fruiting were common it would be poor evidence of heart rot because ordinarily it is no more than a manifestation of advanced decay in the sapwood of the branch. The problem of recognizing infected trees is made difficult by the fact that the fungus does not require conspicuous entrance courts such as wounds, fire scars, or dead tops.

TABLE 5.—Survival of the red rot fungus in branches pruned in 1939 and in unpruned branches, 1949¹

Rot column	Pruned in 1939		Unpruned in 1939	
	Decayed branches	Fungus alive in 1949	Decayed branches	Fungus alive in 1949
Extending into—	No.	Pct.	No.	Pct.
Loose knot only ² . . .	9	0	11	55
Tight knot ²	47	19	35	74
Trunk heartwood	44	77	25	92
Total, or average . . .	100	43	71	77

¹ Based on cultural tests of rot specimens collected during the dissection and examination of 51 pruned trees, and 26 unpruned trees on and adjacent to 14 intensive plots in 5 national forests of Arizona and New Mexico.

² Loose knot is that part of branch overgrown after the branch died, as compared with tight knot, the part embedded before the branch died.

tensive survey (5) reveal that in 31, or 83 percent, the fungus had penetrated the knots principally through the pith cavities. A small dissection study made cooperatively with the U. S. Forest Service in pole stands of the Prescott National Forest during 1952 indicated that of 36 long-standing cases of branch decay, which had reduced the outer branches to stubs, 10 had the rot in the pith cavities (as seen on the surface of pruning cuts) and in 7 of them the rot had reached the trunk heartwood; whereas, of the 26 in which rot was limited to the knot wood, the rot had reached the trunk heartwood in only 4. Some of the latter infections that were limited to wood at the pruning cut invaded the pith cavities in the interior of the knots.

Infections in the knot wood sometimes cause more serious decay in the trunk than those that are limited to the pith cavities. This happens when decay columns leave the knots before reaching the center of the tree, often spreading into the outermost heartwood, and not infrequently into the living sapwood where the fungus acts parasitically and induces a large area of diffused decay and some pitch soaking similar to that shown in the living branch in figure 12.

Although other branch decay fungi (*Fomes tenuis*, *Lenzites saeplaria*, *Polyporus abietinus*, *Stereum pini*, and *Merulius ambiguus* Berk.) are abundant in ponderosa pine, they have never been observed to penetrate knots to an appreciable extent, nor have they been found associated with any heart rot. They are of primary interest because they decay dead branches that otherwise might serve as entrance points for the red rot fungus. This is particularly true in the case of *F. tenuis*. According to unpublished data from the intensive survey in the Black Hills (4) when this fungus was present in less than 10 percent of the dead branches examined the incidence of red rot appeared to be about average for the age and size of trees in the sample. When *F. tenuis* occurred more frequently, the occurrence of rot in dead branches dropped below the average. For example, on 2 plots in 115- to 140-year-old stands in which *F. tenuis* had attacked about 22 percent of the dead branches, red rot was present in only 6, and 13 percent of the standing trees, respectively, whereas the average for that age class was 30 percent. Since the location and extent of decay determine the effectiveness of these fungi in excluding red rot, information on their abundance alone is only suggestive of a protective action.

Evidence that the red rot fungus sometimes becomes arrested or killed before reaching the heartwood of the trunk, especially in connection with breakage or loss of bark, raised the question of the possible result of pruning decayed branches before the fungus had completely penetrated knots. A comprehensive study of this was made on a number of intensive survey plots in Arizona and New Mexico during 1949 (2), the results of which are summarized in table 5. Although not included in the table, evidence was procured during the study that the fungus is more susceptible to drying following pruning if located in pith cavities than in the wood.

Despite the lack of obvious indications of red rot, some method for distinguishing decayed mature and overmature trees and estimating volume losses before cutting has been sought as a guide to marking systems designed to harvest the most defective parts of old-growth*stands first. No practical method has been found. Although the lower and older parts of the trunks of yellow pines rarely are completely clear, decayed branches that were reduced to short stubs are most likely buried in the wood. Inasmuch as red rot does not induce the formation of swollen knots at the site of buried decayed branches such as are associated with red ring rot caused by *Fomes pini* (10), there are no external signs of heart rot in the lower trunks.

Although rotten branch stubs that protrude from the upper trunks can be seen from the ground, they are uncertain indicators of heart rot. It is usually impossible to make the close examination necessary to determine that red rot and not some other branch decay is involved, and that rot is actually present in the heartwood. Unbroken rotten branches on the upper trunks of standing trees cannot be recognized, except when they bear fruiting bodies. Consequently, they are of less utility than branch stubs as

signs of heart rot. Since the red rot fungus attaches the bark firmly to the wood, most branches or branch stubs that have lost appreciable amounts of bark are either sound or infected by some other branch decay fungus and can be disregarded. Differences in bark retention are significant in blackjacks as well as in yellow pines. The only exceptions in which red rot may be present, although the bark has sloughed off, are very old infections in which decay has reduced the exposed wood of branch stubs to a near-friable condition.

Even after trees have been felled estimates of volume losses are subject to error because all heart-rot columns are not necessarily exposed when the trunks are cut into logs. In the absence of surface signs, it is impossible to detect rot in logs cut from the lower trunks when they are sound at both ends. Similar cases of hidden decay in logs from the upper trunks are more likely to be revealed when trees are being trimmed, provided all branches and branch stubs are cut off close to the trunk. The presence of advanced decay in the heartwood or pith cavities of knots is usually reliable evidence of heart rot. Although the extent of rot cannot be estimated from these decay pockets, an exploratory cut can often be made in a long log that will expose any heart rot present; the rot can then be scaled and yet not reduce the resulting two logs to less than merchantable length.

The problem of detection is about the same in immature trees except that trunk infection, or potential rather than existing heart rot, should be the basis for discriminating against undesirable trees during stand improvement or other intermediate operations. Even though there are practically no obvious signs of infection, red rot is more easily found in young than in old trees. Most, if not all, of the dead branches on the former are still attached and relatively near to the ground so that they can be readily removed for close examination.

Red rot infection is negligible in trees less than 40 years old, and it cannot be determined except by systematically pruning and examining a large number of dead branches. Although the rot generally has been active for some time in trees between 41 and 60 years old, it has resulted in little breakage among infected branches. Infections that occurred when the trees were very young, however, are sometimes revealed by the presence of weathered decayed stubs on the lower 4 or 5 feet of the trunks. In view of the disintegrated condition of these stubs oblique cuts into the bark surrounding the stubs are necessary to get firm samples of the branch bases. Typical rot pockets in the pith cavities are indicative of well-established infections.

Bark-covered stubs that occasionally occur higher than 5 feet on 41- to 60-year-old trees are dubious signs of infection, because usually red rot was not the cause of the breakage. However, they are definite suspects. If the broken parts cannot be found on the ground at the base of the tree, the stubs must be removed and examined with the same care given to suspected unbroken branches. Particularly with long

stubs and branches having large basal diameters, some time may be saved by first breaking instead of pruning them. Branches in which there is no infection are thereby eliminated because they resist pressure and break with a crack. On the other hand, branches in the advanced stage of decay offer little or no resistance and break as though waterlogged. Any rot not obvious from this test can be readily recognized in the broken parts. Decayed stubs or branches must then be pruned close to the trunks and the cut surfaces examined. As in weathered stubs, potential heart-rot infection is present if rot is in the pith cavities. Since infection occurs in waves, during favorable periods, decayed branches tend to be located at about the same height on many trees in a stand. Once this height has become apparent on several trees, examination of the remaining stand is facilitated.

In blackjacks between 60 and 100 years of age a much higher proportion of the decayed branches have broken off than in younger trees. Bark-covered branch stubs are relatively reliable signs of the presence of red rot. As in younger trees the broken parts often can be found on the ground at the base of the trees and examined. Pruning is necessary, however, to determine if the trunks have been entered. When decayed stubs are not present, unbroken branches must be tested and examined as in younger trees.

In timber stand-improvement operations it is usually sufficient to know whether or not decay has entered the trunk of a tree, but in pathological surveys and research the intensity of infection must be determined. All dead branches must be pruned and examined and those that show no obvious signs of decay must be peeled to expose early infections.

Red rot can be readily separated from two similar branch decays by the characteristic rot pockets that appear in the pitchy base of the branch, if rot has progressed that far. In cases of incipient branch decay, it can be distinguished by the continuous white mycelial pad (fig. 9) that binds the bark so tightly to the wood that the bark cannot be peeled from the branch without particles of wood adhering. Of the other two branch decay fungi, *Fomes tenuis* forms a tan mycelial pad between the bark and wood, and *Polyporus abietinus* a white to brownish netlike pad, neither of which binds the bark to the wood.

ROT LOSSES IN MERCHANTABLE TIMBER

Evidence that red rot will cause serious economic losses in ponderosa pine under intensive management in the Southwest and Black Hills is indirect and incomplete. Such losses cannot be determined accurately for another 50 to 125 years, or at the end of the rotations for the 2 or 3 age classes forming the bulk of the present second-growth timber. In the meantime, the results of a few defect studies in old growth, in which red rot was separated from other defect, and the intensive surveys of immature stands (4, 5) provide some basis for loss predictions.

Losses in Virgin Stands

First Cuttings

For many years the importance of red rot in virgin stands was based on records collected by Long prior to 1916 on 6 timber-sale areas in the Cinega Ranger District of the Santa Fe National Forest of New Mexico. Red rot cull was found in 0 to 4 percent of the blackjacks and in 3 to 30 percent of the yellow pines, or in 2 and 14 percent of the 2 classes respectively when the areas were combined. Long (26) pointed out that the percentages for yellow pine were low compared with some other areas in Arizona and New Mexico. Although there should have been no doubt that the percentages applied to the number of trees having cull and not to the proportion of gross volumes affected, Long's failure to define infection must have resulted in some misinterpretation. His values, in fact, were so low that they were readily accepted as volume losses.

Later Long made several detailed studies of red rot in which merchantable trees (apparently all trees larger than 11.5 inches diameter breast high with at least one 8-foot log to a 5-inch top) were felled on small strips or plots and cut into lengths determined by the location of decayed branches or branch stubs. The results of these studies were never published, and complete records were found for only one that was made in Madera Canyon of the Santa Fe National Forest during 1917. No heart rot was found in the 25 trees recorded as blackjacks, all but 4 of which were less than 100 years old. In contrast to this, heart rot was found in 41 percent of the 126 yellow pines between 101 to 200 years old and in 76 percent of the 38 between 201 to 300 years old; or an average of 51 percent for the 2 classes combined.

The incidence of red rot among yellow pines cut in Madera Canyon is comparable to that found more recently by the Forest Service in the Cottonwood Wash Mill Scale Study and the Cochiti Grant Defect Study.⁹ Of the 372 trees cut in the 101- to 200-year age class in the 2 studies, 36 to 38 percent had red rot cull, in contrast to 60 to 64 percent of the 281 trees in the 201- to 300-year class. Rot cull amounted to 7 to 10 and 17 to 19 percent of the gross volumes cut in the 2 age classes. In another study made by the U. S. Forest Service in 1939 on the Deer Springs Unit of the Sitgreaves National Forest¹⁰ in which red rot was scaled as a separate defect, rot cull amounted to 10 percent of the gross volume cut in

⁹ Cottonwood Wash is in the Sitgreaves National Forest of Arizona. The logging phase of the mill-scale study was completed in 1936. Red rot was not always scaled and tallied separately from other defect, and percentages given are approximations based on a decay-age relationship for those trees in which rot was distinct. Cochiti Grant adjoins the Santa Fe National Forest of New Mexico. The defect study was made in 1940. Red rot was always scaled separately from other defect. The results of both studies were made available by the Southwestern Region of the U. S. Forest Service.

¹⁰ The data for this study involving 384 trees were also made available by the Southwestern Region of the U. S. Forest Service. Tree ages were estimated according to a modification of the Keen Classification (49) and not determined by ring counts.

Class III trees (150 to 225 years old), and 18 percent in Class IV trees (older than 225 years).

Results of these defect studies probably give a reasonable indication of red rot losses in first cuttings of virgin stands in the Southwest. Comparable losses probably occur in virgin stands of the Black Hills, but apparently no special studies have been made of red rot.

Second Cuttings

An estimate of losses that may be sustained in second cuttings of old-growth stands was obtained in the Wing Mountain Unit Defect Study (77, 39). The logging operation removed approximately 1,334,000 feet board measure of timber from the 456-acre extensive plot. This cut amounted to 49 percent of the volume on the area and 39 percent of the merchantable trees (11.6 inches d. b. h. and larger). No data are available on the amount of cull from red rot or total defect in the original cutting of this Unit, but defect percentages for virgin stands cut recently in the Fort Valley Experimental Forest (39) suggest that total defect amounted to 25 to 30 percent, of which perhaps one-half or two-thirds was caused by red rot, depending largely upon the degree of top utilization.

Most of the unit was marked according to Pearson's improvement-selection system (39), by means of which a large percentage of older blackjacks of all merchantable sizes was removed. In contrast to most of the other U. S. Forest Service timber sales, an appreciable number (132) of trees even younger than 100 years were cut. Cull from red rot was present in 4 percent of these trees and amounted to 1 percent of the gross volumes. In trees between 101 to 200 years of age (83 percent were less than 160 years old), rot was present in 24 percent and accounted for 4 percent of the gross volumes. In trees between 201 to 300 years of age, rot cull was present in 69 percent and accounted for 10 percent of the gross volumes. Red rot cull made up 6.1 percent of the gross volume cut in all age classes.

Table 6 shows the relationship between red rot and age by 10-year age classes. Although the incidence of rot cull increased markedly with age in the three youngest classes shown, the percentage of gross volumes culled because of red rot remained unchanged. Between 131 and 160 years, incidence continued to increase, and there was also a definite increase in volume losses. Relatively few (251 between 161 and 260 years) trees older than 160 years were cut and they have been omitted from the table. The incidence and volume of cull from rot in the older age classes were not as high as would be expected from the trends apparent in the younger trees. The original cut in 1909 must have removed many of the most defective older trees and mortality had been high among the residuals during the 30-year period ending in 1939. Obviously, those that survived for the second cutting contained relatively minor amounts of decay.

In second cuts of old-growth stands, rot losses will probably amount to about one-half the amount suffered in the original harvest operation and they

should decline with each subsequent cutting. As evident from the Wing Mountain Unit data, the magnitude of the losses will depend not only on the age classes originally present in the stands but also on the extent to which mature and overmature trees contribute to later cuts. Light selection or salvage type marking on a 20-year cutting cycle may tend to maintain red rot losses at a seemingly higher level for many years. This will be the case because many defective old trees that would have died between harvest operations spaced at 30-year or longer intervals will live for 20 years, and the cull volumes that would have been included with mortality losses will be charged as a defect deduction from the gross volumes cut.

TABLE 6.—The relationship of incidence and cull volume of red rot to age in trees removed in a second cutting of the Wing Mountain Unit, Fort Valley Experimental Forest, Ariz.

Age class (years)	Trees removed	Red rot cull	
		Incidence	Proportion of gross volume
	No.	Pct.	Pct.
101-110.....	43	2	1
111-120.....	189	7	1
121-130.....	220	14	1
131-140.....	570	23	3
141-150.....	875	27	4
151-160.....	140	37	6

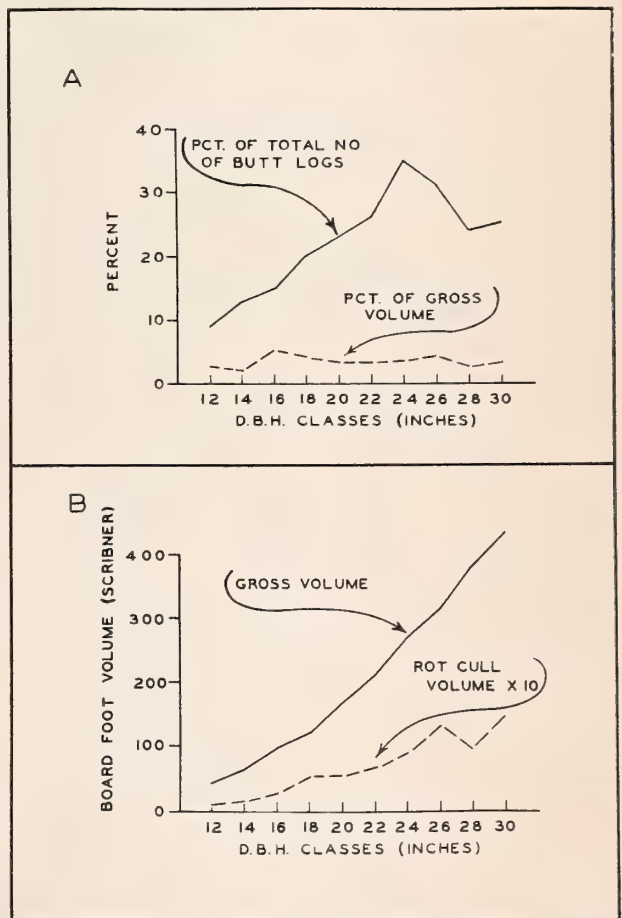
Losses in Second Growth

Because of the large number of 141-to 160-year-old trees cut (table 6), the Wing Mountain Defect Study (39) also provided some indication of the rot that can be expected at the end of a 150-year rotation, which has been considered as the maximum time required to produce sawtimber under management in the Southwest. About 29 percent of the 1,000 odd trees cut in this 20-year age class contained red rot cull amounting to 4.7 percent of the total gross merchantable volume. Butt logs, containing 54 percent of the total gross volume, accounted for 39 percent of the cull volume (a cull percent of 3.4). Upper logs containing 46 percent of the gross volume accounted for 61 percent of the cull volume (a cull percent of 6.3). Inasmuch as a mill-scale study was not made in conjunction with the logging study, no estimates of the volume of hidden decay could be made. It is possible however, that the scale of visible rot resulted in a large enough overrun to compensate for that which was hidden.

The relationship of rot cull in butt logs only to tree size in the 150-year (141-160) age class is shown in figure 14. From Figure 14, A it is apparent that there was a marked decrease in the percentage of logs showing rot cull in trees larger than 24 inches d. b. h. This is explained in part by the fact that some of the

larger trees on the Wing Mountain Unit were open grown and had large living branches extending almost to the ground. In such trees there had been little opportunity for infection and heart rot to develop. It is also apparent that although the percentages of gross volumes deducted for rot showed only slight fluctuations above 16 inches, there seemed to be a downward trend with increases in size. This trend is explained by figure 14, B which shows that, while rot cull volumes increased directly with d. b. h., gross volumes also increased at a more rapid and uniform rate.

Red rot does not occur uniformly over large areas even when there are no appreciable age differences between the small isolated groups of ponderosa pine that make up the stand as a whole. A number of even-aged groups were delineated by Pearson and Wadsworth (41) on the Wing Mountain Unit. Most of the trees in the groups were between 141 and 160 years old, although some were as young as 120.



F-475699

Figure 14.—Relationship of red rot cull in butt logs only to tree size in the 150-year (141-160) age class. Based on approximately 1,000 trees cut on the Wing Mountain Unit of the Fort Valley Experimental Forest in 1939. A, Percentage of logs with rot cull and percentage of gross volumes deducted for this cull. B, Average gross volumes compared with average rot cull volumes (multiplied by 10 to facilitate plotting).

Eight of the groups are listed in table 7. They were selected because a sufficient number of trees were cut to provide a good basis for calculations. Red rot cull was present in 12 to 47 percent of the trees and caused losses of 2 to 8 percent of the gross volumes.

As an indication of losses that can be expected when the present immature stands reach 150 years of age, the Wing Mountain figures may be low. Prior to the 1880's, and possibly for another 10 to 20 years, or during the first 90 to 110 years of their existence, the 141- to 160-year-old trees existed under virgin conditions, inasmuch as little or no logging had been done in the surrounding area. Since results of the intensive survey (5) have indicated that in the Southwest most dead branches below a height of 17 feet on 80-year-old trees are no longer susceptible to decay, in all likelihood, only a nominal amount of rot ever developed in branches below that height on the 141- to 160-year-old trees of the Unit. Any increase in tree infection associated with logging activity must have occurred through branches on the upper trunk, and probably was responsible for rather small volume losses, because of the short time that remained before the trees were harvested.

TABLE 7.—Incidence and cull volume of red rot in trees removed from isolated groups mainly in the 141- to 160-year-age class on the Wing Mountain Unit, Fort Valley Experimental Forest, Ariz.

Group	Trees cut	Average gross volume	Red rot cull	
			Trees	Gross volume
			Pct.	Pct.
	No.	Ft. b. m.		
A.....	55	370	47	8
R.....	31	410	13	2
C.....	106	290	30	5
E.....	35	240	20	2
K.....	52	410	25	7
F.....	28	300	25	5
26.....	25	470	12	2
31.....	73	400	32	5

Analyses of tree dissections made during the intensive survey in the Southwest (5) revealed that red rot is potentially more severe in unmerchantable young blackjacks than in merchantable-sized older trees. A comparison of the amount of rot present in merchantable trees included in the intensive survey and in comparable-aged trees cut on the Wing Mountain Unit gives some idea of the extent to which estimates from the defect study may be low for the Southwest as a whole. A limited basis for such a comparison was obtained by including all merchantable trees on 5 intensive survey plots in 91- to 120-year-old stands. From the incidence of trunk infection in 135 standing trees and the amount of heart rot found in a mechanically selected sample of 20 infected trees, it was estimated that of all the butt logs 18 percent had scaleable rot amounting to 3 percent of total gross volume. Of the 289 trees in this age class cut on the

Wing Mountain Unit, only 5 percent of the butt logs had rot amounting to 1 percent of the total gross volume.

It is anticipated that rot losses will rarely drop below 5 percent in second-growth stands on a 150-year rotation. They may be reduced to one-half this amount, if trees can be cut when they are 120 years old. Earlier cuttings probably would be considered commercial thinnings, and the net effect on losses at the rotation age would depend on whether the marking tended to eliminate or retain infected trees. This estimate does not allow for the possible effect of earlier intermediate operations such as pruning and thinning which will be discussed in connection with control measures in immature stands.

ROT IN IMMATURE STANDS

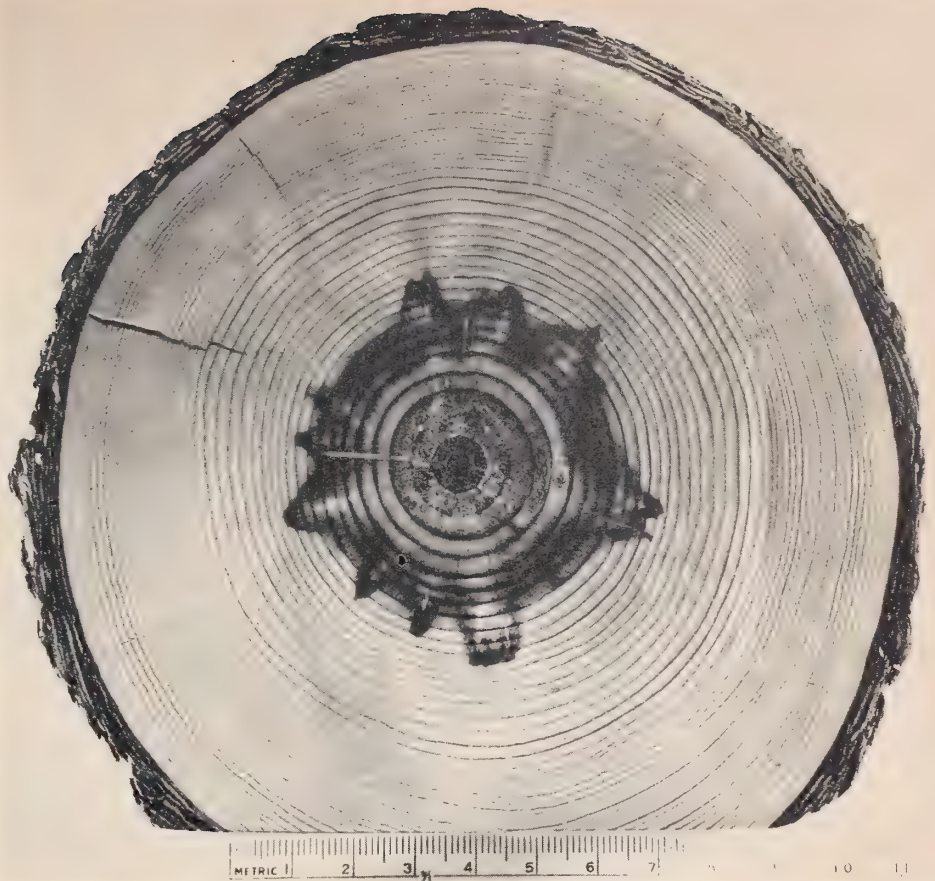
As early as 1915 (24) it was recognized that red rot is just as likely to occur in healthy as in declining yellow pines. Not until 1934,¹¹ however, was it fully appreciated that even young vigorous blackjacks are susceptible to infection. The fact that heart rot is common in mature and overmature trees, and apparently rare in immature trees does not mean that susceptibility to red rot infection is directly associated with the slowing down of physiological processes that characterizes old age. It means only that the probability of infection taking place and heart rot developing increases with age. Consequently, although red rot causes virtually no economic losses in immature timber, it must be considered a disease of all age classes except seedlings and saplings.

The minimum age of infection is determined by the presence of one or more susceptible dead branches. Trunks are usually invaded within a few years after the red rot fungus becomes established in the outer branches. The time then required for the fungus to reach the trunk heartwood is highly variable and dependent on the length of the knots, but it may be short if infection occurs through the pith cavities. Development of heart rot, although rapid in a longitudinal direction, may be retarded radially by the small amounts of heartwood in young stems. Once it is established, however, the fungus may stimulate heartwood formation (fig. 15). It is possible that infections can be well established and active for many years without being readily detected and without causing appreciable volume losses.

If sources of infection remain at a more or less constant level, the progress of red rot in a stand parallels the normal development of ponderosa pine from the sapling stage to maturity. All but the open-grown stands that occur along the margins of the type contain a large number of seedlings per acre initially. For example, stands that originated during 1914 in the Sitgreaves National Forest had 10,000 to 40,000 stems per acre 12 years after establishment (39). Such stands of even-aged reproduction usually are only a fraction of an acre to a few acres in extent because they tend to originate in openings in the forest. During the first 20 years branches below a height of

¹¹ See footnote 3, p. 1.

Figure 15.—Cross section taken at about 25 feet on the trunk of a tree about 100 years old showing red rot in the heartwood, which includes the four innermost rings. The surrounding discoloration in what would normally be sapwood is an early or invasion stage of the decay.



F-475707

2 to 4 feet above ground are shaded out in all but the open stands before reaching appreciable size. Most of these branches are too small to be attacked by the red rot fungus. The lower branches on open-grown trees or trees along the borders of dense groups attain larger size but they live longer and, therefore, are not susceptible to infection until later in the life of the stands. In general then, red rot is rare in stands less than 20 years old. During this period the rate of natural thinning largely determines the extent to which the stands will be susceptible to later infection. Competition for moisture is severe and usually leads to heavy mortality among the less vigorous saplings. Although the stands are still overstocked, most contain less than 5,000 trees per acre when 20 years old. Reductions in the number of stems per acre result in more rapid growth of the remaining trees, and early dominance is expressed by increased height and diameter growth; this is more apparent in the Southwest than in the Black Hills, where many young stands stagnate. As a consequence of improved growing conditions the branches of dominant individuals particularly grow to greater size before being shaded out, most of them being 0.6- to 1.0-inch basal diameter or larger at the time of death. When stands are 40 years old in the Southwest and 60 in the Black Hills, the living crowns have receded to a point 8 to 12 feet or more above the ground, and an

appreciable number of susceptible dead branches are present.

Only a few lower branches are susceptible to infection on 20-year-old trees. Thereafter, the number of such branches increases, eventually leveling off when it includes all that have been dead for 20 years or less. Then as the lowermost branches break off or lose some of their bark and become too dry for decay development additional branches die in the lower crown, and the zone of susceptibility progresses up the trunk. Inasmuch as branch size increases directly with height above ground, and inversely with stand density, relative susceptibility also increases. Thus while trees may have been continuously vulnerable to attack from the time they were 20 years old, they are much more likely to be infected by the time they reach 40 years of age by reason of the greater number and size of dead branches on the trunks. In view of these changes, it is obvious that the incidence of red rot increases during this period under natural conditions, although it may still be low.

When stands have reached an age of about 60 years in the Southwest and 80 in the Black Hills, practically all of the branches below 17 feet have died, and in another 20 years even the highest of these are no longer susceptible to attack. By this time, although the infection potential for butt logs has reached a maximum, few if any of the decayed branches have

broken off and there are no obvious indications that red rot is present. Figure 16 illustrates the appearance of stands during this stage of development. After these ages, decayed branches begin to break off, and the resulting stubs sometimes serve to indicate infected trees. Furthermore, such stubs are usually associated with long-standing infections that have invaded the trunk and some of which may already be established in the heartwood. Beyond this time the status of infection in the first 17 feet of the trunk remains unchanged, except for heart rot that may extend down from a higher entrance point. Branches of increasingly greater size and susceptibility die as the crowns recede above 17 feet. Stands continue to thin out, sound as well as defective trees dropping out as a result of suppression or from the action of a variety of outside agencies. Finally, there remains a relatively open stand of 75 to 150 trees per acre bearing few, if any, external indications of decay on the clear or nearly clear lower trunks.

Intensive Surveys in the Southwest and Black Hills

The intensive surveys in the Southwest (5), Black Hills (4), and the Salmon and Bitterroot National Forests¹² were designed to get estimates of the prevalence and severity of red rot in second-growth stands in terms of butt-log infection (the lower 17 feet of trunks) and associated heart rot. In accordance with the ecological concept of infection, it was assumed that if stands of different ages and densities were sampled, trends in the development of decay could be used to predict volume losses at maturity.

Certain differences in the intensive surveys in the Southwest and Black Hills, which were described in detail in earlier publications (4, 5), limited the extent to which the results have been combined in this publication. These differences resulted from the fact that analyses of the Black Hills' data were practically complete before work started in the Southwest and demonstrated that some procedures could be improved. In the former about one-half of the plots were located in stands that had been thinned. Because of the recognized need for thinning to relieve stagnation in the Black Hills, it seemed desirable to determine the amount of red rot in the residual trees, many of which presumably would be pruned later. It was found, however, that reductions in density led to anomalies that made the samples unsuitable for statistical study. In the Southwest, therefore, the survey was restricted to undisturbed stands. This was a logical change inasmuch as very little second growth had been improved by the crop-tree method

¹² Results of the survey in these forests indicated that red rot was negligible in contrast to the Southwest and Black Hills. An average of only 1.0 percent of the trees were infected on 11 plots in the Salmon National Forest, and 1.8 percent on 9 plots in the Bitterroot, the maximum infection being 7 percent in an 80-year-old stand in the latter forest. Because of the low incidence of red rot, none of the trees were dissected. For these reasons data from the two forests are not included in the remaining discussion.

that had replaced separate thinning and pruning operations (39).

Although infection was determined by pruning and examining dead branches below a maximum height of 17 feet in both regions, the minimum size of trees and dead branches included in the examination was reduced in the Southwestern survey. Preliminary tests of the survey methods in the Black Hills had indicated that by including all trees larger than 3.5 inches d. b. h. and examining all dead branches with a basal diameter greater than 0.5 inch, practically all red rot infection could be detected. Following comparable tests in the Southwest, however, the d. b. h. limit was reduced to 2.5 inches and no minimum diameter was set for branch examination, although branches that were 0.5 inch or smaller were tallied only when they contained red rot.

Some modifications were also made in the method of selecting trees to be dissected. In the Black Hills 10 percent of the plot trees were dissected, regardless of infection. In the first year (1935) they were mechanically selected in order to obtain a representative sample of the size classes present: every tenth tree was picked after the plot trees had been arranged in order of increasing d. b. h. In 1936 they were selected without regard to size by cutting all trees on a transect amounting to one-tenth of the plot area. Particularly in the younger stands, these methods resulted in dissecting many uninfected trees and obtaining little information on red rot.

Consequently, the method of sampling was changed for the Southwestern survey so that 20 percent of the infected trees were dissected. These were mechanically selected by the same procedure used in the Black Hills during 1935. In older stands in which some of the lower branch stubs had been overgrown by the trunk and the results of the examination were inconclusive, a comparable sample was also taken of apparently uninfected trees. In the Black Hills the knots of all dead branches on the dissected trees were collected for later study in the laboratory, whereas in the Southwest collection was limited to those containing red rot.

Survey observations were made in the Southwest on about 5,700 standing trees (230 of which were felled and dissected) on 66 plots and in the Black Hills on about 2,000 trees (206 of which were felled and dissected) on 34 plots. The sample from 41- to 100-year-old stands in the Southwest, which is frequently referred to in the following discussion, amounted to about 3,850 trees (including 177 dissected trees) on 46 plots on the Carson, Cibola, and Santa Fe National Forests of New Mexico, and the Kaibab, Prescott, and Sitgreaves of Arizona.

Infection

Red rot is more abundant in the immature stands of the Southwest than in those of the Black Hills. In that part of 41- to 100-year-old stands larger than 3.5 inches d. b. h., infection amounted to 29 percent



F-475708

Figure 16.—View of an intensive survey plot in a 100-year-old ponderosa pine stand. Forty percent of the trees to a minimum d. b. h. of 3.6 inches were infected below 17 feet. Black Hills National Forest, S. Dak.

in the Southwest as compared to only 15 percent in the Black Hills. Inasmuch as 13 of the 16 plots in this age class in the Black Hills were located in stands that had been thinned and a large number of small and hence uninfected trees removed, differences between the regions are probably even greater. Although additional trees are more likely to be attacked in the Black Hills where maximum butt-log infection is not reached until trees are about 100 years than in the Southwest where the maximum occurs about 20 years earlier, some differences in infection and heart rot probably will be evident at maturity. In general, however, the development of red rot is sufficiently similar to justify application of the results obtained in one region to the other.

The criterion for infected trees (the presence of one or more decayed branches with decay columns extending into the trunks in the first 17 feet or butt-log part of the trees) that has been used in all analyses of the intensive survey data, tends to minimize the relationship that exists between red rot and the normal development of immature stands. According to this standard, trees with only one decayed branch have been given the same weight as those with many

decayed branches in calculating the incidence of infection. Intensification of infection in individual trees, however, is generally reflected by an increase in the proportion of the stand affected.

Relationship to Age

This relationship is difficult to demonstrate by a comparison of stands of different ages. Since the red rot fungus enters trees only through branches that have been dead for 20 years or less, the lower 17-foot parts of the trunks eventually become immune to attack, and the incidence of rot in butt logs does not exceed a certain level regardless of increases in age. Furthermore, environmental factors and the local abundance of fruiting bodies of the red rot fungus may also exert a stronger effect than age, particularly in younger stands. Finally, most samples from stands older than 100 years cannot be alined with the infection trends evident in young stands. This probably may be accounted for either by the generally lower butt-log infection that developed under virgin conditions or by the loss through mortality of a number of infected trees from the older stands before the survey plots were established.

Notwithstanding these limitations, infection was found to be significantly correlated with age ($r=+0.34$) when all 66 survey plots in the Southwest were used. The linear regression equation (percent infection= $10.5+0.19$ age) had no practical utility, however, because of the high standard error of estimate. Also the slope of the regression line indicating an increase in infection of only 1.9 percent in 10 years, appeared to be contrary to expectations and was attributed to the inclusion of the six plots from older stands. Consequently, further analyses were limited to stands that did not exceed an age of 100 years.

For purposes of statistical study a minimum age of 41 years was also set. This limit was originally necessitated by the fact that younger stands were not sampled in the Black Hills. While they were included in the Southwestern survey, it was evident from early tests that infection was not only poorly correlated with age but also with other tree and stand characteristics. This was attributed to the fact that the trees in these stands had been susceptible for such a brief time that incidence of red rot depended almost entirely on whether or not there had been one or more periods especially favorable for the spread and development of the fungus.

In an earlier publication (4) it was reported that butt-log infection in the Black Hills increased with age in thinned stands between 41 and 80 years of age: 5 percent in the 41- to 60-year class, and 10 percent in the 61- to 80-year class of the trees were infected. These percentages were based on averages for all plots and in this form the data could not be tested for statistical significance. A later unpublished analysis¹³ indicated, however, that assuming a linear relationship, there was no significant correlation between infection and age on the 13 plots in thinned 41- to 100-year-old stands. These results tended to confirm a similar analysis of the data collected in the Southwest (5) in which it was found that the coefficient of linear correlation between infection and age for the 46 plots in the 41- to 100-year class was not statistically significant ($r=+0.14$). On the basis of these tests, age was eliminated from further consideration of infection (but not heart rot where the relationship is clear), although it was recognized that a causative relationship existed.

Relationship to Other Characteristics of Trees and Stands

This relationship in the 41- to 100-year age class in both the Southwest and the Black Hills was described at length in earlier publications (4, 5). In the latter region 13 of the 16 plots were located in thinned stands. As has been suggested, in addition to the obvious effect of reductions in densities on infection, thinning alters the proportions of the various size and

vigor classes present in stands to such an extent that normal trends of red rot cannot be determined. For the 13 plots in thinned stands, coefficients of linear correlation between infection and several characteristics of trees and stands were not significant.

Statistical analyses (5) of the data from the 46 plots in 41- to 100-year-old stands in the Southwest revealed that butt-log infection was highly significantly correlated with the percentage of large-branched trees ($r=+0.76$). Large-branched trees in the Southwest were considered to be those having one or more dead branches with a basal d. i. b. greater than 1.0 inch. This index of size was selected mainly for simplicity and ease of application, and it is possible that a more complex one based on the probability of decay occurring in the different branch-size classes would have resulted in a higher correlation. Infection was also highly correlated with the percentage of trees larger than 5.0 inches d. b. h. ($r=+0.76$). Although this index of tree size was found to be superior to average d. b. h., and more readily calculated, it is quite possible that a larger size would have improved the correlation. An inverse relationship between infection and density was also highly significant, the coefficient of correlation for a parabolic curve being 0.58.

Although the relationship of infection to branch and tree size and density was originally illustrated (5) by a composite stand table for all 46 plots in the 41- to 100-year class, as presented in figure 17, this relationship was developed for the data from 18 plots in 41- to 60-year-old stands in the Sitgreaves National Forest.

Table 8 shows some of the characteristics of the three density classes into which the data were divided. Fourteen of these plots were located in pole stands in a large body of virgin ponderosa pine where there had been little logging activity and the only sources of infection were those associated with normal decay activity in old-growth stands. Although the remaining four plots were located in cutover areas, they were not excessively infected. It is obvious that the infection shown is not the maximum that would have

TABLE 8.—Descriptive data for 3 density classes in composite stands, based on 18 survey plots in 41- to 60-year-old stands in the Sitgreaves National Forest, Ariz.

Density class (trees per 0.1 acre)	Mean density	Basis plots	Infected trees	Age	Average tree height to base of crown	Average dead branches per tree	
						Total 0.6 inch and larger	Large (1.1 inch and larger)
Open (75 or less) . . .	No. 41	No. 3	Pct. 53	Yrs. 50	Ft. 15	No. 16	No. 3.0
Medium (76-150) . . .	127	8	23	50	22	9	.7
Dense (151 or more) .	207	7	19	52	22	5	.3

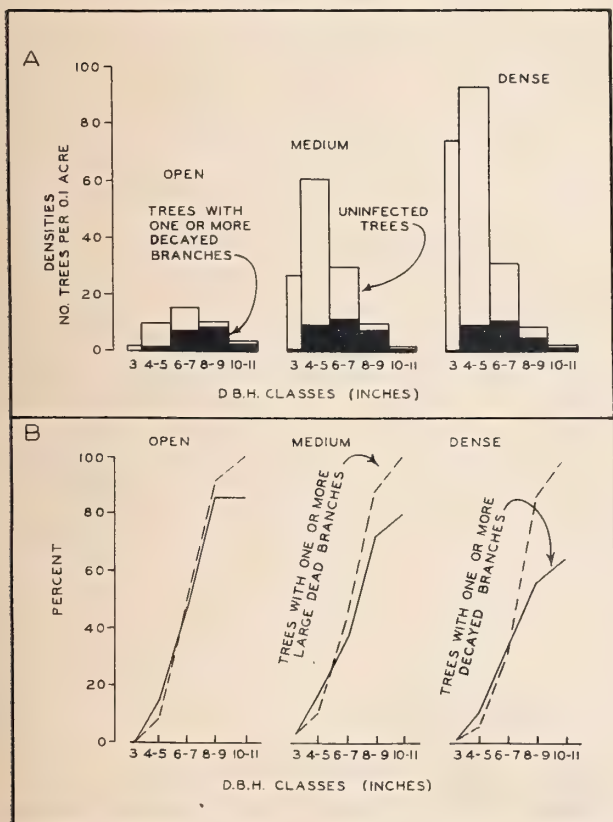
¹³ LARSON, HAROLD V. STATISTICAL ANALYSIS OF THE BLACK HILLS WESTERN RED ROT SURVEY DATA. Graphs, tables, and computations. Undated. [Files, Forest Insect and Disease Laboratory, Albuquerque, N. Mex.]

Development of Heart Rot

developed in butt logs. Presumably that point would not have been reached in all plot trees for another 20 to 40 years, if the stands had not been disturbed.

The bar diagram in figure 17, *A* shows the average number of infected and uninfected trees by 2-inch diameter classes for these density classes. This is supplemented by figure 17, *B* showing unsmoothed curves for the corresponding percentage infection and the percentage of large-branched trees. In addition to showing the close relationship between infection and tree and branch size in stands of approximately the same age but of different densities, the figure indicates that:

- (1) The denser stands contained more infected trees per acre. Over a long period, however, mortality will probably offset this. Furthermore, an increase in butt-log infection is more likely to occur in the open stands, as additional large branches below the 17-foot point die and become susceptible to decay.
- (2) On a percentage basis, red rot infection was higher in open stands. The denser stands contained a large number of small-branched and consequently uninfected trees.
- (3) Regardless of the density, infection percentages were high in trees 8 inches d. b. h. and larger.



F-475700

Figure 17.—Relationship of red rot to d. b. h. in three density classes. Averages for 18 plots in 41- to 60-year-old stands in the Sitgreaves National Forest, Ariz. *A*, Bar diagram showing number of infected and uninfected trees per one-tenth acre. *B*, Unsmoothed curves showing percentages of infected and large-branched trees in the stand.

The amount of heart rot in immature stands is usually small, although it varies widely in different trees. Rot volumes expressed either in cubic or board feet are insignificant. They depend largely upon the cross-sectional areas of decay that may remain negligible for many years in immature trees that contain only small cores of heartwood. For these reasons, the length of rot columns has been used as the most satisfactory expression of heart rot for purposes of analysis.

As might be expected from the limited infection present, heart rot was rare in the sample from 21- to 40-year-old stands. Of the 31 infected trees in this age class that were dissected in the Southwestern survey, only 2 had heart rot averaging 0.01 foot.

Once it is established in the trunk, heart rot development is primarily a function of time, and the length of rot columns appears to be closely associated with age in the 41- to 100-year class. Changes in length with age for the 60-year period were sufficiently pronounced to warrant 20-year classes for the dissected trees. The incidence of heart rot and the average length of rot columns per dissected tree in these classes are shown in table 9. The table is based on 177 trees that were dissected on the 46 plots in 41- to 100-year-old stands in the Southwest. A comparable summary for the Black Hills survey indicated that none of the 13 trees in the 41- to 60- and none of the 37 in the 61- to 80-year age classes had heart rot in the butt logs. Of the 24 trees in 81- to 100-year-old class, however, 8 were infected and 3 of them had heart rot, the average length of which was 1.46 feet per infected tree.

An opportunity to get additional information on heart rot in the 41- to 100-year age class occurred in connection with the pole and sawtimber inventory of the Prescott National Forest during 1952. Three of the one-quarter acre inventory plots in the 61- to 70-year-old stands of the Prescott District were clear cut and the 147 felled trees were dissected to expose all red rot in the trunks. Because of the objectives of the inventory, decay measurements were not limited to butt logs. This fact explains the higher incidence of infection and heart rot than were found in the intensive surveys (5).

TABLE 9.—Heart rot in butt logs that entered through dead branches below a height of 17 feet, based on 177 trees dissected on 46 plots in 41- to 100-year-old stands in the Southwest

Age class (years)	Mean age	Dissected trees		Average total length of rot columns per dissected tree	
		Total	With heart rot		
	<i>Yrs.</i>	<i>No.</i>	<i>No.</i>	<i>Pct.</i>	<i>Ft.</i>
41-60.....	52	121	39	32	0.47
61-80.....	66	30	13	43	1.20
81-100.....	92	26	11	42	3.04

The results are considered sufficiently similar to those obtained in the survey to present as an example of the relationship of infection and heart rot to tree size in immature stands, in which there is practically no variation in infection associated with age. Figure 18 shows the percentage of the trees that were infected and that had heart rot in four size classes. It is apparent from the bar diagrams that heart rot was well established in the Prescott District, and that it was closely related to size in the even-aged stands. Figure 19 shows, however, that although the average lengths of the rot columns per tree are appreciable, because of the small amounts of heartwood present, virtually no volume losses are involved at this age. Most of the heart rot was so located that it would not have been discovered if the trees had been cut for sawtimber or poles in a commercial thinning. Of the 20 merchantable trees with heart rot, 14 had decay columns that would not have been exposed if they had been cut into 17-foot sawlogs. Of the trees suitable for poles 11 had heart rot and 8 had columns that would not have shown at either the butt or top ends of poles.

No entirely satisfactory estimates of the rate of heart rot development in 41- to 100-year-old stands are available. A comparison of trees dissected in 1939 on 4 of the 18 plots in 41- to 60-year-old stands in the Sitgreaves National Forest with a comparable number of unpruned infected trees dissected adjacent to these plots in 1949 (2), suggested that the incidence of heart rot among infected trees had increased from 11 to 75 percent during the 10 years, and that the average total length of rot columns in trees with

heart rot had increased at a rate of about 1.5 feet per decade. Inasmuch as this average figure included some new cases of heart rot, which contributed little to the total lengths, it is obvious that it shows slower development than can be expected after all potential heart rot infections have become established in the heartwood of the trunks.

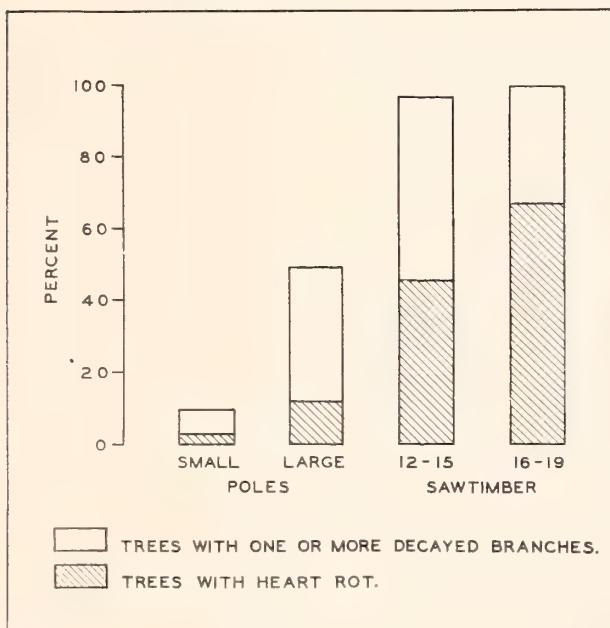
A similar comparison between trees dissected during the intensive survey in the Prescott National Forest during 1938 and 1939 (5) and those dissected in conjunction with the pole and sawtimber inventory in 1952 suggested about the same increase (1.6 feet per decade) in average length. At the rate of 1.5 feet per decade, the total length of rot columns in the butt logs of trees with heart rot can be expected to average about 9 feet in a 100-year-old tree (compared to 7.2 feet per dissected tree shown for the 81- to 100-year class in table 9) and at least 15 feet in a 150-year-old tree. Most columns of such lengths would be exposed at either the stump or 17-foot cuts, if the trees were made into sawlogs, and the scaleable rot would cause an appreciable reduction in gross volumes. In general, about 50 to 75 percent of the trees that are infected at maturity will have heart rot in the butt logs.

CONTROL

Now that the period of heavy liquidation of old-growth ponderosa pine is passed and lighter cuts, closer utilization, and better slash disposal methods are being applied even in virgin stands, it is entirely possible that a decline in the rate of red rot infection will become apparent in young second-growth, i. e., that which originated in 1919 and 1929 in the Southwest. Until accurate information on the trend of infection has been obtained, however, it must be assumed that an aggressive program of indirect control is the best policy to follow.

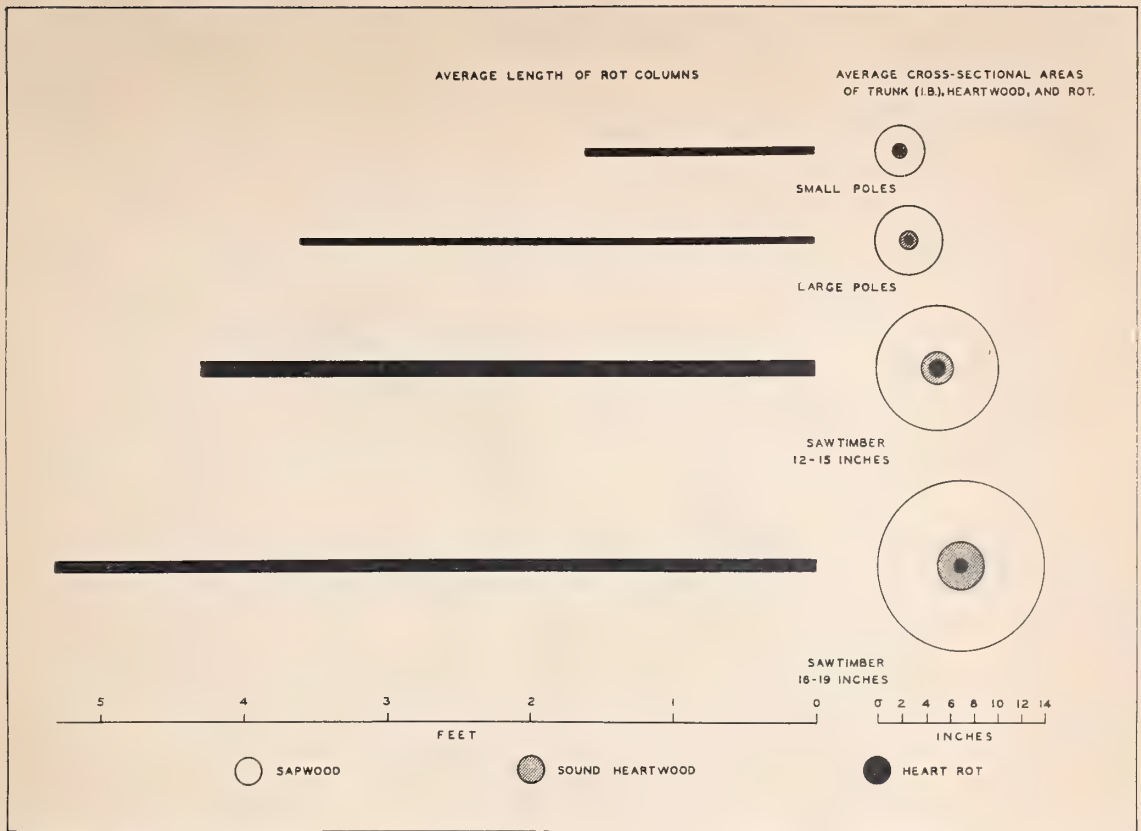
Unless the amount of butt-log infection can be reduced, losses of about 5 percent can be anticipated when the present immature stands are harvested for sawtimber at 150 years. Fortunately, marked reductions in red rot can be effected by the application of sound silvicultural principles to the management of second-growth stands. Recent developments have demonstrated that measures formerly considered to be too intensive for practical application are now accepted stand-improvement practices.

Recommendations for control, which were based on existing knowledge of the progress of decay in relation to the normal development of second-growth stands, were presented for both the Southwest and the Black Hills in earlier publications (4, 5). They are now largely of academic interest in view of the recent advances in the management of immature stands and the accumulation of new information on decay. The recommendations for the Black Hills were based upon the fact that stands were being thinned and pruned in separate operations, whereas those for the Southwest were made applicable to the crop-tree method of stand improvement. In both regions they were limited to the rot problem in the lower 17 feet of the trunks.



F-475701

Figure 18.—Relationship of the incidence of red rot infection and heart rot to the size of trees in the Prescott District of the Prescott National Forest. The d. b. h. range for small poles is 3.6 to 6.5 inches, and for large poles 6.6 to 11.5 inches. Based on 147 trees on 3 one-quarter acre plots that were dissected in conjunction with the Prescott Pole and Sawtimber Inventory.



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Figure 19.—Relationship of the average lengths and cross-sectional areas of decay columns in trees with heart rot to size in the Prescott District of the Prescott National Forest. Based on 147 trees on 3 one-quarter acre plots that were dissected in conjunction with the Prescott Pole and Sawtimber Inventory.

Following the intensive survey in the Black Hills during 1935 and 1936, Moberg¹⁴ spent several months in that region testing control methods that could be included in stand-improvement operations in progress. His final recommendations, which were incorporated in timber stand improvement regulations for Region 2 of the U. S. Forest Service (7), included a number of departures from previous instructions for thinning and pruning. In thinning operations, the revised instructions permitted the removal of uninfected trees, which were poor risks because of large living or dead branches, as well as the infected trees. In pruning operations, the maximum size of trees that could be pruned was reduced from 10 to 7 inches d. b. h. In general, Moberg concluded that when timber stand-improvement operations were undertaken in young second-growth stands the favoring of small-limbed trees not exceeding 7 inches d. b. h. automatically resulted in the elimination of a large number of infected or susceptible trees.

For the Southwest the recommendations for control were more general owing to the fact that the intensive survey had provided evidence that infections became

¹⁴ MOBERG, T. R. APPLICATION OF THE BLACK HILLS WESTERN RED ROT SURVEY TO THE TIMBER STAND IMPROVEMENT PROGRAM OF THAT REGION. 16 pp. March 10, 1938. [Type-written. Files, Forest Insect and Disease Laboratory, Albuquerque, N. Mex.]

established at an early age and often occurred in small, fine-limbed trees (5). Although no age or size limits were prescribed, it was suggested that maximum prevention could be obtained only by pruning small-branched trees initially at an early age and subsequent pruning operations sufficient to protect the trunks to a height of 17 feet. It was also suggested that wherever possible proposed crop trees should be examined before pruning and those with infections entering the trunk eliminated from further consideration. Finally, it was recommended that high stand densities be maintained for the first 80 years to inhibit the growth of lower branches.

When the control recommendations were made, pruning was justified only as a measure for protecting previously uninfected trunks from subsequent attack. It was recognized that potential infection could be reduced to some extent by the removal of decayed branches before the rot had entered the trunks. Because of the rapid development of red rot such cases were not numerous. The failure of the red rot fungus to reach the trunk heartwood from some decayed branches had already given rise to speculation regarding the therapeutic effect of pruning, but no basis existed for including this possibility in discussions of control.

Results of a study on the effect of pruning on red rot in 1949 (2), the findings of which have been sum-

marized in table 5, indicated that although the fungus dies naturally in some infections pruning arrests it or results in its death in an appreciable number of the decay columns that have entered the trunks in stands less than 60 years old. Red rot can, therefore, be markedly reduced by pruning according to existing silvicultural instructions in stands younger than that age. The earlier pruning is started the more complete will be the protection against red rot. When less than the standard 17 feet of the trunk can be pruned in a single operation, the ideal interval between subsequent treatments is about 10 years if most new infections are to be disposed of before they have penetrated the trunk for any distance.

In current stand-improvement work in the Southwest, pruning is restricted mainly to young stands in which few crop trees are larger than 6 or 7 inches in d. b. h., and in most stands they are considerably smaller. Provided subsequent pruning will be possible at fairly short intervals, near-maximum protection against butt-log infections should be achieved.

Interest in thinning has been increasing in the Southwest for the past 5 or 6 years, because of mounting evidence that growth rates are not being maintained in immature timber. If the small stems that would be cut could be utilized as poles, posts, and other piece products, thinning would be economically feasible and probably would replace the crop-tree method as an intermediate treatment for the denser stands. In that event, the Black Hills' findings would be generally applicable to the Southwest, although a satisfactory pathological program cannot be developed until management and silvicultural requirements have been determined.

Even under ideal conditions it is unlikely that pruning will prevent all butt-log infection. An idea of the benefits that can be expected, however, is furnished by the 150-year-old trees cut on the Wing Mountain Unit of the Fort Valley Experimental Forest (11). As already reported, butt logs contained 54 percent of the total gross volumes of these trees and 39 percent of the rot volumes. Although some of the rot in the butt logs probably entered the trunks above 17 feet, it is reasonable to assume that if most infections below this point had been prevented, rot volumes would have been reduced by about 35 percent, and the proportion of gross volumes lost because of heart rot would have been 3.1 percent instead of 4.7. In terms of the combined annual cuts for the Southwest and the Black Hills, this difference represents a substantial saving. Greater benefits may be expected when the present immature stands reach maturity because butt-log infection is considerably greater than that in trees now 150 years old, and can be expected to result in larger proportions (probably at least 50 percent) of heart rot for the trees as a whole unless preventive action is taken.

SUMMARY

Red rot caused by *Polyporus anceps* is the major defect in merchantable stands of ponderosa pine in the Southwest (Arizona and New Mexico) and the Black Hills of South Dakota. Its regional occurrence as a

serious heart rot of this species is unique. It causes insignificant losses to ponderosa pine in other western regions. Although it is abundant on the slash of many conifers throughout this country and Canada, it rarely, if ever, attacks living trees.

Studies of red rot in the Southwest date from 1913. By 1915 sufficient evidence had been gathered to indicate that slash decay was the principal source of heart-rot infections in living trees and that these infections occurred through dead branches.

For many years the red rot fungus as it occurs on ponderosa pine, mainly in the Southwest and Black Hills, was called *Polyporus ellisianus*. Laboratory studies indicate that specimens bearing this name are identical to *P. anceps*. The studies suggest that there may be several varieties or races. Sporophores that darken with drying are predominant in collections from ponderosa pine in the Southwest and Black Hills. Isolates from these regions also appear and behave differently in culture than eastern isolates, and are probably adapted to the environmental conditions of ponderosa pine stands. Designation of varieties or races is not justified on the basis of present information.

The red rot fungus fruits abundantly on decaying dead material in contact with the ground. The flat white fruiting bodies develop annually during the summer rainy season. Windborne spores, or fragments of the fungus on the bodies of insects, lodge in small openings in the bark of dead branches and lead to the development of white pads between the bark and wood. The wood of branches is directly invaded from the rapidly expanding pads. When the fungus reaches the branch bases the rot concentrates into slender, highly pigmented pockets. Branches larger than 1.5 inches in basal d. i. b. are about 5 times more susceptible to attack than smaller branches in the Southwest, and about 20 times more susceptible in the Black Hills.

Branches may be attacked as soon as any part of them dies and may remain susceptible for about 20 years, provided they retain most of their bark. Living branches sometimes are infected through dead secondaries.

After reaching the branch bases the fungus progresses through the knots into the heartwood of the trunks. It is apparently the only decay fungus attacking dead branches of ponderosa pine that is able to penetrate the pitch-infiltrated wood of knots, probably because of its greater tolerance for extractive substances of knot wood. Most rot (60 to 80 percent), however, reaches the heartwood through the pith cavities and not through the wood of knots. Failure of some infections to develop into heart rot may result from the activity of other branch-decay fungi, breakage of branches or loss of bark, and also from pruning.

Although red rot is difficult to detect in living trees because of fruiting habits of the fungus and failure to form swollen knots or other external signs, familiarity with the appearance of decay in knots and dead branches aids in locating hidden pockets of rot in sawlogs and in estimating trunk infections and heart rot in young trees.

Estimates of losses in ponderosa pine under management are based on the results of a number of defect studies and intensive surveys in the Southwest and the Black Hills. Losses in gross volumes will probably amount to about 7 to 10 percent in trees less than 200 years old and at least 15 percent in older trees cut in the remaining virgin stands. They will probably drop to about one-half these amounts in second and subsequent cuts, depending upon the rate at which the mature and overmature trees are removed. Losses will probably remain at a seemingly higher level where light selection or salvage type marking is followed. In second-growth stands, losses will rarely drop below 5 percent in a 150-year rotation. They may be reduced to one-half this figure if trees are cut when 120 years old.

Intensive surveys of red rot in immature stands of the Southwest and Black Hills made between 1935 and 1938 indicated that red rot is more serious in the Southwest than in the Black Hills.

Although rot infection increases with the age of the tree, this relationship is not evident in 41- to 100-year-old stands where infection varies within wide limits because of the effect of other factors, and where only the first 17 feet of trunks was studied. In general, infection is negligible in younger stands. The infection in older stands apparently is not indicative of what may be expected when the present young stands reach that age. Infection in 41- to 100-year-old

stands is directly related to dead branch size and tree size, and inversely related to density. These relationships, which were statistically significant, are demonstrated by stand tables for 41- to 60-year-old stands in the Sitgreaves National Forest.

Heart rot volumes in 41- to 100-year-old stands are usually negligible. Data on the extent of heart rot are given for 177 infected trees in the 41- to 100-year age class that were dissected during the intensive survey in the Southwest, and for 147 additional trees in 60- to 70-year-old stands in the Prescott National Forest. Between 41 and 100 years the average length of rot columns in affected trees appears to be increasing about 1.5 feet per decade. At this rate, trees with heart rot can be expected to have columns averaging 9 feet per tree at 100 years or 15 feet at 150 years of age.

Control measures formerly considered too intensive for practical application are now accepted stand management practices. In the Southwest current stand improvement is restricted mainly to young stands containing small trees. Provided the pruning necessary to clear the trunks to 17 feet is spaced at close enough intervals, near-maximum protection against red rot will be achieved. Ultimately thinning may replace the release cutting of the crop-tree method in the Southwest, in which case findings for the Black Hills will be generally applicable.

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