1936

The Tympanis Canker of Red Pine

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YALE UNIVERSITY · SCHOOL OF FORESTRY

BULLETIN NO. 43

THE TYMPANIS CANKER OF RED PINE

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Yale University

1936

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2012

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FOREWORD

THIS investigation was a joint project between the Osborn Botanical Laboratory and the School of Forestry in Yale University, and the Division of Forest Pathology, Bureau of Plant Industry, in cooperation with the Northeastern Forest Experiment Station, United States Department of Agriculture.

The work was carried on by the writer during the years 1933 to 1936. The data pertaining to the southern Connecticut study areas were taken at various times throughout this period. Observations in the Lake States were limited to 1934, in New York to 1935, and in Ohio, Pennsylvania, and New Jersey to 1936. It is realized that the relative shortness of the period of observation makes it impossible for some of the findings given herein to be of an exhaustive nature; rather, they may be considered as indicative of the present status only of a forest tree disease which may be regarded differently in the light of cumulative data obtained through future investigations.

The writer wishes to express his sincere appreciation to Professors J. S. Boyce and R. C. Hawley of Yale University and to Dr. Perley Spaulding of the Division of Forest Pathology, United States Department of Agriculture, for their kindly and instructive criticism and valuable advice in the planning, execution, and presentation of the entire study. In addition he wishes to acknowledge the cooperation of Dr. T. W. Childs and Mr. H. G. Eno of the Division of Forest Pathology; Professors H. J. Lutz and R. B. Friend, and Mr. R. T. Clapp of Yale University; Dr. J. W. Groves of the Department of Botany, University of Toronto; Professor D. V. Baxter of the School of Forestry and Conservation, University of Michigan; Professor H. H. York of the Department of Botany, University of Pennsylvania; Professor L. O. Overholts of the Department of Botany, Pennsylvania State College; Dr. G. D. Darker of the Farlow Herbarium, Harvard University; Dr. F. J. Seaver of the New York Botanical Garden; Mr. R. Heim of the Museum National d'Histoire Naturelle, Paris; and Mr. N. F. Buchwald of the Royal Veterinarian and Agricultural College, Copenhagen.

The original manuscript was submitted as a dissertation in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Yale University.

THE TYMPANIS CANKER OF RED PINE

INTRODUCTION

IN the administration of any forest tract, the silviculturist finds his attention drawn to a multitude of problems which might seem somewhat irrelevant to the layman. In reality, however, he must combine these problems with those of a strictly silvicultural nature and consider their solutions as essential to the performance of his work. Thus, he must have information on the pathological and entomological relations and interrelations of all the tree species with which he is dealing. To the degree that he avails himself of such information will he insure himself against the loss of the materials and labor that have gone into the building of his forest.

The operation of the Eli Whitney Forest *(21)* in and near New Haven, Connecticut, has afforded the staff in charge with repeated examples of the necessity for these extra-silvicultural studies and their application. One such example marked the incidence of the investigation reported in this paper.

In the winter of 1932-33, R. C. Hawley, silviculturist in charge of the Eli Whitney Forest, observed an area in the forest where the red or Norway pines *(Pinus resinosa* Sol.)[1] were dead and dying. Shortly thereafter, J. S. Boyce, R. B. Friend, P. Spaulding, and the writer examined the area. No evidence of primary insect infestation could be found but there was every indication that the disturbance was of fungus origin. The necessity for immediate information on the cause, general features, and control of the disease was obvious. This paper presents the results already secured.

Red pine is today one of the most valuable and widely used coniferous trees for both reforestation and afforestation work in and near its natural range. It has a variety of uses, among which are construction material, piling, and pulp wood. The commercial importance of the wood undoubtedly has been a factor in determining the value of the tree, but the ease with which it is grown in the nursery, the high survival of the planted seedlings,

1. The scientific names of all American forest trees mentioned in this paper are in accordance with Sudworth (3*1*). Unless otherwise denoted the common names are also those recognized by him. For *P. resinosa* the preferable common name is "red pine" rather than "Norway pine" because of the much wider usage accorded the former name.

the apparent freedom from injurious elements, and the rapid growth rate during the early years of its life have augmented its position.

A particularly strong point in favor of red pine, and a contributory cause for its general use, is that the species has been relatively free from insect infestation and fungus diseases. Other forest tree species, particularly the eastern white pine[2] (*Pinus strobus* L.), other considerations being equal, would probably far outdistance red pine in value as a tree for forest planting. The necessity of protecting white, or five-needle, pines against the white pine blister rust disease, caused by *Cronartium ribicola* Fisch., has lessened the planting of eastern white pine to some extent and caused favorable consideration to be given to the planting of trees of less intrinsic value. The remarkable degree of freedom from pests that red pine evidenced in natural stands brought it quickly into favor. That this approval was not illogical is shown by the many citations pertaining to the vigor and health of red pine stands. Dana (*15, p. 21*), Woolsey and Chapman (36, *p.* 7), Reed (*28, pp. 12-15*), and Kittredge (25, *p. 13*) all agree that red pine is a particularly desirable species for planting because it appears to be almost immune to insects and diseases. Moreover, Anderson *et al.* (4, *p.* 77) in their check list of the diseases of economic plants in the United States, give only four types of fungus diseases upon living red pines: (1) canker-forming organisms, only one—*Cronartium comptoniae* Arth.; (2) needle-inhabiting fungi, only one genus—*Coleosporium* spp.; (3) damping-off fungi, three—*Corticium vagum* Berk. and Curt., *Fusoma parasiticum* Tubeuf, and *Pythium debaryanum* Hesse; and (4) heart rot fungi, four—*Fomes pinicola* Fries, *Polyporus schweinitzii* Fries, *P. sulphureus* Fries, and *Fomes (Trametes) pini* (Thore) Lloyd. These fungi are not peculiar to red pine but are, in contrast, somewhat ubiquitous in their occurrence. While collectively their possibilities of damage to the species may be considerable, yet in actual practice all of them (with the exception of the damping-off fungi which can be locally controlled in nurseries) may be more or less disregarded. They are native diseases and it may be safely assumed that the red pine has gradually acquired or built up the ability to grow and thrive in spite of them. Friend and West (*16, p.* 35) review the subject of insect infestation of red pine and state that, "Before the introduction of the shoot

2. In this paper the name "eastern white pine" is applied to *Pinus strobus* rather than the name "northern white pine" as given by Sudworth (*31*). The western white pine, *P. monticola* D. Don., actually ranges as far north as does the eastern white pine; therefore, the common name northern white pine is considered inappropriate for *P. strobus*.

moth (*Rhyacionia buoliana* Schiff.) red pine was favored over white for forest planting because of the supposed freedom of the former from serious insect pests and fungous diseases and because, in addition, it has numerous good qualities of its own."

The relatively small number of known parasites of red pine and their apparent innoxiousness, with the possible exception of the shoot moth, over a period of years have created in the popular mind the concept that this species is practically immune to all injurious factors. While it may be granted that experience with the tree in its native habitat and under natural growing conditions has justified this assumption, yet it must also be realized that such a conclusion cannot be countenanced without further substantiation when the species is planted in artificial stands outside of its optimum ,natural range.

ECONOMIC ASPECTS OF A NEW DISEASE

I is readily evident that the possibilities for damage to forest plaritings of red pine by any new disease are tremendous. The large areas of land, often outside of the botanical range of the species, which have been planted pure with it offer ideal conditions for the fostering and rapid dissemination of epidemic disturbances. Any new disease, whether caused by a recently introduced parasite or by a native organism with a suddenly acquired virulence, is capable of widesprea.d damage which in a short time may ruin the planting work of many years.

A brief discussion of some of the factors antecedent to and predisposing a species to a disease may well be inserted here. It is a generally accepted fact that any increase in the cultivation and production of any plant species is liable to be accompanied by an increase in the incidence of many parasitic diseases. With respect to the increased danger of disease in forest trees under intensive management, Boyce (8) *p.* 14), in his observations on forest pathology in Great Britain and Denmark, very aptly sums up the situation as follows: "It is axiomatic in crop production that intensive culture increases the danger from disease and timber growing in western Europeis decidedly intensive. . . . Pure stands are the most susceptible to fungus and insect attacks, consequently much of the ,voodland in Great Britain, consisting of pure planted stands . . . , is inherently susceptible to disease."

Champion *(13)* opposes this interpretation of European experiences in the following statement: "I frequently attempted to collect records of specific instances proving the much advertised drawbacks and losses due to pure crops as such and the results were most unsatisfactory. It seemscertain that a great deal of the discredit is ascribable, not to purity of crops as such, but to mistakes in management, above all to planting up extensive areas with a species outside its natural distribution either as regards climate or soil, to planting on soils perhaps potentially suitable, but rendered unsuitable by undue exposure or other forms of faulty treatment, to using unsuitable strains of seed or planting stock, to failure from fungus or insect attack or whatever cause, to establish the new crop and soil cover quickly, and so on." In other words, Champion asserts that purity of crop is not the only cause of the failure of many pure stands in Europe and then lists a few of the other causes which may be operative along with purity. Certainly his statement cannot be interpreted as removing all of the discredit from purity itself; rather does it implicate other causes which alone may have, been conducive to failure but also may have been rendered more active when combined with purity of planting.

Boyce's position is further strengthened by the findings of Ackers (I) to the effect that pure European larch (*Larix europaea* D. C.) plantations in southern England were more heavily diseased by the European larch canker organism (*Dasyscypha willkommii* [Hartig] Rehm) than were adjacent mixed plantations of larch and Douglas fir (*Pseudotsuga. taxifolia* [LaM.] Br.). His data are startling in their simplicity. On the same site were three adjoining 16-year-old plantations, A, B, and C. A and C were mixtures of larch and Douglas fir, half and half; B was pure larch and was between A and C. The number of larch stems having cankers bad enough to affect their market value was determined for each plantation. In A, 18 per cent of the trees were cankered; in C there were no cankers; and in B from 40 per cent to 64 per cent of the trees were cankered. Inasmuch as in this particular instance, purity of planting is the only variable, it is rather difficult to avoid the conclusion that the greater amount of disease in the pure stand, B, than in either of the mixed stands, A and C, must be attributed to the purity of the stand; or, conversely, that the greater freedom from disease in the mixed stands is a result of some benefit derived from growing the two trees together. Hiley (23, *p.* 72), also working with the larch canker in England, emphasizes the fact that the lessened amount of canker in mixed stands of European larch and various other trees is because soil conditions remain better there than in pure stands, thus promoting a more vigorous development of the larch which, in turn, is reflected in a decreased susceptibility to disease.

The application of these ideas to American forestry is readily apparent. Our silvicultural practices are not yet as intensive as they are in Europe but they are nevertheless gradually approaching the European conditions. The application to the artificially reproduced plantations of pure red pine, such as those in this vicinity, is even more pronounced. This tree has been planted pure in regions outside of its optimum range, on sites which undoubtedly are not always suitable, and the seedlings have originated from seed which in many cases has not come from areas exactly similar in climate.

All of these factors-the present extensive planting of red pine in regions and on sites new to the species, the expected future increase in such plantings, the timber value of red pine, the past freedom from insect and fungus pests, and the probable increase in susceptibility to such diseases as the intensity of culture increases-all of these factors make the following investigation both timely and necessary.

THE DISEASE

GENERAL FEATURES

AS stated in the introductory section, a disease of red pine caused by a parasitic fungus was found in southern Connecticut during the winter season of 1932-33. The writer has already published a note (19) telling of the discovery and giving a few preliminary observations. The present paper is a complete report of the investigations conducted to determine the seriousness of the disease.

In the first notice the causal organism was identified as *Tympanis pinastri* Tul. (32, *pp.* 151-153), a fungus never before considered as a serious parasite. Since that time a modification of the concept of the species, *T. pinastri*, has made it questionable whether one can refer this pine-inhabiting fungus to that name (17). A discussion of the taxonomic features of the fungus is reserved for treatment in a subsequent portion of the paper.

HOST PLANTS

Careful examination of many natural stands and plantations of red pine, eastern white pine, Scotch pine *(Pinus sylvestris* L.), pitch pine *(P. rigida* Mill.), jack pine *(P. banksiana* Lam.), Austrian pine *(P. nigra* Arn.), and western yellow or ponderosa pine *(P. ponderosa* Laws.), has failed to disclose the disease on any but the first two species-red pine and eastern white pine. Of these two it is significant only on the former. Occasional branch and stem cankers had been observed on eastern white pine for several years previous to the discovery of the disease on red pine, but the cankers were always on trees greatly weakened through suppression, poor soil, root competition, or some other similar cause. Upon eastern white pine, then, the disease was not considered dangerous; on the contrary, it was thought to be beneficial in that it presumably hastened the death of trees that could never produce timber even if allowed to maintain themselves. It is a practical certainty that, had the disease remained only on this species, it would have continued to be designated as of no economic importance. When it made its appearance upon red pine, however, and in the short time of less than a decade killed or permanently injured hundreds of plantation trees, it could be no longer disregarded.

Macroscopic Characteristics

On red pine the disease first manifests itself by the formation of cankers on the main-stem only of trees between the ages of 10 years and 30 years. Younger trees have been exposed to the disease without becoming infected, but older trees are not present in the localities where conditions favorable to infection exist. Subsequent investigations may enlarge these age limits, but present data indicate that they are inclusive. The cankers may range in size from very small ones (Plate I) up to those which extend over two full main-stem internodes.[3] The smallest canker found was 3.5 inches in length and 1 inch in width. The largest was 36 inches long and 8.4 inches wide. The long axes of the cankers are always parallel to the main stem of the tree. A typical canker is shown in Plate II.

The cankers are almost entirely annual, the exact seasonal relationship and rate of development being unknown because of the impossibility of securing such data. All of the cankers found were produced in or prior to

3. For the purposes of this study the terms "node," "internode," and "whorl" are used with the following connotations. A "node" is that portion of the stem or branches of a pine tree at the junction of two successive years' growth in height or in length. A "whorl" designates all branches originating at a single node. An "internode" is that portion of the stem or branches which separates two adjacent nodes—i.e., the distance between two successive whorls—and constitutes one full year's longitudinal extension of a stem or branch. It is realized that these definitions are not in complete accord with the approved botanical meanings of the terms. In the absence of available alternatives and because of the apparent acceptance in current forestry and forest-pathology literature of the terms as herein used, the writer feels that this nomenclature is justified.

1931 and usually acquired full size in the year of their origin. However, circumstantial evidence indicates that canker growth takes place during that portion of the season after the host tree has completed its annual cambial activity as expressed in radial increment. Reference to Plate III shows that all the 1930 radial growth was made before infection which occurred in 1930. According to Kienholz (*24, p. 85*), in 1931 red pine near Keene, New Hampshire, began cambial growth in early May, reached a first maximum June 2, decreased slightly, and reached a second maximum July 9. Growth ceased in early October. He does not state the seasonal limits of most rapid cambial activity, but undoubtedly a high percentage of the annual growth layer was formed prior to the July 9 maximum. His data show that 96 per cent of the annual leader elongation was made between May 15 and July 15. Baldwin (*6, p. 684*), working with red pine at Ithaca, New York, shows that height growth there took place from the last week in April to the second week in July. It seems reasonable to expect that most of the radial increment would be added during the same period that height increment takes place, although the writer has been unable to find any outright statement in the literature to uphold this view. Inasmuch as Kienholz found that the maxima of cambial growth of red pine were on June 2 and July 9, the assumption that red pine in this region makes most of its radial increment in the period from May to July, inclusive, cannot be far wrong. It follows that canker growth must take place after that time and prior to the radial growth of the following year. Slight vegetative growth of the fungus would be expected during the coldest winter months. Therefore, the time of canker formation may be assumed to be late summer, autumn, and early winter, or possibly very early in the spring before tree growth begins.

Even though the canker continues to increase in size for only one season the causal organism does not die at the end of that season. In 1935 fresh fruiting bodies were collected on cankers originating in 1928, showing that the parasite was still viable in the diseased tissue seven years after infection. Moreover, repeated isolations of the fungus from the margins of cankers have been successful up to five years from the time of origin. Just why the parasite is unable to maintain its growth in the stem over a period of more than one year is problematical. It does not lose its viability so the limiting factor must be some host response which prevents further fungus invasion.

With respect to its annual nature this Tympanis canker of red pine is similar to the cankers of Douglas fir caused by *Phomopsis pseudotsugae* Wilson (*34, 35*) and by *P. lokoyae* Hahn (*18*). Boyce (*9*), in referring to the latter disease, says, "The cankers are apparently annual, developing during the dormant season of the host and gro\ving for one dormant season only." The analogy between the latter disease of Douglas fir and the Tyro.. panis canker of red pine is doubly significant. Both are annual cankers and are produced when the growth activities of their respective hosts are at a minimum.

The cortex and cambium over the infected area die soon after invasion by the fungus hyphæ so that the centers of the cankers are depressed to the extent of the thickness of the annual growth rings since the year of infection (see Plate III). The surface of a young canker is smooth, but within two or three years the bark over the canker cracks and may become shredded, exposing the sapwood beneath. Most main-stem cankers of coniferous hosts caused by other fungi are apt to be marked by considerable sur.. face resin flow, or resinosis. With this canker, however, resinosis is usually slight. Occasionally resin will exude on the canker surface next to the callous layer and may even be evident on the bark and wood at the center of the canker. The wood beneath the infected tissue usually becomes more or less resin impregnated. This feature is partially responsible for the dark color of the centers of the decorticated cankers shown in Plates IV, V, and VI.

The canker margin may be quite definite, or again it may be highly indeterminate. It may be delimited by a slightly raised callous formation, or it may gradually shade off and become indistinct in the bark scales of the host. Because of this variation it is frequently impossible to define the canker limits accurately without removing the cortical layers. If the bark on a cankered stem is removed, however, the margin is clearly marked, as shown in Plate IV. As a general rule, cankers on vigorously growing trees are more distinct than those on less thrifty individuals. This difference is explained by suggesting that the host response to infection in vigorous trees is more rapid than in slowly growing trees. Moreover, since the central portion of a canker is sunken to the extent of the thickness of the annual growth layers since infection, it is obvious that this depression will be much greater on rapidly growing trees than on slowly growing ones. On all trees the cankers are apt to be somewhat obscure and may be overlooked easily unless the observer scrutinizes the main-stems carefully.

The cankers are usually of the nongirdling type. They are elongated, roughly elliptical in outline, and are always centered at the main-stem nodes. Reference to Plates I to V illustrates these features clearly. Complete girdling of the stem occasionally results from the coalescence of two or more cankers having their origin at the same node. One case of this kind is shown in Plate VI. The narrow tongue of living tissue extending downward marks the division between two cankers which have coalesced to girdle and kill the tree. Such an occurrence is the exception rather than the rule.

Cankers range in height on the stems from 3 feet to 16 feet with the great majority of those observed occurring between the heights of 7 and 10 feet. They thus constitute a serious blemish in the mid portion of the basal 16-foot log of each infected tree. Moreover, the open faces of the cankers offer ideal infection spots for secondary staining and wood-rotting fungi which extend up and down the bole to distances far beyond the actual limits of the canker. The external evidences of infection do not convey a complete picture of the injury to the bole.

On eastern white pine the manifestations of this disease are somewhat different than on red pine. Cankers may occur either on the main-stem or on branches of any unthrifty, smooth- and thin-barked tree. Die-back of twigs and small branches is occasional but the majority of cankers on this host are of the type illustrated in Plates VII and VIII. The cankers are always centered at the nodes and in outline and general features closely resemble those on red pine. The one most striking difference is that the bark over the cankers on eastern white pine seldom becomes cracked or shredded. The bark dies just as rapidly, but remains tightly adherent to the underlying wood. Little attention has been given to secondary fungi following canker formation on this host. Cursory examination has disclosed the presence of staining and rotting fungi in the wood under a few cankers, but slight importance can be attached to either the cankers themselves or to their secondary effects on eastern white pine.

MODE OF INFECTION

As previously stated, cankers on both hosts are always centered at a node. Generally there is only one dead branch marking the point of infection but occasionally two or even three branches may be present at or near the center. This condition immediately suggests that the parasite gains admittance to the main-stem through the avenue of adhering lateral branches. Moreover, the absence of any cankered tissue upon these centrally located branches indicates that the fungus occurs there as a saprophyte, grows as such through the dead branches into the living main-stem, and there assumes its pathogenic rôle and causes the formation of cankers. Experimental proof of this theory is lacking, but innumerable observations in the field offer evidence of its authenticity.

RATE OF CANKER FORMATION

Dissection and analysis of 358 red pine stem cankers collected in southern Connecticut show that all of them originated in the four years from 1928 to 1931, inclusive. They were of the annual type so theirtotal size represents one year's growth. Table I presents the essential data concerning the size of cankers segregated into groups according to the year of origin.

There are two striking features of canker formation suggested by these data. First and foremost is the rapid growth of the fungus. It is remarkable that in one year a fungus is able to penetrate and kill the cambium for a

TABLE I. SIZE OF RED PINE CANKERS IN SOUTHERN CONNECTICUT

Year of origin	*Number*	*Percentage o/total*	*Length (inches)* *Max.*	*Min.*	*Av.*	*Width (inches)* *Max.*	*Min.*	*Av.*
1928	7	2.0	8.0	6.0	7·3	4.0	2.0	2.6
1929	5	1.4	10.0	6.0	7.8	3·0	2.0	2.2
1930	321	89.6	36.0	3·5	12.4	8·5	2.0	4·3
1931	25	7·0	20.0	5·0	10·4	6.0	2.0	3·5
Total	358	100.0	36.0	3·5	12.2	8·5	2.0	4.2

maximum distance of 36 inches up and down the main-stem of a living tree. It must be remembered that the mycelium is growing both upward and downward in the tree from the point of origin at the same time, so the figures on canker size are double those for mycelial growth in anyone direction. The other striking feature is that cankers produced in 1930 are materially larger than those originating in the other three years. Furthermore, those produced in 1931 are larger than those appearing in 1928 and 1929. Later in this paper evidence will be produced to show that, because of drought, the red pine trees bearing these cankers were most vigorous in 1928 and 1929, less so in 1931, and least vigorous in 1930. These data on canker size, therefore, suggest that the rate of growth of the fungus in the cortical tissues, as reflected in the overall size of cankers, is dependent upon the vigor of the infected trees.

Growth of the fungus laterally is approximately at the same rate on either side of the point of origin. Longitudinal growth is not so uniform, however. It may be extremely erratic. For example, in the formation of a canker 24 inches long the fungus may have grown 18 inches downward and only 6 inches upward, or these figures may be exactly reversed. In most cases the upward and downward growth is equal but the unequal type is frequently encountered. The cause of this variation is not known. Repeated observations have shown that apparently it is not correlated with any of the physical characteristics of the host-age, vigor, exposure to light and wind, etc.-nor is it associated with any uniform environmental factors.

DISTRIBUTION

On red pine the present known distribution of the disease is quite widespread and yet sporadic. The three worst known infection centers are in southern Connecticut in the towns of Hamden, Branford, North Branford, Orange, Woodbridge, Bethany, and Middlebury, in western New York in the town of Canadice, and in the Saginaw State Forest near Ann Arbor, Michigan.[4] Smaller infection areas have been located at the Ashokan Reservoir in the towns of Olive and Hurley, New York; near the village of Alder Creek, in the town of Boonville, New York; in the Harvard Forest at Hamilton, Massachusetts; in the Goddard Memorial Park, Potowomut Neck, Warwick, Rhode Island; at the Ohio State Sanatorium, Mt. Vernon, Ohio; in the plantations of the York Water Company, York, Pennsylvania; on the Nolde Estate and the Horst Estate, Reading, Pennsylvania; and on the Winston Estate and the Borie Estate near Gladstone, New Jersey. The disease is actually causing appreciable damage only at the first three centers. Typical cankers and authentic fruiting bodies of the fungus have been found at the other places as well, but in relatively small quantities.

On eastern white pine, occasional cankers caused by this disease have been found over a wider area, but in no instance can any damage be charged to it. Records of its occurrence as a parasite on this host are available at Warwick, Rhode Island; Windsor, Bethany, and Hamden, Connecticut; Frostburg, Maryland; Petersham, Massachusetts; Gambier, Ohio; Brigh-

4. Information concerning this infection center is through the courtesy of D. V. Baxter. In a red pine stand planted in 1921,562 trees out of the 652 examined were cankered. Eighty-four per cent of the dominant trees, 89 per cent of thecodominant trees, 88 per cent of the intermediate trees, and 80 per cent of the suppressed trees were cankered. Such high canker incidence in all crown classes indicates that this entire plantation was stagnated and that the growth of the upper crown class trees was probably greatly reduced over what it should have been to maintain the trees in good vigor. These data were secured too late to incorporate them into the body of the paper, but their inclusion would not have materially changed the figures and would not have affected the conclusions.

ton, Boonville, and Syracuse, New York; and West Gorham, Maine. On eastern white pine, infection is known to occur on both natural, and plantation-grown trees, but on red pine only the latter have been found to be cankered. On both tree species, the distribution of the fungus as a saprophyte is known over a much greater area than is listed above.

Extensive scouting of red pine stands, both planted and naturally reproduced, wherever the species exists in northeastern United States has failed to disclose the presence of the disease anywhere on naturally reproduced trees and has shown that it occurs in those plantations only which are south of the optimum natural range of the species. It is thought that the present limits of the geographical distribution of the disease are fairly well defined, but that future work will indicate many more spot infections within these limits.

THE CAUSAL ORGANISM

NOMENCLATURE

THIS disease of red and white pines is caused by a fungus belonging to the genus *Tympanis* of Tode,[5] the order *Pezizales*, and the family *Dermateaceae*. According to common usage both in Europe and in North America the parasite has been referable to the species, *T. pinastri* Tul. (32, pp. 151–153). The writer used this name in an earlier notice of the disease (19). Groves (17), however, has recently studied some of the American species of the genus *Tympanis*, and has come to the conclusion that Tulasne's name, *T. pinastri*, can be applied only to that fungus occurring on the true firs *(Abies* spp.). It is abundantly and widely distributed in northeastern North America on the balsam fir *(A. balsamea* [L.] Mill.). So far as is known, it is always purely saprophytic, no record of its occurrence even as a weak parasite having come to the writer's attention.

If Groves's delimitation of *T. pinastri* is to be accepted, the species of Tympanis occurring on pines in North America lacks a specific name until its identity with known European species is proved, or until it is described as a new species. Cultural comparison with fresh European material is essential before any final decision can be made. Therefore, the fungus causing this new disease is designated *Tympanis* spp. until further work on its identity is completed.

5. Tode, H. 1. (1790.) Fung. Meek., *1*: 23.

Description of the Fungus

The apothecia (Plate IX, Fig. 5; X, Fig. 1), or the perfect stage, of the fungus causing this disease of red and white pines are erumpent through the bark, single or cespitose in clusters of from 2 to 25, irregularly circular in outline but often compressed into various shapes, almost sessile to well stalked, up to about 1 mm. in diameter and 2 mm. in height. The hymenial surface is dull to shiny black, concave when young, plane to convex when old. The margin is distinct when young, becoming less apparent with age but never disappearing. The excipulum is dull black or occasionally slightly pruinose. The consistency is hard or horny when dry, becoming cartilaginous or leathery when moist.

The internal tissue is plectenchymatous with a firm gelatinous matrix. Groves (*17*) suggests that this matrix is essentially the greatly thickened walls of the interwoven hyphæ. Toward the outside the consistency becomes more dense until the surface is a hard black crusty layer. The subhymenial zone is narrow and indistinct. The asci (Plate IX, Fig. 6; X, Figs. 3, 4) are cylindric to cylindric-clavate, narrowed below to a short stalk, very thick walled when young, but having this wall compressed as the spore contents increase in volume with age, 68–135 $\times$ 12–17 μ (Av. 105 $\times$ 13 μ). They are usually filled completely with minute secondary ascospores (Plate IX, Figs. 6, 7, 8) which are one-celled, hyaline, straight, or slightly curved, 3–5 $\times$ 1–2 μ. Occasionally in the younger asci, from 1 to 4 primary ascospores (Plate IX, Figs. 6, 9: X, Fig. 4) may be observed. They are from 3 to 9 septate, hyaline, ovate to narrowly elongate, with rounded ends, constricted at the septa, 11–25 $\times$ 3–5 μ (Av. 15.6 $\times$ 3.7 μ), and are always imbedded in a mass of secondary ascospores. Plate X, Fig. 4, shows one primary ascospore near the base of an ascus. The paraphyses (Plate IX, Fig. 6) are hyaline, septate, rarely branched, filiform below, about 2 μ in diameter, swollen at the tips to 4.5–5.0 μ, and glued together over the asci to form a thick, dark yellow or brownish epithecium.

Of considerable interest is the method by which the secondary ascospores are formed in the ascus. The most complete and lucid investigation of the matter is that presented by Brefeld (*10, pp. 48–50; 11, pp. 290–297*). He states that in certain species of Tympanis he has observed the secondary ascospores budding off the primary ascospores in much the same way that yeast plants bud or sprout to form new plants. He concludes that the formation of such secondary spores is merely the result of the germination of the primary ascospores while still in the ascus. His theory is partially substantiated by the fact that when the secondary ascospores themselves germinate they produce more conidia similar to themselves. Such conidia are shown in Plate X, Fig. 7, a photomicrograph of a germinating secondary ascospore on malt agar medium 72 hours after sowing. Brefeld did not examine any species of Tympanis occurring on pine, but his results when working with other species of the genus should be applicable to the pine-inhabiting members of the genus. However, no one has observed the formation of the secondary ascospores in the ascus in *Tympanis sp.*

Suggestion that the primary ascospores are produced first in the ascus is given by the fact that the size of all asci containing primary ascospores is well to the lower end of the range in ascus size. Asci observed with 1 to 4 primary ascospores in them varied in size from 68.0-88.6 × 6.2–10.2 μ (Av. 81 × 9 μ). Inasmuch as the average size of all asci measured was 105 × 13 μ, it is readily apparent that the smaller size of those asci with primary ascospores is due to their morphological immaturity. The writer suggests that the great increase in ascus size with age may possibly be a result of internal pressure, developed by the formation of the innumerable secondary ascospores within a closely confined space. Such an assumption is difficult to prove but seems plausible.

The size of asci containing primary ascospores is based on measurements of 32 asci-all that were found to contain such spores in the course of this study. The size of all asci is based upon 500 measurements. The discrepancy between these population sizes was unavoidable because of the scarcity of asci with primary ascospores.

The pycnidial, or imperfect stage, fructifications of *Tympanis sp.* are much less abundant in nature than the apothecia. In pure culture on malt-extract agar medium, however, they are common. Taxonomically the imperfect stage is considered to belong to an undescribed species referable to the genus *Pleurophomella* of Von Hohnel.[6]

The pycnidia (Plate IX, Figs. 1, 2; X, Fig. 2) are erumpent, single or grouped on a stroma in clusters of 4 to 20, dull to shiny black, spherical to cylindric or conic, the single ones up to 1 mm. in height and somewhat less in width, the cespitose groups up to 2 mm. both in height and in width. The consistency and tissue structure are the same as in the apothecia.

The conidiophores (Plate IX, Fig. 3) are hyaline, septate, occasionally branched, 15-25 × 1.5-2.0 μ, bearing conidia both terminally and laterally at the septa. The conidia (Plate IX, Fig. 4) are hyaline, usually straight but rarely slightly curved, 2-4 × 1-2 μ.

6. Hohnel, H. von. (1914.) Sitzb. Akad. Wien., *123:* 123.

Cultural Studies

The growth of *Tympanis sp.* on 2 per cent malt-extract agar in test tubes was carefully studied. Isolations were made from the inner bark at the edge of cankers on both white and red pines, from single asci, from single secondary ascospores, and from single conidia produced on both hosts. In all cases the cultural characteristics were essentially identical. Growth was moderately rapid and uniform. Young colonies were appressed, whitish, butyrous or yeast-like, with a marginal fringe of nonbutyrous hyphæ. Older colonies darkened to a yellow or light brown and became even more appressed, sodden, and almost slimy. Black hemispherical masses of stromatic tissue appeared on the surface. They had the same leathery consistency that is found in the tissue of the apothecia and pycnidial stromata in nature. Many of them remained as sterile masses of undifferentiated hyphæ, but others developed into pycnidia producing typical conidia. No apothecia appeared in any culture.

Inoculation Experiments

In order to demonstrate experimentally the parasitism of this fungus on red pine, 221 inoculations and 35 checks were made on thrifty 14-year-old red pine trees in southern Connecticut in May, 1934. The inoculum was from pure cultures of *Tympanis sp.* from inner bark, from single asci and from single secondary ascospores from both red and eastern white pine cankers. The cultures were on 2 per cent malt-extract agar. No natural infection was present in the stand where the inoculation experiments were performed, but cankers were prevalent throughout the general locality.

The following technique was employed. The place to be inoculated was first rubbed to remove all loose bark scales and débris and then sterilized by washing with cotton soaked in 70 per cent ethyl alcohol. Incisions were made with a sterile scalpel by gently slitting the bark parallel to the long axis of the stem or branch and raising the phloem from the xylem on one side of the slit. The entire incision was approximately one-half inch long. The inoculum was then inserted in the incision with a sterile needle. Then the bark was gently pressed down so that the only external evidence of the operation was a small almost-closed slit. Finally the incision was wrapped with cotton, moistened with sterile distilled water, and bound securely with grafting tape. These bandages were left on for one month and were moistened periodically with sterile water during that time.

Inoculations were made on series of 6 trees with inoculum from 6 different sources which are listed in Table 2. Each seventh tree was a check in that the technique was identical but sterile 2 per cent malt-extract agar was inserted in the incision in place of inoculum.

The first 48 inoculations and 8 checks were on main-stem internodes midway between the nodes and consisted of 4 inoculations per tree-all at the same level, but each one facing to one of the four cardinal directions, north, east, south, and west. In Table 2 these inoculations are referred to as "on internodes." The second series of 54 inoculations and 9 checks was made on all the living lateral branches of one whorl on the main-stern-varying from 4 to 6 inoculations per tree. The incisions were one inch from the main-stem on the top side of the branch. In Table 2 these inoculations are referred to as "on intact branches." The third series of 58 inoculations and 10 checks was made on all the living lateral branches of one whorl on the main-stem, but the branches were each girdled at the distal end of the first internode. To prevent too rapid desiccation the girdled area was coated with Bordeaux paint composed of equal portions of Bordeaux mixture and linseed oil. In Table 2 these inoculations are referred to as "on girdled branches." The fourth and last series of 61 inoculations and 8 checks was made on all the living lateral bran.ches of one whorl on the main-stem, but the branches were completely severed at the distal end of the first internode. The cut surfaces were coated with Bordeaux paint. In Table 2 these inoculations are referred to as "on severed branches." The technique in the latter two series was identical with that in the second series except for the girdling and severing of the inoculated branches.

The inoculations were examined in September, 1934, May, 1935, and October, 1935. The final data are recorded in Table 2. It is apparent that the parasitism of the fungus is demonstrated by the fact that 32 cankers were induced on the stem internodes, and one each on intact branches and girdled branches-on 15 per cent of the total. Considering the main-stem inoculations alone, 32 out of 48, or 67 per cent, were successful. These cankers \vere all small-the largest being 5 inches long and 2 inches wide-but they were very definitely cankers of typical form and the fungus was fruiting freely on all of them. When no canker was present the fruiting bodies were in and around the incision where the inoculum was placed. When cankers were present the fruiting bodies were distributed from the center to the margin of the diseased tissue.

The apothecia produced on these inoculations were typical of those occurring naturally except that they were usually much smaller-averaging about ½ mm. in diameter as compared with 1 mm. for those occurring

TABLE 2. INOCULATIONS ON RED PINE WITH TYMPANIS SP.

Inoculum from		*On internodes*			*On intact branches*			*On girdled branches*			*On severed branches*			*Total*	*No. of*	*No. with*
Host	*Origin*	*No.*	*Cank.**	*Apoth.**	*No.*	*Cank.*	*Apoth.*	*No.*	*Cank.*	*Apoth.*	*No.*	*Cank.*	*Apoth.*	*No.*	*cank.*	*apoth.*
Red pine	Ascus	8	3	4	8	0	4	10	0	2	12	0	8	38	3	18
Red pine	Inner bark	8	4	6	8	0	5	10	0	4	11	0	6	37	4	21
Red pine	Ascospore	8	7	8	10	1	7	9	0	7	8	0	7	35	8	29
White pine	Inner bark	8	7	8	10	0	10	10	1	7	12	0	8	40	8	33
White pine	Ascus	8	8	8	9	0	9	10	0	6	9	0	6	36	8	29
White pine	Ascospore	8	3	4	9	0	7	9	0	6	9	0	3	35	3	20
Total		48	32	38	54	1	42	58	1	32	61	0	38	221	34	150
Checks		8	0	0	9	0	0	10	0	0	8	0	0	35	0	0

* Cank. = canker present; Apoth. = apothecia present.

naturally. Typical asci and secondary ascospores were abundantly present in all of them and the original fungus was reisolated into pure culture from them. According to Koch's postulates, which involve the isolation into pure culture of the causal organism from the diseased plant, the production of the disease by inoculating healthy plants' with a pure culture of the organism, and finally the reisolation of the organism from the inoculated plants, the pathogenicity of *Tympanis sp.* on red pine is conclusively demonstrated.

It was hoped that the writer's theory of the method of infection through the avenue of dead lateral branches would be strengthened by the results of the inoculations on intact, girdled, and severed branches. The failure of all but two of these inoculations to produce main-stem cankers was disappointing, but the presence of typical fruiting bodies on 112, or 64 per cent, of the 173 inoculations of this kind showed that the fungus was still alive. The vigor of the inoculated trees is considered to have been too high to allow the fungus to penetrate into the main-stem and form cankers. The frequent occurrence in nature of *Tympanis sp.* fruiting bodies on dead lateral branches of red pines close to the main-stem but with no parasitic action resulting in canker formation is an example of just such a condition.

All of the check incisions were completely callused over and healed by the time of the last examination. This is considered conclusive evidence that the wounding of the tissue with the scalpel in making the inoculation slit was not responsible for the production of cankers. Twenty of the inoculations themselves were almost healed at the last examination. The inoculum apparently died in these twenty before it became established in the tissue.

Because of the relative unimportance of the disease upon eastern white pine, no inoculations were performed on that host. However, the fact that the inoculum secured from eastern white pine cankers induced cankers on thrifty red pine trees when artificially inoculated into them is considered proof of the pathogenicity of the fungus associated with cankers on this species. To have also inoculated eastern white pines would have been interesting, but the value of the results of such inoculations would have been large!y academic.

RELATION OF THE DISEASE TO RED PINE STANDS

MOST of the field work on the Tympanis canker disease has been conducted in the red pine stands on the Eli Whitney Forest, where the disease was first observed. The writer's preliminary note *(I9)* was based entirely upon data taken there. The information embodied in the remainder of this paper may be considered as pertaining directly to the Eli Whitney Forest unless another locality is specifically mentioned. It may be of value, therefore, briefly to characterize the red pine plantations in this Forest.

GENERAL DESCRIPTION OF THE RED PINE PLANTATIONS IN THE ELI WHITNEY FOREST

The plantations in which the disease has been found and studied were established between 1914 and 1920, inclusive, on land which previously had been used for agricultural purposes, such as pasture, meadow, orchard, or cultivated ground. The soil undoubtedly may be considered as suitable for red pine growth. Hicock *et al.* (22, *p. 750)* state that, "In general, the soils of Connecticut, and probably of much of the surrounding region, may be classed as good to excellent for the production of red pine."

The seed source for all of the plantations was in the Lake Champlain section of New York. This region is in many respects similar climatically to southern Connecticut, but it should be borne in mind that it is on the average at least 5° F. colder there than it is in southern Connecticut. Whether or not a difference no greater than this can be considered significant with regard to red pine seed is a question not conclusively answered by any work to date. Bates (7), however, in referring to his experiments with red pine on the effect of seed source upon the resulting seedlings says, ". . . the present experiment is expected to show that in the long run, after being planted under natural conditions, only seed from the same portion of the range develop into trees which are fully adapted to a given region or planting site."

Moreover, the instructions issued by the Swedish Forest Service *(20)* with regard to the source of pine seed used in artificial reforestation in Sweden are that, "Pine seed shall not be sown in a district where the normal temperature for the summer deviates more than 0.5° C. (0.9° F.) from the corresponding temperature in the region where the seed was collected." This statement concerning Swedish practice, along with Bates' generalization from his work, indicates that the climatic difference between the Lake Champlain and the southern Connecticut districts may be sufficient to unfavorably influence plantations established in the latter locality from seed collected in the former. However, the need for a coniferous tree such as red pine for reforestation in southern New England, the obvious inability to get another satisfactory tree any better suited to the climate than red pine, and the lack of a red pine seed source any more satisfactory than the Lake Champlain region make it imperative that, for the present, red pine planted in southern Connecticut should be grown from Lake Champlain seed.

The plantations were composed largely of 2-1 transplants, but in a few instances 2–2 stock was used. The spacing was roughly 6 feet in all cases, giving a density of approximately 1,200 trees per acre.

During the years 1914 to 1916 red pine was planted only in pure plantations, but beginning with 1917 it was also planted in alternate row mixtures with eastern white pine. At the close of the 1920 planting season a total of 526 acres of pure red pine plantations and 298 acres of mixed red and eastern white pine plantations were established on the forest. Of this total area only 97 acres, or 18.5 per cent, of the pure plantations and 64 acres, or 21.5 per cent, of the mixed plantations were examined in the present study. Infection was found on 84 acres, or 86.5 per cent, of the pure plantations and on 6 acres, or 9.5 per cent, of the mixed plantations.

In the course of the examination of these plantations certain definite relations and interrelations with various environmental factors have been brought out regarding the incidence of the disease. These data are segregated and presented in the following sections.

PLANTATIONS VERSUS NATURAL STANDS

The known distribution of this disease on red pine is in southern New England, eastern, central, and western New York, northern central New Jersey, eastern Pennsylvania, central Ohio, and southern Michigan. All of these localities are south of the natural optimum range of red pine, which is a boreal species and ranges from eastern and central Canada southward into the Lake States, New York, and central New England, and even extends as isolated trees at the higher elevations into Pennsylvania and West Virginia *(31)*. The disease has never been found in naturally reproduced stands nor has it been found in plantations growing within the optimum natural range of red pine. In contrast, it has been found only in plantations south of the optimum natural range of the species. The disease is at present, therefore, attacking only planted trees in a zone which may be characterized as an artificial southern extension of the range of red pine.

PURE VERSUS MIXED PLANTATIONS

As previously stated, infection was found on 84 acres of the 97 acres of pure red pine plantations examined and on 6 acres of the 64 acres of mixed plantations examined. All of the infection in the mixed stands was considered light in that only an occasional tree of the intermediate or overtopped crown classes was cankered. In no instance were dominant or codominant trees of such stands infected. In the pure stands, however, conditions were entirely different. Many of the dominant and codominant trees were cankered and the percentage of infection in some stands was very high. Infection was considered medium to heavy on 45 acres and light on 39 acres. The contrast in the degree of infection in the pure and the mixed stands is so marked that one is led to assume that admixture of red pine with eastern white pine is a definitely limiting factor to infection. One qualifying condition exists which may have some bearing on this relation. All of the mixed plantations examined are at least 2 or 3 years younger than the older pure plantations in which the disease is prevalent. Therefore, the same degree of competition is not present in the mixed plantations that is found in some of the pure. Moreover, in the mixtures red pine is in this region generally dominant over eastern white pine during the early life of the plantation. It is probable that the red pine in the mixed stands on the Eli Whitney Forest is at present somewhat more thrifty than similar trees in pure stands. The greater amount of disease in the pure stands may be partially attributable to factors other than purity, but observations up to the present indicate that one result of planting red pine in pure stands in southern Connecticut may be an increase in the incidence of the Tympanis canker. That such should be the case agrees with the previously stated ideas of Boyce (8) and Hiley (23) and the data of Ackers *(I)*, and is not irrelevant to the conclusions of Champion *(I3)*. Inasmuch as the relation of disease incidence to purity of stand is a controversial matter, the present data may be regarded as indicative only. However, under the existing conditions in the southern Connecticut plantations there is much less infection in mixed stands than in pure.

GOOD VERSUS POOR SITES

For the purpose of this study the average height of 20 dominant and codominant trees in each study area was used in detecting and measuring differences in site quality. The method was that set forth by Bull *(I2)*. The data upon which his publication is based were secured from pure red pine plantations in Connecticut, so his results were considered readily applicable to the present problem. The technique is simple. The average height of the 20 selected trees and their total age from seed are secured. Then the height is computed to which the trees would have grown for any arbitrarily selected standard age-for which 15 years was used. Therefore, the site index figure for each plot is the average height which 20 dominant and codominant trees on that plot have or did have at the total age of 15 years. Plantations of varying sizes and ages are thus adjusted to a common basis and any difference in the site index figure may be attributed to some factor or factors in the site itself.

A summary of all the infection data accumulated in the study is given in Table 3, where the southern Connecticut study areas are arranged in order of ascending site indices and the data are presented by crown classes. Even though the number of different sites included here is not large, it is believed that they offer a representative selection of the growth conditions in pure red pine plantations in this region. For the three New York infection areas exact age data were not available; therefore, site indices for them are not included. General observations in the Canadice area indicate that a site index figure for the plantation listed in Table 3 would be very low as compared with the southern Connecticut sites. The heavy infection at Canadice, New York, may then be regarded as occurring on a poor site.

Consideration of the southern Connecticut areas alone shows that there is no hard and fast relation between site and infection. Thus, only 2.6 per cent of the trees on the site with an index of 12.50 were infected, and 23.4 per cent and 31.6 per cent were infected on the sites with indices of 18.35 and 19.30, respectively. This indicates that plantations on relatively poor sites may be almost free of infection whereas plantations on relatively good sites may be heavily diseased. Such a condition is undoubtedly the result of the action of other limiting factors.

In Table 4 the infection data for the southern Connecticut areas, which are presented in detail in Table 3, have been analyzed to emphasize the effect of site. The 14 areas with known site indices are equally divided into two groups of 7 each with 17.75 the line of division and the average percentage of infection on each group of sites is given for each crown class and for all classes. There is twice as much infection of dominant trees on the poor sites as there is on the better sites. As the crown class is lowered the effect of site becomes less until in the overtopped class there is practically as much infection on the better sites as on the poorer sites. However, for all classes there is slightly more than 1½ times as much infection on the poor sites than on the better sites.

Because of the small number of sites included in this study, a statistical analysis of the data in Table 4 is not presented. The variation in the percentages of infection on sites above and below 17.75 is so great that there

Site index	Aspect and slope*	Dominant trees No.	Dominant trees Infected No.	Dominant trees Infected Per cent	Intermediate trees No.	Intermediate trees Infected No.	Intermediate trees Infected Per cent.	Overtopped trees No.	Overtopped trees Infected No.	Overtopped trees Infected Per cent	Total trees No.	Total trees Infected No.	Total trees Infected Per cent
						Southern Connecticut							
12.50	W–mod.	268	2	0.8	42	6	14.3	2	0	0.0	312	8	2.6
13.24	E–st.	96	15	15.6	21	12	57.1	5	1	20.0	122	28	23.0
13.40	E–gen.	198	42	21.2	42	33	78.6	29	25	86.2	269	100	37.2
14.20	W–gen.	801	133	16.6	162	54	33.3	106	55	51.9	1069	242	22.6
17.00	SE–gen.	167	24	14.4	47	26	55.3	23	15	65.2	237	65	27.4
17.35	E–gen.	293	0	0.0	35	4	11.4	20	6	30.0	348	10	2.9
17.65	S–gen.	748	106	14.2	136	65	47.8	215	98	45.6	1099	269	24.5
17.85	W–gen.	187	15	8.0	36	16	44.4	40	21	52.5	263	52	19.8
17.90	W–mod.	618	14	2.3	118	12	10.2	30	6	20.0	766	32	4.2
18.35	SE–st.	195	18	9.2	39	20	51.3	31	24	77.4	265	62	23.4
19.25	N–st.	196	1	0.5	24	5	20.8	27	11	40.7	247	17	6.9
19.30	Level	214	42	19.6	29	21	72.4	26	22	84.6	269	85	31.6
20.78	SW–gen.	1137	0	0.0	321	0	0.0	89	5	5.6	1547	5	0.3
21.30	E–gen.	319	0	0.0	44	3	6.8	24	2	8.3	387	5	1.3
Total		5437	412	7.6	1096	277	25.3	667	291	43.6	7200	980	13.6
						Canadice, New York							
	W–mod.	488	108	22.1	452	128	28.3	124	32	25.8	1064	268	25.2
						Ashokan Reservoir, Olive, and Hurley, New York							
	S–gen.	697	0	0.0	224	3	1.3	78	7	9.0	999	10	1.0
						Boonville, New York							
	S–gen.	198	1	0.5	177	1	0.6	61	0	0.0	436	2	0.5
Grand total		6820	521	7.6	1949	409	21.0	930	330	35.5	9699	1260	13.0

* mod. = moderate; gen. = gentle; st. = steep.

is some question as to the significance of the averages. However, they are at least indicative of the fact that dominant trees on the better sites are less susceptible to infection than those on the poor sites. Moreover, the ratios of the infection percentages on the sites below 17.75 to those on sites above 17.75 point to another significant relationship. They suggest that while a lessening of vigor resulting from poor site quality is a factor in determining the amount of infection, particularly in the dominant crown class, decreased vigor resulting from competition alone is also highly significant. In other words, low vigor may be induced by either poor site or by competition

TABLE 4. COMPARISON OF INFECTION ON GOOD AND POOR SITES

Crown Class	*Site index* Below 17.75 Av. per cent infection	Above 17.75 Av. per cent infection
Dominant	12.0	5.7
Intermediate	42.5	29.4
Overtopped	42.7	41.3
All	20.0	12.5

among individuals on all sites, and each alone or both together make for increased susceptibility to this disease.

Available data do not make it feasible to attempt any comparison of red pine growth figures in southern Connecticut with those for the tree growing naturally farther north. General observations indicate that red pine growth in this region is as good as, if not better than, it is anywhere else in the country. However, there are no stands of mature red pine in southern New England, and the suitability of any tree species planted outside of its optimum range cannot be determined until stands of it have attained economic maturity.

RELATION OF INFECTION TO CROWN CLASSES

The data concerning the individual condition of trees. as measured by their dominance or lack of dominance in the stand show that there is a marked relation of canker incidence to crown class. In taking the data in the field each tree examined was placed in one of four crown classes-dominant, codominant, intermediate, and overtopped *(14)*. In the analysis of the infection data no appreciable difference could be detected between the trees in the first two groups-dominant and codominant-hence, they were thrown together and listed as "dominant."

Reference to Table 3 shows how regularly the degree of infection varied with the crown class. In southern Connecticut a total of 7,200 trees was examined, of which 5,437 were in the dominant class, 1,096 in the intermediate, and 667 in the overtopped. The percentage of infection increased from 7.6 in the dominant class to 25.3 in the intermediate and 43.6 in the overtopped. In the entire northeastern region a total of 9,699 trees was examined of which 6,820 were in the dominant class, 1,949 in the intermediate, and 930 in the overtopped. Here, too, the same regular increase in the percentage of infection occurred—from 7.6 in the dominant class to 21.0 in the intermediate and 35.5 in the overtopped.

When the separate study areas are considered individually, the same inverse ratio between infection and crown class holds true in all cases except those where so few trees were found in the overtopped class that no value can be attached to the data concerning them, or where conditions are such that only small differences in thrift exist between the crown classes. Thus, on the first plot listed in Table 3 there were only two trees in the overtopped class and, by chance, neither was infected. On the Canadice, New York, area infection is almost equally severe in all classes, but happens to be highest in the intermediate class. On this particular area an almost unparalleled lack of expression of dominance was apparent and even the dominant trees were in only slightly better condition than the overtopped. The general lack of vigor in the stand undoubtedly had much to do with the even distribution of infection throughout the classes.

Somewhat parenthetically, it may be stated that in young red pine plantations as they occur in the Northeast, the expression of dominance is a latent character. The result is that plantations of the ages studied herein are largely composed of codominant trees from which it is difficult to select those individuals most suitable for final crop trees. Thus, of the 9,699 trees examined in this investigation, 6,820, or 70.3 per cent, were dominant and codominant; 1,949, or 20.1 per cent, were intermediate; and 930, or 9.6 per cent, were overtopped. Inasmuch as the great majority of these trees were spaced approximately 6 feet by 6 feet at the time of planting, it seems probable that a spacing of 8 feet by 8 feet may result in an earlier expression of the inherent growth possibilities of individual trees.

The Relation of Infection to Aspect and Slope

The aspect and slope data on all the study areas are given in Table 3. In determining the aspect a compass was used and the direction of the general slope recorded as the nearest cardinal direction or midpoints between them —i.e., north, northeast, east, southeast, etc. The slope or gradient was read with a clinometer and then classified under the following terms (*14*):

Level	0°	to	3°
Gentle	3.1°	to	8°
Moderate	8.1°	to	16°
Steep	16.1°	to	26°

In case of any considerable variation in either aspect or slope on a plot it was assigned to that category where it most nearly fitted.

A brief reference back to Table 3 shows that there is no particular relation between the degree of infection and either aspect or slope. This lack of uniformity is even more strikingly brought out in Table 5 where the 17

TABLE 5. ASPECT AND SLOPE ARRANGED IN ORDER OF THE DEGREE OF INFECTION

Percentage of infection	*Aspect*	*Slope*
0.3	SW	gentle
0.5	S	gentle
1.0	S	gentle
1.3	E	gentle
2.6	W	moderate
2.9	E	gentle
4.2	W	moderate
6.9	N	steep
19.8	W	gentle
22.6	W	gentle
23.0	E	steep
23.4	SE	steep
24.5	S	gentle
25.2	W	moderate
27.4	SE	gentle
31.6	–	level
37.2	E	gentle

areas are arranged in the order of the degree of infection found on them. It will be noted that as far as slope is concerned both the lightest and the heaviest infections occur on gentle slopes. One of the heaviest infections is on the level, yet, on 2 of the 3 steep plots infection is almost as bad as on the level. The arrangement of the aspects also suggests that they are a minor feature in determining the amount of disease.

The data concerning aspect are summarized in Table 6 and those concerning slope in Table 7. Reference to these tables shows even more clearly that infection is not related to any particular aspect or slope. It is realized that the basis in number of study areas is very low and that little reliance can be placed on these conclusions until they are borne out by extended field work. However, the limited data on hand do give an indication that neither aspect nor slope is of any particular importance in determining the amount of disease in any one stand.

TABLE 6. RELATION OF INFECTION TO ASPECT

Aspect	*No. of plots*	*Average percentage of infection*
N	1	6.9
E	4	16.1
SE	2	25.4
S	3	8.7
SW	1	0.3
W	5	14.9
level	1	31.6

TABLE 7. RELATION OF INFECTION TO SLOPE

Slope	*No. of plots*	*Average percentage of infection*
level	1	31.6
gentle	10	13.7
moderate	3	10.6
steep	3	17.7

RELATION OF INFECTION TO SOIL REACTION

In recent years considerable emphasis has been attached to the important bearing of soil reaction upon the favorableness of any site for the growth of a particular plant. Wherry (*33*) has worked out the soil-reaction preferences of many different plants and states that in general the *Coniferales* are acid-preferring plants. Alway, Kittredge, and Methley (*3*), working with natural red pine stands in northern Minnesota, found that the reaction of the litter, duff, and leafmold varied from a pH value of 4.0 to 4.7. Plice (*27*) gives the reaction of the forest-floor litter under red pine stands near Ithaca, New York, as pH 4.15 and of composite soil samples from about 4 inches depth under a red pine plantation near Urbana, Illinois, as pH 4.8. These data on red pine soil acidity, along with the oral and written expressions of the opinion of various foresters acquainted with the natural growing conditions of red pine stands, indicate that red pine prefers an acid soil and that the pH values of the soil under native red pine stands would probably be within the limits of 4.0 to 6.0.

Unpublished data on the soil reaction of red pine plantations in southern Connecticut, taken in 1928 and 1929 by M. F. Morgan, H. A. Lunt, and H. Bull of the Connecticut Agricultural Experiment Station, show that the range of pH values is from 4.2 to 5.3 with over 95 per cent of the recorded values falling between 4.4 and 5.0. The plantations in which Tympanis cankers have been found are included among those from which these data were taken. It may be concluded, therefore, that the soil reaction of the diseased plantations in southern Connecticut falls well within the limits of normal soil acidity under naturally reproduced red pine stands where none of the disease is present. However, there is a possibility that the pH values of the diseased plantations may be grouped at one end of the range of pH values for all plantations. No way of checking upon this possibility was available without the duplication of much of the work so it was not done. It should not be prematurely discounted that the worst infection centers may have been upon the least acid soils; but neither should one overlook the fact that Hicock *et al.* (*22, p. 730*) found that in Connecticut there is no correlation between soil reaction and red pine growth in plantations. This finding, coupled with the fact that the incidence of Tympanis canker varies inversely with the thrift and crown class of red pine, indicates that in southern Connecticut no correlation exists between soil reaction and the incidence of the disease.

Relation of Infection to Climatic Factors

Dissection of the 358 cankers referred to in Table 1, shows that they originated in the four years between 1928–31 inclusive. Seven, or 2.0 per cent, originated in 1928; 5, or 1.4 per cent, in 1929; 321, or 89.6 per cent, in 1930; and 25, or 7.0 per cent, in 1931. None of any earlier or later date were located in southern Connecticut at any time during the investigation. In western New York at Canadice a few cankers were found which dated back to 1926 but the data concerning their origin are too fragmentary to allow of more than cursory discussion. The following observations, then, will pertain almost entirely to the southern Connecticut infection zone.

The sharp increase in the amount of infection in southern Connecticut in 1930 suggested that a definite relation might be found between general climatic conditions and this abruptly appearing epidemic. Precipitation was selected as the variable to be compared with the incidence of the disease in southern Connecticut.

A summary of the precipitation at the New Haven, Connecticut, weather station from its inception in 1873 is given in Table 8. While the data given here are not exactly applicable to any one infection area yet they are equally

TABLE 8. PRECIPITATION (INCHES) AT NEW HAVEN, CONNECTICUT

Month	*Average means 1873–1927*	*1928*	*1929*	*1930*	*1931*	*1932*	*1933*
January	3.98	1.92	3.49	2.86	3.17	5.63	1.73
February	3.94	4.90	4.42	3.27	2.04	2.51	4.15
March	4.22	2.98	4.19	3.50	5.27	6.28	6.60
April	3.70	5.11	7.25	2.09	3.98	1.93	4.64
May	3.70	2.26	3.94	5.45	5.90	2.64	2.00
June	3.12	6.09	1.57	2.43	5.33	2.16	2.26
July	4.19	7.86	2.44	1.65	3.99	2.79	3.58
August	4.54	3.51	4.17	1.35	3.31	3.88	7.39
September	3.49	3.85	1.31	0.47	4.60	3.55	5.05
October	3.75	1.38	3.75	2.50	2.23	5.51	2.64
November	3.54	3.59	2.22	6.73	0.85	6.45	0.90
December	3.87	1.60	4.35	2.42	3.54	2.25	4.51
Annual total	46.19	45.05	43.10	34.72	44.21	45.58	45.45
June to September, inclusive	15.34	21.31	9.49	5.90	17.23	12.38	18.28

pertinent to all. Moreover, they constitute the only available source of such information within the confines of the infection zone.

From 1873 to 1927, inclusive, the New Haven station recorded an annual average rainfall of 46.19 inches, which was approximately equally distributed over the months of the year, varying from a low of 3.12 inches in June to a high of 4.54 inches in August and averaging 3.85 inches per month. In 1928 the annual rainfall was 45.05 inches; in 1929, 43.10 inches; in 1930, 34.72 inches; in 1931, 44.21 inches; in 1932, 45.58 inches; and in 1933, 45.45 inches. In other words, in the years before, during, and after the appearance of the disease the annual rainfall was only slightly below the average annual mean for the preceding S4 years *except in I930 when it dropped to* 34.72 *inches*—a deficit of 11.47 inches, or 24.8 per cent, from the long-time mean of 46.19 inches. This one-quarter decrease in moisture marks the well-known drought of 1930 in this region, which manifested itself in widespread injury and death to many forms of plant life, including trees *(30).* It is not surprising that there should be a disease outbreak under such conditions, for it is a well-known fact that drought weakens plants and makes them susceptible to parasitic diseases which under normal circumstances would not be injurious. Boyce (9) has shown that drought conditions prevailing in northern California in 1929 were directly responsible for the outbreak of the Douglas fir canker caused by *Phomopsis lokoyae.* With respect to this new disease of red pine, then, the fact that 89.6 per cent of the cankers studied originated in 1930 may with small reason for doubt be correlated with the large deficiency in rainfall for that year.

Examination of the monthly precipitation data discloses another significant fact. The greater portion of the deficiency in 1930 occurred from June to September, inclusive, during that part of the year when plant growth and consequent use of water are at a maximum. As compared with an average long-time precipitation of 15.34 inches for these 4 months, in 1930 there were only 5.90 inches. Moreover, in 1929 during the same period only 9-49 inches of rainfall occurred. The 1930 deficiency, therefore, may be considered as an addition to that of 1929 and, hence, the injurious effects to vegetation may be regarded as the resultant of an accumulated deficit. This sustained reduction of the moisture supply undoubtedly lowered the thriftiness of the planted red pines and made them more susceptible to any disease for which the vigor of the host is a limiting factor.

The 1928 and 1929 cankers were on intermediate and overtopped trees, suggesting that in years of normal or slightly subnormal precipitation this disease may occur sporadically, but will probably be restricted to the lower crown classes unless some factor other than abnormal climatic conditions causes a lowering of vigor. The appearance of more cankers in 1931 than in the years preceding 1930 probably was the result of a lag of the deleterious effects of the drought into the following year of approximately normal precipitation.

The reason for the absence of any cankers originating prior to 1928 is that relatively little planting of red pine was done in this region before 1910, so that few plantations of the requisite age and size for infection by the disease were present before the 1930 epidemic. Infection is thought to occur through lower dead branches; therefore, at young ages before the appearance of many such dead branches, the chances of infection are greatly reduced. This offers the most logical explanation for the absence of early cankers.

A different line of reasoning may be applied to explain why no cankers have originated since 1931. With conditions for infection as favorable as they were in 1930-so favorable that about nine-tenths of all the diseased trees in southern Connecticut became infected in that year-it is entirely possible that most of the low-vigor trees are already infected and that the remaining uninfected ones are sufficiently vigorous to ward off the disease. Such an idea is highly theoretical, but seems rather plausible. It does not lend itself to proof, but in the absence of recent infection it is also difficult to disprove.

RELATION OF INFECTION WITHIN A CROWN CLASS TO VIGOR AS EXPRESSED IN HEIGHT AND DIAMETER INCREMENTS

In the course of routine examination of the southern Connecticut red pine plantations, it was frequently observed that two adjacent trees which were almost identical would differ in that one would be infected and the other not. It is always possible, even probable, that such a condition might result from the accidental chances of natural infectioll. However, it was thought advisable to attempt some explanation of this variation. Accordingly, 100 pairs of adjacent trees as nearly identical in every respect as could be determined from careful observation and examination were selected at random in several different plantations. Of each pair one tree was free of infection and the other had one stem canker of 1930 origin. Both members of each pair were thus similar in crown class, soil, aspect, slope, age, spacing, etc. Of the 100 pairs, 25 fell into the dominant class, 40 in the codominant, 23 in the intermediate, and 12 in the overtopped.

For each tree the total height and the diameter at breast height were secured. Then the height increment for the two five-year periods, 1924–28 and 1931–35, was determined. For the same periods the diameter increment was secured by removing a median core at one foot from the ground with an increment borer and measuring the exact diameter growth with a small caliper. The 1924–28 data are considered to be a measure of the growth rate and condition of the tree previous to the heavy infection period of 1930; and the 1931–35 data a measure of the growth rate and condition after the infection period.

In Table 9 the average height and diameter increments for infected and uninfected trees are given by crown classes and for all trees, and the growth rate in the five-year period, 1931–35, is compared with that in the period 1924–28. For dominant uninfected trees height growth is reduced 15.2 per cent and diameter growth 55.9 per cent. The reduction increases as the crown class is lowered until the height growth of the overtopped trees is reduced 38.7 per cent and diameter growth 64.7 per cent. For infected trees it will be observed that the percentage reduction is in every case greater than it is for the uninfected trees.

These differences in the growth rates before and after the period of infection are statistically analyzed in Table 10 in which $S =$ the standard deviation of the units in each sample, $Sa =$ the standard deviation of the average for each sample and $Sxy =$ the standard deviation of the difference of the averages of the two samples.[7] That the differences are significant is indicated by the fact that the values in column 10 are in every case greater than three times the values in column 11—in other words, the differences of the averages exceed by over three times the standard deviation of the difference of the averages. From the statistical point of view this is considered proof that the differences shown are not the result of variation in sampling, but are caused by some other factor. The conclusion is that the rate of growth for all trees whether infected or not is significantly less in 1931–35 than it was in 1924–28. Furthermore, the growth rate of the infected trees was reduced more than that of uninfected trees.

In Table 11 the growth of infected trees is compared with that of unin-

7. These values were derived from the following formulæ taken from Wright, W. G., 1925. Statistical Methods in Forest Investigative Work. Bul. 77, Forestry Branch, Dept. of Interior, Canada, p. 36.

$$S = \pm\sqrt{\frac{\Sigma d^2}{n}}\,;\; Sa = \pm\frac{S}{\sqrt{n}}\,;\; Sxy = \pm\sqrt{\frac{Sx^2}{nx} + \frac{Sy^2}{ny}}$$

TABLE 9. REDUCTION IN THE GROWTH RATE OF PAIRED TREES SINCE THE PERIOD OF INFECTION

Condition	*Crown class*	*Basis*	*Av. ht. increment in feet*		*Per cent reduction**	*Av. diam. increment in inches*		*Per cent reduction**
			1924–28	*1931–35*		*1924–28*	*1931–35*	
Infected	D	25	7.4	6.1	17.6	1.94	.68	65.0
Uninfected	D	25	9.2	7.8	15.2	2.29	1.01	55.9
Infected	CD	40	7.3	5.6	23.3	1.64	.41	75.0
Uninfected	CD	40	8.9	7.5	15.7	1.97	.72	63.5
Infected	I	23	6.4	4.0	37.5	1.56	.43	72.4
Uninfected	I	23	7.9	6.0	24.1	1.91	.68	64.4
Infected	O	12	5.4	3.0	44.4	1.29	.26	79.8
Uninfected	O	12	7.5	4.6	38.7	1.67	.59	64.7
Infected	All	100	6.9	5.0	27.5	1.65	.46	72.1
Uninfected	All	100	8.6	6.9	19.8	2.00	.78	61.0

* On basis of 1924–28 growth.

TABLE 10. STATISTICAL ANALYSIS OF THE DIFFERENCES IN THE GROWTH RATES BEFORE AND AFTER THE PERIOD OF INFECTION

1 Condition	2 Crown class	3 Basis n	4 Av. increment 1924–28	5 Standard deviation S	6 Sa	7 Av. increment 1931–35	8 Standard deviation S	9 Sa	10 Difference of averages	11 Sxy
					Heights					
Infected	D	25	7.4 ft.	±1.38	±0.28	6.1 ft.	±1.47	±0.29	1.3 ft.	±0.40
Uninfected	D	25	9.2 ft.	±1.43	±0.28	7.8 ft.	±1.25	±0.25	1.4 ft.	±0.38
Infected	CD	40	7.3 ft.	±1.06	±0.17	5.6 ft.	±1.25	±0.20	1.7 ft.	±0.26
Uninfected	CD	40	8.9 ft.	±1.32	±0.21	7.5 ft.	±1.36	±0.21	1.4 ft.	±0.30
Infected	I	23	6.4 ft.	±1.19	±0.25	4.0 ft.	±1.19	±0.25	1.4 ft.	±0.35
Uninfected	I	23	7.9 ft.	±1.39	±0.29	6.0 ft.	±1.44	±0.30	1.9 ft.	±0.42
Infected	O	12	5.4 ft.	±1.14	±0.33	3.0 ft.	±1.07	±0.31	2.4 ft.	±0.45
Uninfected	O	12	7.5 ft.	±1.55	±0.45	4.6 ft.	±1.33	±0.38	2.9 ft.	±0.59
Infected	All	100	6.9 ft.	±1.15	±0.12	5.0 ft.	±1.25	±0.13	1.9 ft.	±0.17
Uninfected	All	100	8.6 ft.	±1.37	±0.14	6.9 ft.	±1.33	±0.13	1.7 ft.	±0.19
					Diameters					
Infected	D	25	1.94 in.	±0.29	±0.06	.68 in.	±0.18	±0.04	1.26 in.	±0.07
Uninfected	D	25	2.29 in.	±0.26	±0.05	1.01 in.	±0.29	±0.06	1.28 in.	±0.08
Infected	CD	40	1.64 in.	±0.32	±0.05	.41 in.	±0.15	±0.03	1.23 in.	±0.06
Uninfected	CD	40	1.97 in.	±0.39	±0.06	.72 in.	±0.20	±0.03	1.25 in.	±0.07
Infected	I	23	1.56 in.	±0.38	±0.08	.43 in.	±0.22	±0.05	1.13 in.	±0.09
Uninfected	I	23	1.91 in.	±0.40	±0.08	.68 in.	±0.26	±0.05	1.23 in.	±0.10
Infected	O	12	1.29 in.	±0.36	±0.10	.26 in.	±0.12	±0.03	1.03 in.	±0.15
Uninfected	O	12	1.67 in.	±0.39	±0.11	.59 in.	±0.31	±0.09	1.08 in.	±0.14
Infected	All	100	1.65 in.	±0.33	±0.03	.46 in.	±0.17	±0.02	1.19 in.	±0.04
Uninfected	All	100	2.00 in.	±0.36	±0.04	.78 in.	±0.25	±0.03	1.22 in.	±0.04

TABLE II. COMPARISON OF THE GROWTH RATE OF INFECTED AND UNINFECTED TREES BEFORE AND AFTER THE PERIOD OF INFECTION

Crown class	*Basis (pairs)*	*1924–28* *Uninfected*	*Infected*	*Per cent difference**	*1931–35* *Uninfected*	*Infected*	*Per cent difference**
				Average height increments in feet			
D	25	9.2	7.4	19.6	7.8	6.1	21.8
CD	40	8.9	7.3	18.0	7.5	5.6	25.3
I	23	7.9	6.4	19.0	6.0	4.0	33.3
O	12	7.5	5.4	26.7	4.6	3.0	34.8
All	100	8.6	6.9	19.8	6.9	5.0	27.5
				Average diameter increments in inches			
D	25	2.29	1.94	15.3	1.01	.68	32.7
CD	40	1.97	1.64	16.8	.72	.41	43.1
I	23	1.91	1.56	18.3	.68	.43	36.8
O	12	1.67	1.29	22.8	.59	.26	55.9
All	100	2.00	1.65	17.5	.78	.46	41.0

* On basis of growth rate of uninfected trees.

fected trees for the periods before and after infection. The data here show two things. First, in the period before infection, 1924-28, the trees which were to become infected were growing appreciably slower than those which were to escape infection; second, in the period after infection, 1931-35, the difference between the growth rate of infected and uninfected trees was greater than it was in 1924-28.

The comparison in Table 11 was tested statistically as in Table 10 and the differences were found to be equally significant. Therefore, it may be definitely stated that the trees which escaped infection were making more rapid growth and hence were more vigorous both before and after the period of infection than were those that became infected.

The conclusions which may be drawn from the data presented in Tables 9-11 are both varied and significant in the interpretation of the causes and effects of infection. The 1924-28 data represent the vigor of all trees in the southern Connecticut plantations before plantation closure, before the 1930 drought, and before the period of Tympanis canker incidence. Conversely, the 1931-35 data are representative of conditions after these three separate factors had become operative. It is impossible to segregate the effects of each factor; hence, the results must be considered in the light of all three collectively. \Vith respect to the uninfected trees alone, the reduction in their gro\vth rate may be attributed to both plantation closure and the 1930 drought, \vith the former probably most effective. However, the greater reduction of the growth rate of infected trees than of uninfected trees cannot be attributed to the presence of cankers alone although it is probable that the presence of a stem canker on a tree would have a detrinlental effect on the vigor and growth rate of the tree. But it is also probable that inasmuch as in the 1924-28 period-before infection, closure, and drought were operative -the trees which were to become infected were less vigorous than those which were to escape infection, they might have been more affected by the injurious and weakening consequences of both closure and drought than were their more vigorous neighbors. It is logical to assume that if two trees or two living organisms of any kind are subjected to the same degree of unfavorableness, the less vigorous of the two will suffer most acutely. All trees were less vigorous after 1930 than they were before, but the infected trees certainly sho\ved a greater reduction than the uninfected. Regardless of the decrease in the growth rate of all trees after 1930, it is evident that in all crown classes the less vigorous individuals \vere more susceptible to infection than their faster gro\ving neighbors. It may be concluded, therefore, that irrespective of other factors the vigor of an individual tree largely determines its susceptibility to the Tympanis canker disease. Of the 100 pairs of trees studied, the infected members were certainly less thrifty before, during, and after the infection period.

GENERAL DISCUSSION OF THE FACTORS CONTRIBUTING TO INFECTION

It has been pointed out that this new disease of red pine is known to occur only on plantation trees south of the optimum range of the species, that its incidence is much higher in pure stands than in mixture with white pine, that it is worse on the poorer sites than it is on the better ones, that the lower crown classes are more susceptible than the upper ones, that the indications are that slope, aspect, and soil reaction are of little consequence, that any injurious or weakening environmental factor such as a severe drought has a direct and positive bearing on infection, and, finally, that susceptibility to infection is inversely correlated with the vigor of individual trees. From these conclusions the inference has been drawn that the causal organism, *Tympanis sp.*, is only weakly parasitic and can only enter the stem and cause canker formation when the host trees have their general vigor lessened by some factor or complex of factors in the environment. This inference is strengthened by the small size of the inoculation cankers artificially produced on vigorous trees. The organism even though inserted into the stems could not cause large typical cankers there because of some inhibiting factor within the host. It is furthermore strengthened by the widespread natural occurrence of the causal organism as a saprophyte as compared with its restricted occurrence as a parasite. Throughout the range of the eastern white pine, which corresponds over large areas with the range of red pine, *Tympanis sp.* occurs frequently. It has never been found by the writer on the lower dead branches of living red pine naturally reproduced, but in all the plantations examined in southern New England and New York it is common on such branches. It will be found fruiting within one inch of the stem usually, but unless the tree becomes weak enough to allow infection, the fungus dies as the bark of the branches loosens and sloughs off. Such conditions are exhibited in all of the red pine plantations 15 to 30 years old that the writer has examined in regions south of the optimum natural range of the species. It is highly probable that in many of these plantations, if conditions for tree growth become unfavorable, the fungus will shortly drop its saprophytic rôle and assume that of an active and destructive parasite. In southern Connecticut the 1930 drought was the deciding factor. In other areas other factors may predominate. General observation indicates that one of the contributory causes of the high infection at Canadice, New York, was insufficient spacing at the time of planting, coupled with the lack of thinnings later. The net result was that the plantation stagnated at an early age and the disease became epidemic in it.

Reasons why the present known distribution of the disease is limited. to those regions which may be considered as an artificial southern extension of the range of red pine are somewhat obscure. It would seem not to be a result of growing the tree in pure plantations alone, else infection of trees in such plantations would occur farther north than it has been found. No Tympanis cankers have been found in plantations in northeastern New York, in northern Vermont, in central Massachusetts, in southern New Hampshire, or in the northern portions of the Lake States. Therefore, artificial planting and growing conditions alone cannot be held responsible for the appearance of the disease. It certainly is not dependent on any limitations in the distribution of the causal organism or to its failure to act as a parasite at northern latitudes because it does occur on eastern white pine, often as a parasite, over much of the optimum range of red pine. Therefore, it seems possible that this restricted distribution may be caused by differences in the climatic environment of the host tree in its optimum range and in those areas to the south where it has been planted. A discussion of these differences and their possible effects on the incidence of the disease may be of value in understanding its geographical distribution.

A partial picture of the climatic differences between areas where red pine grows best naturally and where the heaviest known infection occurs on plantation trees is available in Figure 1. Five climatographs are shown here -the two at the top constructed from data taken by the Weather Bureau of the United States Department of Agriculture at Hemlock, New York, and New Haven, Connecticut,and the three at the bottom from weather data taken in northern Minnesota, northeastern New York, and western-central Maine. The northern Minnesota climatograph represents an average of-the data taken at Cass Lake and Itasca State Park, the northeastern New York an average of the data taken at Lake Placid Club and Keene Valley, and the western-central Maine an average of the data taken at Rumford and North Bridgeton. In all cases the data for the different places are averages for all the years since the inception of the respective weather-bureau stations. The Hemlock, New York, data are considered appropriate to the Canadice, New York, infection area; the New Haven, Connecticut, data are considered appropriate to all of the southern Connecticut infection centers; and the other three graphs are considered to be representative of three

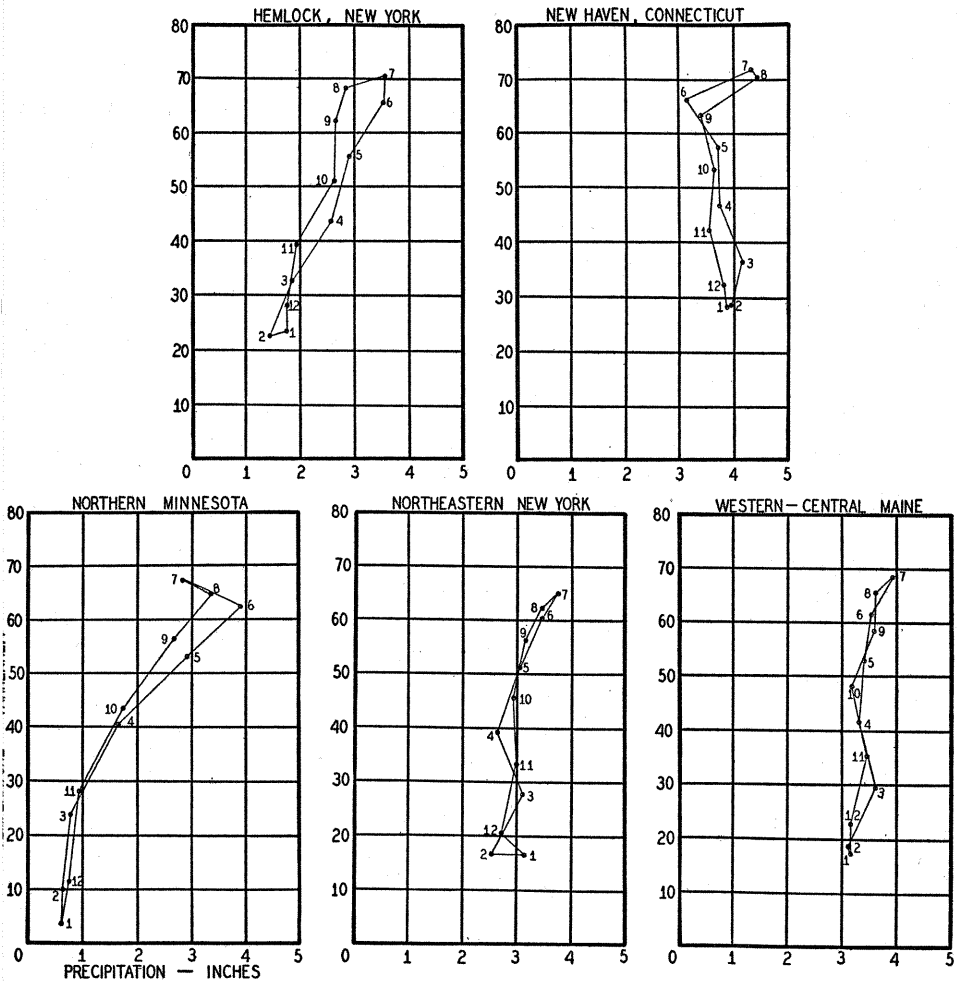

FIG. 1. Climatographs of areas where badly diseased plantations of red pine occur—Hemlock, New York, and New Haven, Connecticut—and of areas where red pine grows well naturally and where no disease has been found—northern Minnesota, northeastern New York, and western-central Maine. The average monthly temperatures in degrees Fahrenheit are plotted on the vertical axes and the average monthly precipitation figures in inches on the horizontal axes. The numbered points on the graphs correspond to the months of the year—1 for January, 2 for February, 3 for March, etc. The lines connecting successive numbers serve only to give a closed figure representing the average annual climatic conditions existing at any one place or in a region.

widely separated regions in northern United States where red pine grows well naturally and is one of the commercial forest tree species. The two upper graphs represent climatic conditions in areas where red pine does not occur naturally other than as occasional scattered trees, but is found extensively in planted stands and where disease conditions are severe. The three lower graphs represent climatic conditions in regions where red pine occurs and grows well naturally, as well as in plantations, and where no infection has yet been found.

Examination of these climatographs shows that as far as precipitation is concerned the largest monthly variation and the smallest annual total occur in the northern Minnesota region where red pine is an important natural component of forest stands and where no infection has been found. The average annual precipitation and its distribution over the year is approximately the same in western-central Maine where no infection occurs and at New Haven, Gonnecticut, where a large amount of infection is present. It is obvious, therefore, that no correlation exists between average moisture conditions alone and the known distribution of the disease.

If the charts are compared with reference to temperature conditions, however, an association is unmistakingly evident between higher monthly and annual temperature and the presence of the disease. The coldest months at Henllock, New York, and New Haven, Connecticut, have average temperatures of approximately 23° F. and 28° F., respectively; and the warmest months average approximately 71° F. and 72° F., respectively. In comparison, the coldest months in northern Minnesota, in northeastern New York, and in western-central Maine have average temperatures of approximately 4° F., 17° F., and 18° F., respectively; and the warmest months have average temperatures of approximately 67° F., 65° F., and 69° F., respectively. Without further discussion it is apparent from these data and from the position and shape of the climatographs that the total annual heat is greater in the disease areas than it is where no disease occurs.

Conjectures only may be advanced as to whether or not there is any causative relation between these higher temperatures and the incidence of disease. It seems reasonable to believe that, inasmuch as red pine has its optimum range well to the northern part of the United States and into Canada, the species has the ability to withstand temporary unfavorable conditions, such as severe drought, whenever it is growing within this optimum range. Conversely, it may be argued that one of the reasons the species has not spread naturally farther south is because it is not fitted to cope with unfavorable circumstances arising there periodically. Thus, red pines planted in southern Connecticut have grown well under the influence of the even rainfall and moderate temperature as long as no serious deviation from the normal occurred with respect to these features. But when they were subjected to the drought of 1930, it is possible to conceive of them as being unable to withstand the effects of insufficient moisture as well as they might have done farther north. Their vigor was thereby reduced and they became susceptible to infection by the Tympanis canker fungus. The writer makes no claims for this theory other than that it is not unreasonable and that it does serve to explain why trees within the optimum range are free of infection and those to the south are heavily infected.

Bates (7), in discussing the results of a study designed to determine the relative merits of red pine seed from different localities, states that, "It is probably true that the southern portion of the range of Norway pine, even though it receives more rainfall than the northern portion, is less favorable for growth because of greater extremes of temperature, higher evaporation, and greater liability to drought." Even though he does not produce evidence to bear out this statement, the fact that he makes such a statement indicates that the writer's theory is not improbable.

Another possible explanation for the restriction of the Tympanis canker to plantations south of the optimum range of red pine may be advanced. Planted red pines in southern New England grow more rapidly during their early life than do planted or naturally regenerated trees farther north. The excellent soil conditions (*22, p.* 750), the higher temperatures and uniform rainfall and the longer growing season are the principal factors responsible for this increased growth. It is possible that the more rapidly trees are growing, the more they are weakened when any environmental change suddenly lessens their rate of growth. When a plantation closes and competition becomes a factor in determining growth, it seems plausible to expect that the resulting shock to the individual trees will be greater in the rapidly growing southern plantations than it is in the slower growing northern plantations. If such be true, planted red pine in southern New England should be in a less thrifty condition during the period of adjustment after the closing of the plantation than would similar trees in northern New England. They would, therefore, be more susceptible to disease even under normal weather conditions. The southern Connecticut red pine plantations where infection occurred in 1930 had closed only a few years prior to that time. The trees may have been weakened through the shock of closing and the drought of 1930 accentuated their unthrifty state more than it did in the northern stands.

DAMAGE TO INDIVIDUAL RED PINE TREES

FROM the point of view of the individual tree composing a plantation or stand, this new disease is capable of causing two types of injury: (1), primary infection, resulting in the creation of stem cankers which either permanently disfigure the tree or cause its outright death; and (2), secondary effects which may be manifested in breakage by wind and snow or in extensive decay of the boles by fungi which gain entrance through the open cankers. Each type of defect will be separately discussed.

Death or Permanent Disfigurement of Infected Trees

As previously stated in the review of the macroscopic characteristics of the disease, the large majority of cankers on red pine caused by *Tympanis sp.* are of the nongirdling type. It follows naturally and logically that instances of death of the infected tree should be relatively few. Such is the case. Complete girdling with its consequent destruction of the conductive function of the phloem tissue results either when two or more cankers are centered at the same node and coalesce to form an encircling zone of infected bark (Plate VI), or when a single canker extends around the stem, as occasionally happens. After girdling is effected, death of the tree may be expected within one year, or at most by the end of the growing season following that in which girdling took place. The slight ability of the disease to girdle trees is indicated by the fact that out of 682 infected trees, only 26, or 3.8 per cent, were girdled. Furthermore, of these 26 girdled trees, 16 were girdled through the combined activity of two or more cankers. The remaining 10, or 1.5 per cent of the total number of infected trees, represent the small number girdled by a single canker.

Occasionally, isolated infected dead trees or a small group of dead and dying infected trees may be found in the southern Connecticut plantations. While the evidences of canker formation are unmistakable on them, it is believed that their loss cannot be charged specifically to *Tympanis sp.*, although the fungus may have been a partial agency. Some other plausible theory of the cause of their deaths can always be advanced. Dead and dying groups are usually found among exposed ledges and rock outcroppings, particularly when these formations occur on slopes where rapid run-off of surface and subsoil moisture is facilitated. Many of these trees are apt to exhibit stem cankers, but conversely many will have no indications of infection. The writer's opinion is that death under these circumstances may be attributed to lack of moisture or nutriment because of the shallow soil over the ledges. Again, single infected dead trees commonly occur, but one may see uninfected dead trees close by. Examination will show that suppression and competition may be considered responsible for death in both cases. The presence of the disease on these poorly conditioned trees may have hastened death to a slight degree, but it cannot be regarded as the sole cause.

In the event that death does not follow canker formation, a permanent defect of the stem is usually produced. Even if the above mentioned secondary effects of infection do not become apparent, an unmistakable blemish is created. Resin infiltration of the sapwood below the face of the canker constitutes a permanent disfigurement even if the canker is covered with a callous layer. In the dissection of red pine stems taken from the infection area at Canadice, New York, numerous completely healed lesions were found. *Tympanis sp.* could not be isolated from them, but circumstantial evidence strongly points to it as the original cause of the injury. Lumber sawed from such logs would be subject to serious degrade because of the pitch pockets and extensive discolored areas. The inference is that infection always results in some degree of permanent injury.

Breakage at the Cankers

It is logical to expect that the formation of stem cankers will be reflected in a lessening of the strength of the infected stems. Breakage of uninjured stems of plantation-grown red pines by ordinary wind and snow storms in this region rarely occurs. Close planting and evenage result in an almost level and uninterrupted crown canopy which offers slight chance for any storm to exert severe lateral pressure on the stems. The pressure which is exerted, however, is sufficient to cause the breakage of the stems of infected trees at the cankers. In heavy infection centers several adjacent trees may snap off, thus opening up the canopy considerably and making the trees near by more subject to storm injury. In Plate XI, Fig. 1, is an infection center in Woodbridge, Connecticut, where several dead trees have broken over at the cankers. All of the dead trees shown in the picture were infected. In Plate XI, Fig. 2, is a single tree in Branford, Connecticut, showing breakage at the canker.

Up to the present time breakage of this type is not prevalent. In only two or three small areas is group breakage apparent. Single broken trees are exceedingly sporadic. Nevertheless breakage does constitute one serious potential consequence of infection.

Decay by Secondary Fungi

Within a year or two after infection the bark on a canker cracks and shreds so that the sapwood beneath is exposed to the ravages of other fungi which may be considered as secondary in that they gain entrance only after *Tympanis sp.* has killed the bark. From the point of view of the amount of damage caused by them, however, these so-called secondary fungi are of primary importance. Some idea of their prevalence in southern Connecticut is given in Table 12, in which data on 884 cankers are presented. Decay of the bole under the face of the canker had started in 594, or 67.2 per cent, of them. This shows that deterioration of the stem by decaying organisms is already prevalent and undoubtedly will become more so as the years since infection increase.

TABLE 12. RELATION OF WOOD-ROTTING FUNGI TO RED PINE CANKERS

Crown class	*Number of cankers*	*Number with stem decay present*	*Percentage*
Dominant	371	251	67.7
Intermediate	312	179	57.4
Overtopped	201	164	81.6
Total	884	594	67.2

The exact extent of this decay up and down the boles of living trees was not determined because the affected trees were thought to be too small for the data to have any practical significance. However, the writer has dissected trees 6 inches and less in diameter in which most of the sapwood and a considerable portion of the heartwood was typically decayed for two and occasionally three full internodes. It is highly improbable that any trees now in this condition in young plantations will ever reach the age of merchantability. If they should remain alive until that time, the decay would have advanced so far as to make the bole unmerchantable.

Decay of cankered boles is caused largely by two fungi, *Poria versipora* (Pers.) Fries and *Radulum spathulatum* (Schrad. *ex* Fries) Bres. The general appearance of these two fungi is shown in Plate XII.

Cultures made from decayed wood on malt agar medium have in many cases turned out to be one of these two fungi. Many cultures were contaminated with molds, yeast, and bacteria, but no appreciable decay can be attributed to organisms belonging to these groups of fungi. In addition, cultures of other fungi which have not as yet been identified have been occasionally secured. The possibilities of finding a large number of wood-rotting fungi in these decayed stems are almost limitless, but present data indicate that the two fungi named above are the ones of primary importance.

Considerable discoloration of the sapwood in and adjacent to the open cankers is caused by one or more wood-staining fungi, particularly by members of the blue-staining group. No attempt has been made to isolate and determine any such fungi. Their presence is often of slight importance because of the fact that actual decay by other fungi is already prevalent in the same tissue invaded by the staining organisms.

DAMAGE TO RED PINE STANDS—ECONOMIC LOSS

THE idea that the percentage of infection in a stand is the sole criterion of economic loss is no longer held, and in its place has risen the sensible concept that infection or even death of single trees does not constitute loss unless it eventually results in a reduction of the final crop, or in a lowering of its quality. Meinecke (*26, pp. 285–286*) in 1928 clearly states this principle as follows: "Loss can have only one meaning in forestry, that of economic loss, which in turn is practically synonymous with loss in wood production. . . . The criterion by which the loss must be gauged is not the actual number or per cent of trees killed but the effect of the killing on the condition promising the best obtainable wood production. The loss, therefore, concerns not the present but the future value. It affects the expectation value of the stand." Snell (*29*), in 1931, restates this new evaluation of loss from a disease and also attempts an estimate of the actual expectation value of the crop and its reduction by the disease.

The writer's discussion of this red pine disease has thus far dealt largely with the percentage of infection and the types of injury to be expected. Inasmuch as most of the cankers formed are of the nongirdling type, actual and outright killing of the infected tree by the causal organism is relatively rare. Nevertheless, each infected tree loses its potential value at maturity because the open cankers offer entrance to the stem for secondary staining and rotting fungi which largely render the bole unfit for lumber. The butt log constitutes the principal value to be expected from plantation-grown red pine trees. This new disease usually damages the butt log and hence appreciablyreduces the expectation value of an infected tree even though the tree may remain alive for an indefinite period.

In an artificially reproduced plantation the component trees theoretically are spaced at the time of planting so as to secure the most rapid accretion of high quality product that is COlnmensurate with the site and the species. Silviculturally, a stand so grown should produce the greatest possible amount of lumber in the shortest rotation. 'fhinnings-or other intermediate cuttings should be so timed as to always maintain the highest level of productivity.

Assuming that the plantations where this disease at present occurs have been operated on this principle, then damage or loss must be evaluated according to the degree that the disease has upset or hindered the fulfillment of the species productivity. Total infection percentages such as those given in Table 3 represent damage only to the extent that the disease removes crop trees or impairs their quality. The amount of damage is directly dependent on the distribution of the infected trees in the stand rather than on the total percentages of trees infected.

Figures 2 and 3 are diagrammatic representations of the condition's pertaining in two plantations of red pine in southern Connecticut. It is realized that consideration of them will not show or even approximate the conditions that will be true at the time the plantations are mature. As long as one is working with a biotic factor the best that can be done is to reduce the present circumstances to a static condition and yet not lose sight of the fact that ceaseless changes are going on.

In Figure 2 is represented a plantation established in 1916 from 2-2 stock spaced 6 by 6 feet. In 1934 when the data were taken the stand had a total age of 23 years. A slight ridge runs across the short axis of the plantation with its crest approximately following the twentieth row from the left. Theslope and aspect to the left of this ridge are gentle and westerly, to the right,gentle and easterly. The infection is concentrated on the western slope and is negligible on the eastern. There are 152 selected and pruned crop trees on the area of which 16, or 10.5 per cent, are infected. On the western slope 74 of the 152 crop trees occur, of which 15, or 20·3 per cent, are infected.

What is the actual damage? First, one may say that the 16 infected crop trees, representing 10 per cent of all the crop trees in the plantation, constitute a loss. They had been selected as the most vigorous individuals in the stand and had been pruned at a direct expenditure. Inasmuch as infection damages the butt log of a tree it is obvious that by the time these trees

FIG. 2. Diagrammatic representation of a badly diseased red pine plantation in southern Con- ticut. Each letter designates a single tree and gives the crown class—D, dominant; C, codomi- ıt; I, intermediate; and O, overtopped. A dash denotes a dead tree and a blank space an opening the stand where no tree is present. A large outer circle indicates that the tree is diseased. A dot ler a letter shows that the tree has been pruned. The area inside the closed lines represents that tion of the plantation which the disease has caused to be understocked. The spacing in the plan- ion is approximately 6 feet.

reach the age of maturity they will be rendered unmerchantable through decay centered at the cankers. A total of 10 per cent of the pruning cost in this plantation is certainly a loss.

In Figure 3 is represented another plantation established in 1914 froin 2–1 stock spaced 6 by 6 feet. In 1934 the total age of this stand was 24 yeats. The aspect is southerly and the slope level to gentle. A highway bordered by scattered hardwood trees parallels the upper edge. The death of many trees along the road and the conspicuous blank areas in the plantation may be largely attributed to the effects of shade and root competition from these trees. Some of the openings inside the stand are caused by old apple trees which are or have been present. A ledge of rock lies just above and to the left of the large group of dead diseased trees in the upper central part of the figure. Undoubtedly much of the low vigor of the trees on this area may be charged either to the effects of competition with vigorous hardwood trees or to poor soil conditions caused by surface ledges. The soil near and over these ledges is shallow and dries out quickly in dry periods.

There are 102 pruned crop trees on the area of which only 5, or 4.9 per cent, are infected. It is obvious that only about 5 per cent of the pruning cost can here be considered a loss as compared to 10 per cent in the plantation represented by Figure 2. Considering both areas represented in Figures 2 and 3 as a unit, there are 274 pruned crop trees of which 21, or 7.7 per cent, are infected by *Tympanis sp.* Inasmuch as these two areas are among the worst infection centers that have been observed in southern Connecticut, it may be concluded that the heaviest loss of selected crop trees to be expected in any single plantation in this region from one severe infection period, such as that induced by the drought of 1930, will not run over 10 per cent and probably will be somewhat less.

In a great many young red pine plantations in this country today no attempt has been made to select crop trees, and possibly none will be made until late in the life of the stand. For such plantations it is obviously impossible to express damage in terms of the percentage of infection on selected crop trees. Furthermore, even when such a course is possible, the figure arrived at may not really represent damage for in many cases the infection or even the removal of a crop tree results in slight loss because other trees are available to fill its place in the stand. If such is the case, the only loss is that represented by the cost of pruning or other cultural operations plus the difference in value of the crop tree and the tree that will take its place. In view of these considerations the writer has undertaken to estimate the economic loss in the plantings represented in Figures 2 and 3 by the

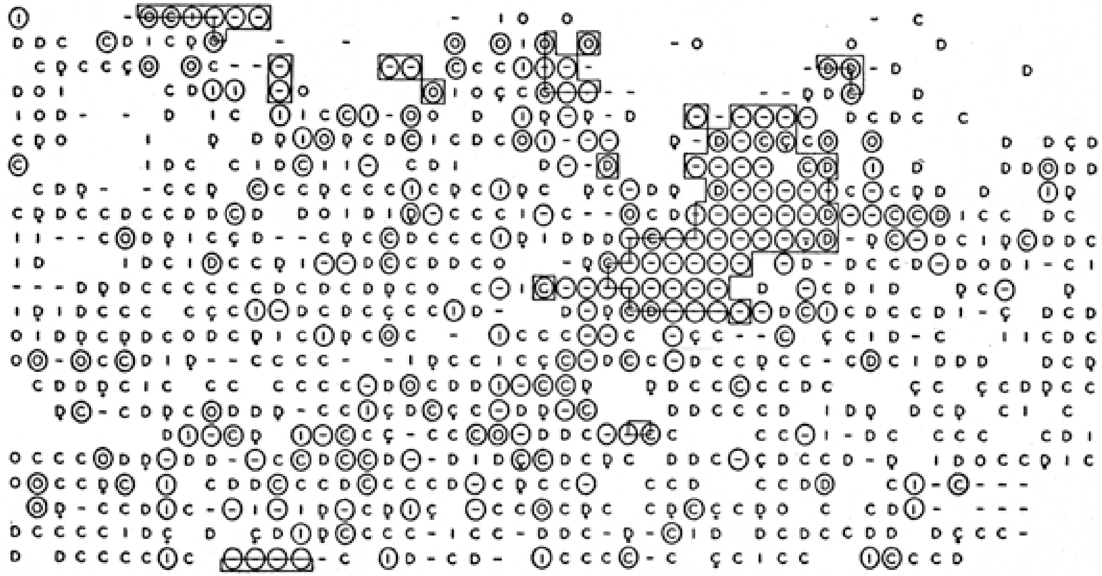

FIG. 3. Diagrammatic representation of a portion of another badly diseased red pine plantation in southern Connecticut. The data explaining Figure 2 are applicable to this figure.

method used by Meinecke (26) in evaluating the loss to young stands of western yellow pine in California caused by the rust fungus, *Cronartium comandrae* Peck.[8]

With the assistance of Professor R. C. Hawley, the writer has outlined in Figures 2 and 3 that portion of the surface of the plantations on which infection has resulted in the loss of the growing stock. In other words, the areas inclosed by the solid lines are those on which .it is estimated no merchantable trees will be present at the time of economic maturity of the two stands. Areas understocked or completely unstocked from other causes are disregarded in this study. Then, through the use of a planimeter, the percentage of the total area reduced to an unstocked condition by the disease is easily secured. The plantation represented by Figure 2 has an area of 1.2 acres of which 0.057 acre, or 4.8 per cent, will have been denuded by the disease. The portion of another plantation represented by Figure 3 also has an area of 1.2 acres of which 0.072 acre, or 6.0 per cent, \villhave been denuded. From these data and this line of reasoning it seems reasonable to conclude that the expectation value of the crop on these two plots has been decreased approximately 5 or 6 per cent through the agency of the Tympanis canker.

The remainder of the infection scattered over the t\VO plantations-i.e., all infection not included inside the closed lines in Figures 2 and 3—may be regarded as constituting a beneficial thinning to the stands. It is more irregular than a voluntary thinning would be, but after allo\ving for its unevenness the writer is of the opinion that it is of decided value to the residual trees. Furthermore, if light infection may be considered virtually as a thinning or as a partial thinning, it may result over a long period of time in an actual monetary saving to the operator in stands where the wood removed in thinning has little or no sale value. That is, it is conceivable that infection might act as a natural thinning agent to a sufficient extent that the money saved in thinning operations might exceed the economic loss suffered by the plantation. Such an idea is at present purely theoretical, but its possibilities should not be discounted prematurely.

It is evident from the small amount of economic damage caused by the Tympanis canker on two of the areas in southern Connecticut (Figs. 2, 3) \vhere infection is most severe, that the disease cannot be considered serious

8. Meinecke discusses this disease under the name of *C. pyriforme* (Peck) Hedge. and Long, but Arthur (5) has since that time decided that the nomenclature given above .is correct.

enough to be a limiting factor in the production of red pine in this or a similar locality. However, if the incidence of the disease is definitely dependent, as it seems to be, on the southern extension of the range of red pine, it is probable that if the tree is planted in sufficient quantity farther south in the United States, this disease may be more serious there than it is in southern New England. Therefore, the Tympanis canker should be considered as a possible cause of severe damage to red pine planted south of this region.

CONTROL MEASURES

ANY discussion of control measures for a forest tree disease known for such a short period of time as this red pine canker has been known, must of necessity be somewhat theoretical-at least in the sense that no experimental evidence has been secured concerning the effectiveness of the recommended measures. However, in the carrying on of the several phases of this investigation certain definite tendencies of the disease have been observed. The process of controlling the disease narrows down to the application of any silvicultural methods which might combat these natural proclivities of the causal organism. In so far as the methods suggested are sound and economically practicable they deserve adoption into the accepted forestry procedure for handling red pine.

It is obvious that no measures for the control of the disease are necessary unless red pine is grown within those areas where it is subject to infection. The causal organism is much more widely spread than is the disease which, as previously stated, occurs only in plantations south of the optimum range of red pine, while the fungus is common over much of the optimum range. In particular, the control measures suggested are based largely on data taken in southern Connecticut; therefore, their application is recommended especially for that region. However, it is always possible, even probable, that the disease will appear in regions where it is now unknown; therefore the use of the suggested measures may be of value wherever red pine is planted.

During the past two decades the forest pathologist has become increasingly cognizant of the fact that for many diseases the only possible control measures are those which may be effected through direct application of silvicultural practices in forest management. This red pine canker falls in that category. No specific and extra measures are necessary but the application and timing of the ordinary practices may be most efficacious. The various aspects of the control of the disease may be discussed under four headings:

(1) Planting practices,
(2) Pruning operations,
(3) Thinnings,
(4) Sanitation measures.

The one predominant concept responsible for these principles of control is that any factor or practice which will improve the vigor of the individual trees composing a stand will at the same time decrease the probability of disease. For instance, it has been shown that a positive relation exists between drought and canker incidence in southern Connecticut. Obviously, it is impossible to prevent the appearance of droughts, but it is reasonable to expect that any measure which will increase the resistance of red pine trees or stands to drought injury will be reflected in a decrease in susceptibility to the disease.

PLANTING PRACTICES

There are two ways in which planting practices may be made to favor control of this disease. They are, first, the establishment of red pine in mixed, rather than pure, plantations, and, second, the use of an 8-foot spacing rather than of the 6-foot or less which has been used so frequently in the past.

Infection data referred to previously in this paper show that there is much less disease on trees planted in mixture with white pine than there is on those in pure stands. In most of the mixed plantations examined the two species were in alternate rows. Better silvicultural practice would be to plant red and white pines in alternate strips of about three rows each. There is no reason to believe that the same beneficial effects secured from alternate row planting in the control of this disease will not be obtained from alternate strip planting. Certainly, if such a practice will stimulate better growth of either or both species, it should give an appreciable degree of control of the disease.

The use in pure red pine stands of an 8-foot spacing at the time of plantation establishment should have a dual effect, one of which will be indicated here and the other discussed under pruning and thinning operations. Wider spacing should lessen root competition among the individuals in a stand and by so doing should increase their general vigor during the early life of the stand. The more vigorous red pine trees are, the less susceptible they are to infection. Therefore, this practice should act as a curb to the disease.

PRUNING OPERATIONS

In the discussion of the mode of infection by the Tympanis canker fungus it was indicated that dead lateral branches probably afford entrance to the stem. The inference, then, is that the removal or pruning off of the lateral branches before they die or become of extremely low vigor will offer protection against the disease. Obviously, it is not economically practicable to prune all the trees in a plantation, but forest property owners and operators are more and more recognizing the value of pruning selected crop trees in a stand. The principle is that the enhanced value of a log from a pruned tree over one from an unpruned tree more than justifies the cost of pruning. Therefore, it is perfectly feasible to recommend as a control measure that all crop trees should be carefully selected for freedom from disease and that the successive pruning operations on them should be so timed that the large majority of branches to be removed will still be alive when cut off. On the Eli Whitney Forest, pruning of crop trees has been planned so as to secure a 16-foot butt log with a minimum of knots confined to a small central core. The pruning is done in three successive operations, the first removing the branches to a 7-foot level, the second to 12 feet and the third to 17 feet. When the trees are planted with a 6-foot spacing, many of the lateral branches die from shade suppression before they are removed. If, however, the spacing is increased to 8 feet, the probabilities are that few lateral branches will die before the stem reaches the pruning size. The avenue of infection will thus be removed before the disease has had a chance to infect the pruned trees. Therefore, wider spacing and timely pruning may be regarded as an excellent form of insurance against the infection of selected crop trees.

THINNINGS

In a properly managed stand, judicious thinning naturally follows pruning in order to maintain the growth rate and general vigor of the pruned trees at the highest possible level. The practical difficulty which usually interferes with scheduled thinnings is that early thinning of young stands of red pine is neither profitable nor even self-supporting because of the slight market value of the small diameters removed in such an operation. The rule-of-thumb ordinarily followed in thinning is to perform the operation as soon as it will yield financial returns. The use of the 8-foot spacing should help solve this problem because it would defer the time of thinning until the trees to be removed are larger and have an enhanced value on the market. From the point of view of the disease, thinnings should be regularly performed so as to keep the vigor of the crop trees above the level at which they will become susceptible to infection.

As indicated in the previous paragraph one of the results of thinning is that it serves to maintain the vigor and growth rate of the crop trees. Another no less valuable result is that proper thinning may serve to insure a stand against drought injury. Adams (2) found that a moderate thinning of a 20-year-old eastern white pine stand and a light thinning of an 18-year-old Scotch pine stand in northern Vermont caused a decrease in the percentage of available soil moisture when the moisture content of the soil was high and an increase in the percentage of available soil moisture when the moisture content of the soil was low. The decrease under high soil-moisture conditions he attributes to more rapid surface evaporation resulting from greater air movement in the thinned stands, and the increase under low soil-moisture conditions he attributes to a lessening of transpiration because of the reduction in the density of the stand.

Irrespective of the soundness of his interpretation of the causes for this reaction to thinning, the fact remains that his data show that in dry seasons, or in periods of drought, more soil moisture is present in thinned stands than in similar unthinned stands. If such a relation holds true for eastern white pine and Scotch pine stands in northern Vermont, there is no reason for thinking it would not be equally valid when applied to red pine stands in other sections of the country. Stickel *(30)*, working with hemlock-hardwood stands in southern Connecticut, found that on the poorer sites, open stands -i.e., frequently thinned stands-exhibited less drought injury during and after the 1930 dry period than did similar denser stands. Thus, his work with different species in another region substantiates the data and conclusions of Adams. Therefore, it may be stated that judicious thinning of red pine stands probably will reduce their susceptibility to drought injury and will thereby insure them against one of the major causes of lessened vigor and of increased disease susceptibility.

SANITATION MEASURES

Blanket sanitation rules have been frequently recommended as an integral part of the control program for many diseases. With certain types of forest tree diseases such measures are undoubtedly highly efficient, but for the Tympanis canker of red pine, little can be gained by such a program. The causal fungus is widespread throughout the range of red and eastern white pines and the total amount of inoculum produced by it is so large that the removal of occasional cankered trees would not appreciably reduce the chances of infection of healthy trees. Attempts at eradication may be regarded as of no value. However, when a thinning operation is carried on in a stand, diseased trees should be removed in preference to uninfected trees. The average vigor of the residual stand is thereby heightened.

SUMMARY AND CONCLUSIONS

RED pine is today accepted as one of the most important native coniferous trees for reforestation in northern and eastern United States. Its silvicultural chara.cteristics have been the principal features responsible for this evaluation, but its freedom fr01TISerious insect pests and fungus diseases has been a contributory factor. Therefore, any outbreak of anew disease calls for immediate attention and thorough study in order to determine the significance of the new factor.

A new disease of red pine has recently been found in southern Connecticut, Rhode Island, eastern Massachusetts, \vestern and central New York, northern New Jersey, eastern Pennsylvania, central Ohio, a.nd southern Michigan. It is of serious consequence only on plantation-grown red pine, but it also occurs occasionally on eastern white pine. On the former host it is characterized by axially elongated, annual main-stem cankers which are always centered at the nodes. Infection takes place through adhering lateral dead branches and the growth of the fungus after it gains entrance to the stem.is usually very rapid-Le., cankers up to three feet in length may be formed in one year's time. Infection of red pine has been found only where the tree has been planted south of its optimum range.

The causal organism belongs to the genus *Tympanis* of the family *Dermateaceae* and the order *Pezizales*. Further investigation is necessary before it can be described as a new species or definitely identified as one of the previously described species of this group. In the mean,vhile it is referred to as *Tytnpanis sp.* Its morphological and cultural characteristics are given.

The pathogenicity of the causal organism has been established through isolation into culture, inoculation into healthy tissue, the production of small but undeniable cankers, and the reisolation of the original organism from the artificially induced lesions. All of the checks remained sterile and healed rapidly.

Data are presented to show that the disease occurs only in plantations south of the optimum range of red pine; that it is much more severe in pure plantations than in mixed; that it may occur on all sites, but is generally worse on poor sites than on good sites; that in any stand it is more prevalent on the lower crown classes than on the upper; that there seems to be little, if any, relation between its incidence and aspect, slope, and soil reaction; that in southern Connecticut there is a remarkable relation between its appearance as an epidemic in 1930 and the serious moisture deficiency of that year; and that infection is inversely related to vigor as expressed in height and diameter growth of paired trees.

The conclusion is reached that *Tympanis Spa* is a weak parasite of red pine and can only cause disease when the host is weakened by some environmental factor or complex of factors. The hypothesis is suggested that the presence of the disease only in plantations south of the optimum range of the host may be a result of the fact that a warmer climate exists there than is found within the optimum range of red pine. This warmer climate undoubtedly increases the injurious effects of a severe drought and thereby favors disease outbreaks.

Individual infected trees may be killed outright by the girdling of the main-stem or may remain alive indefinitely. A permanent disfigurement of the bole of the tree is the usual result and may be effected through resin infiltration of the wood under the canker, through decay of the wood by secondary fungi gaining access through the open cankers, through the discoloration of the sapwood by staining organisms, or through the breaking of the main-stem at the cankers.

Economic loss, or damage to stands, is evaluated in two ways—percentage of infection of selected and pruned crop trees, and the degree of understocking produced in a plantation through infection. Expressed in either way the loss probably will not exceed 10 per cent of the expectation value of the crop. In individual plantations a light, scattered infection may be regarded as a beneficial thinning and possibly may even result in a monetary saving to the operator.

Methods of control for the disease are considered. Mixed planting with white pine, an 8-foot spacing, and judiciously timed pruning and thinning operations, are regarded as offering an appreciable degree of control. No eradication or particular sanitation measures are recommended.

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PLATES

PLATE I

SMALL stem canker on red pine from southern Connecticut. This is the smallest canker found and could be easily overlooked. The canker surface was flattened and separated from the healthy tissue by a slightly raised margin. Approximately X 2.

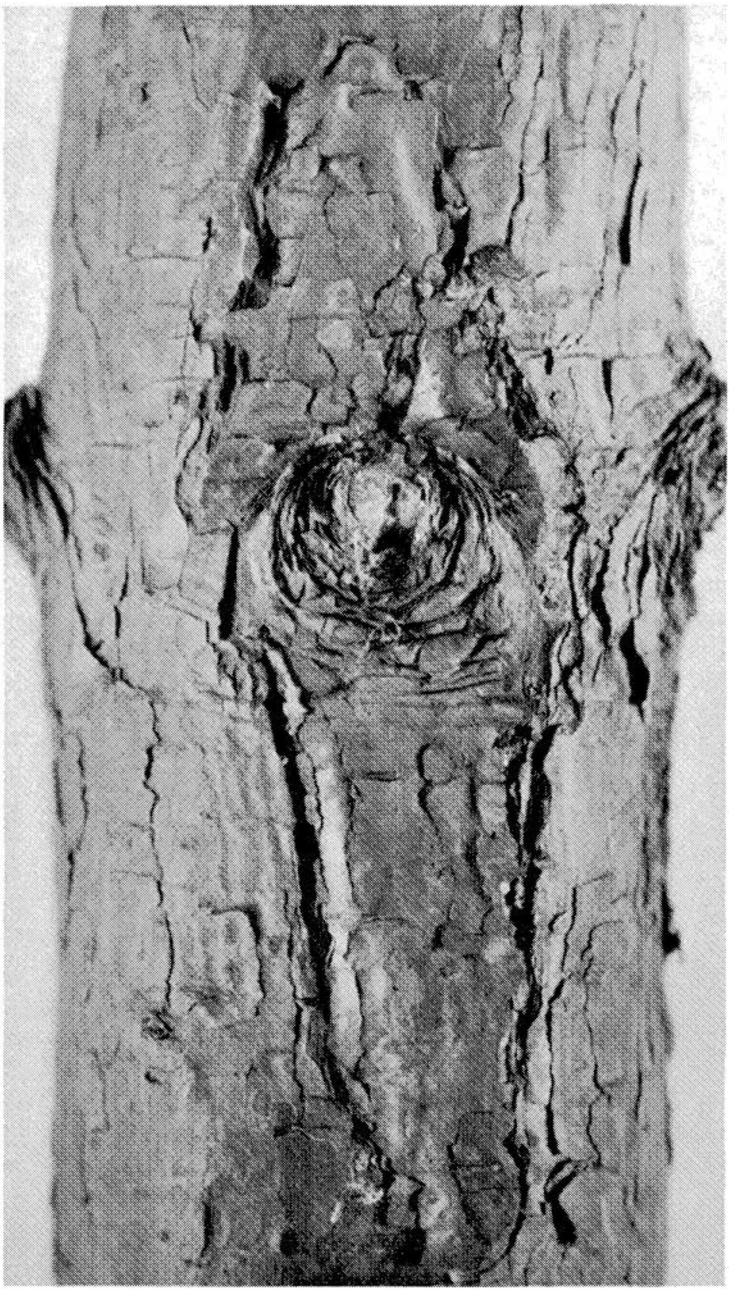

PLATE II

TYPICAL stem canker on red pine from southern Connecticut. The small black bodies scattered over the canker surface are the apothecia or fruiting bodies of the causal organism. The bark is opening up at this stage and can be easily removed from the canker face. Approximately natural size.

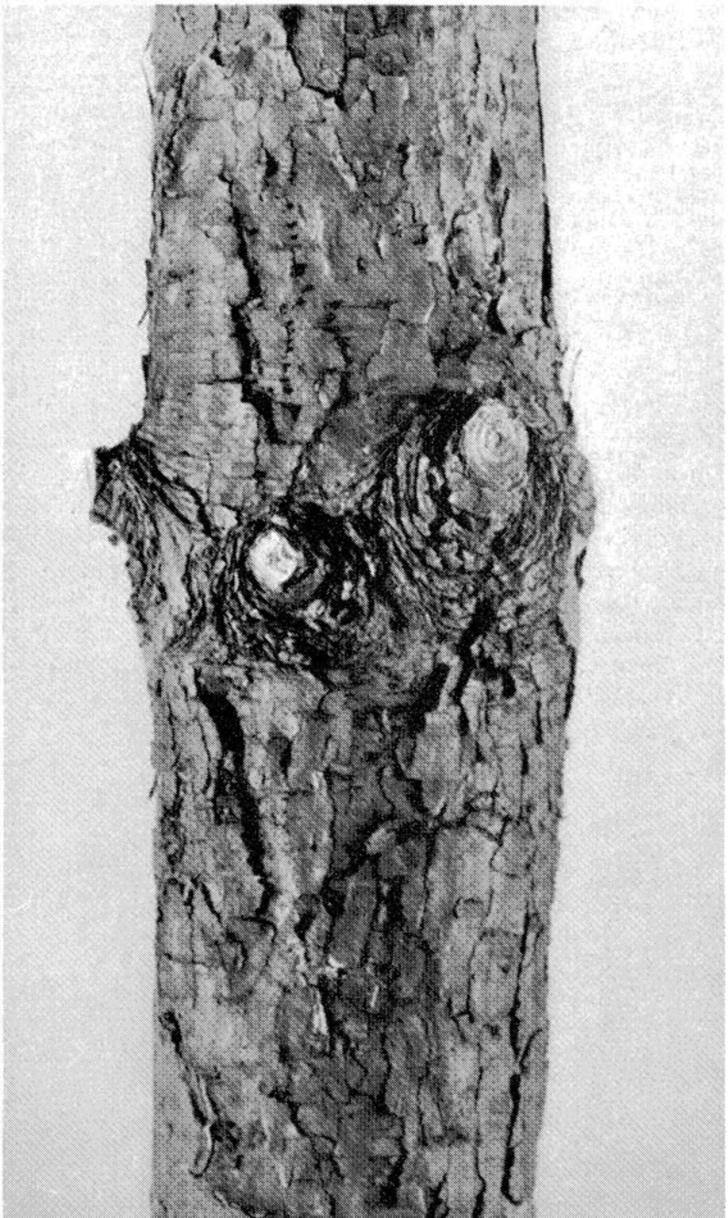

PLATE III

TRANSVERSE sections at one-inch intervals through a stem canker on red pine from southern Connecticut showing typical malformation and discoloration. The sections are arranged consecutively beginning at the upper left and going from left to right. This canker originated in 1930 and was removed from the tree in August, 1935. Note that the 1930 annual growth ring is of equal width on the canker face and on the back side where no injury took place. The bark was removed to bring out the exact canker limits more clearly. The discoloration of the wood below the canker surface is partially caused by resin infiltration, but is predominantly an indication of decay. Approximately one-third natural size.

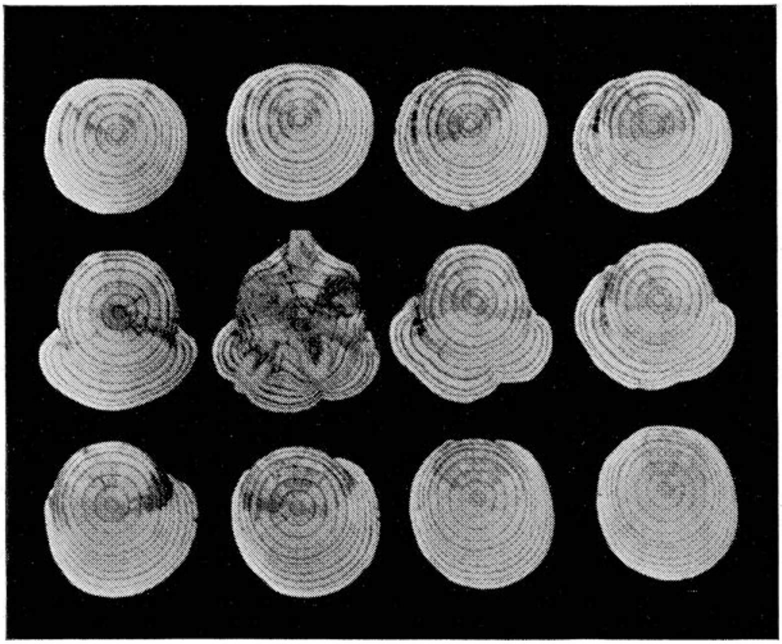

PLATE IV

TYPICAL stem canker on red pine from southern Connecticut with the bark removed to show the surface malformation. Approximately one-half natural size.

PLATE V

EXTERNAL and internal appearance of a stem canker on red pine from southern Connecticut. On the right a lateral surface view of the canker with the bark removed. On the left a median longitudinal section through the canker with the visible limits of decay indicated by the pencil line. Approximately one-half natural size.

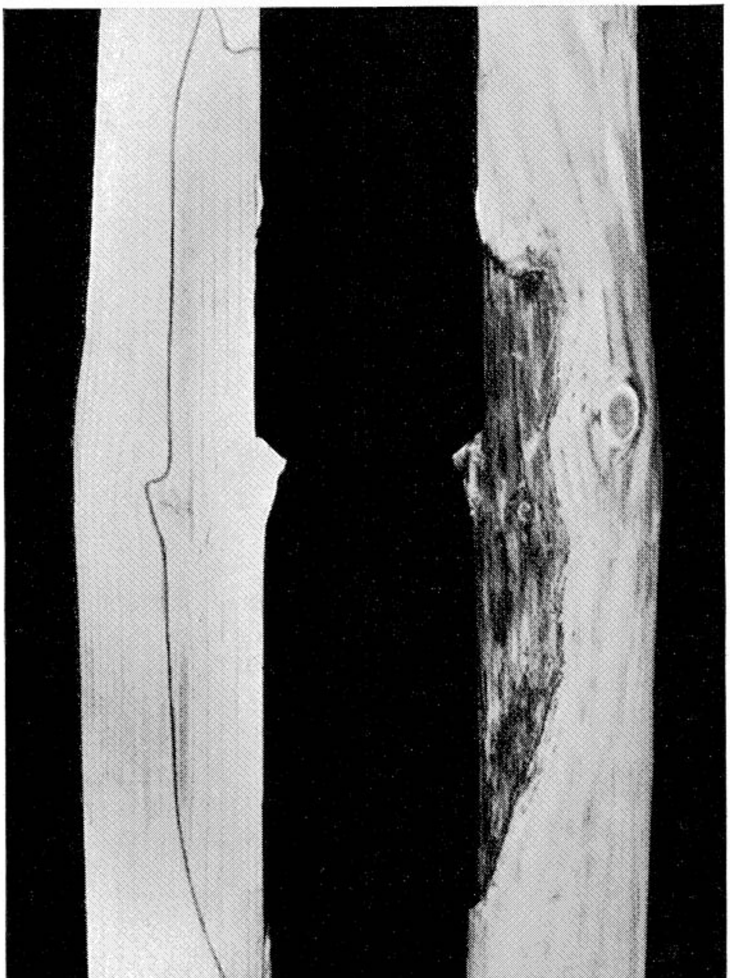

PLATE VI

A COMPLETELY girdled stem of a red pine from southern Connecticut. Two cankers coalesced to produce this result. Excessive decay is indicated by the dark, mottled color of the wood at the lower left. The bark was removed to bring out the exact detail. Approximately one-half natural size.

PLATE VII

TYPICAL stem canker on eastern white pine from northern Connecticut. The erumpent black bodies on the canker surface are the apothecia of the causal organism. Note that the bark is not cracked or shredded, but remains tightly adherent to the underlying wood. Approximately $\times$ 2.

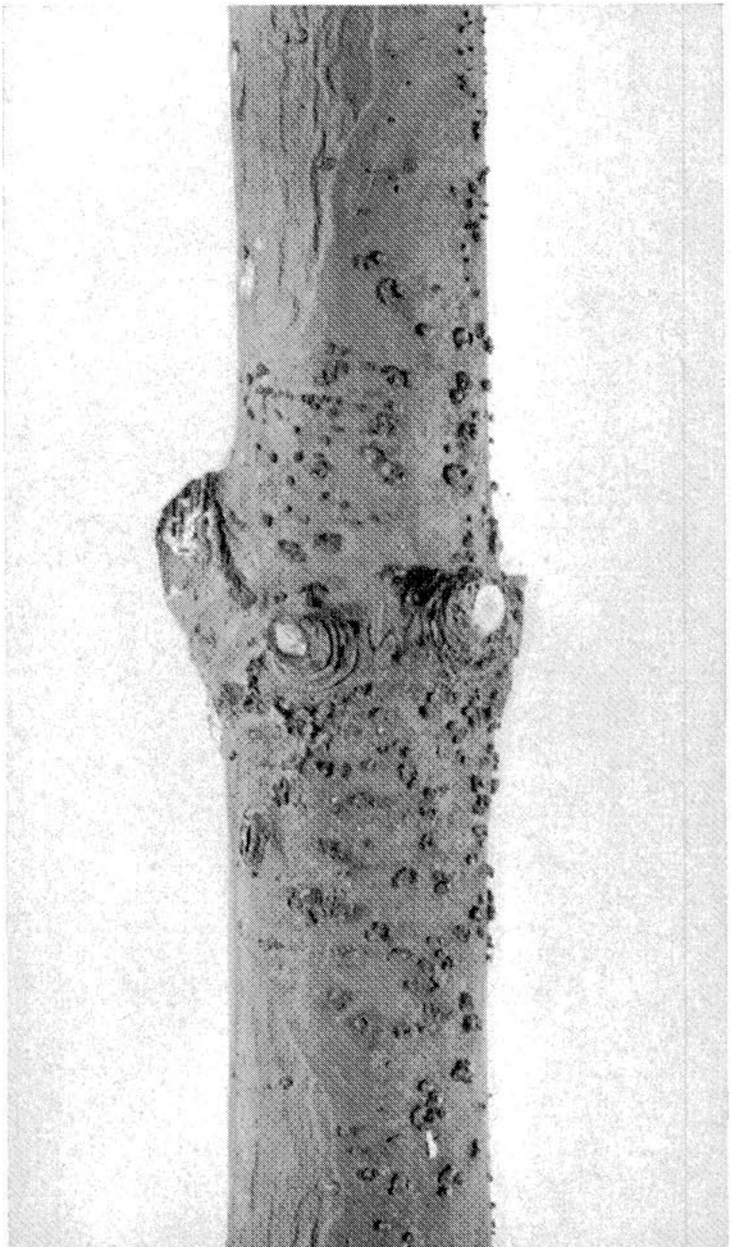

PLATE VIII

BRANCH canker on eastern white pine from central Massachusetts. The apothecia of the causal organism are also visible here as in the preceding plate. Approximately × 3.

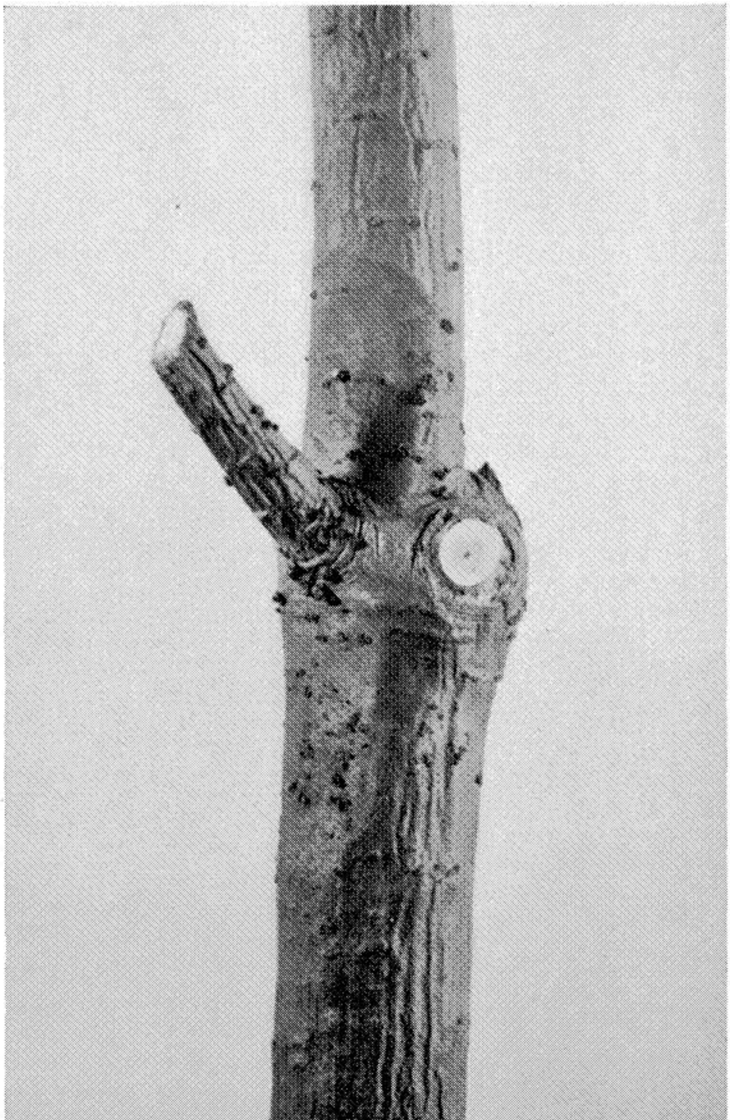

PLATE IX

Tympanis sp., the causal organism of this new disease of red pines. Figures 1, 2, and 5, freehand; 3, 4, 6, 7, 8, and 9, with camera lucida.

Fig. 1. Median longitudinal section of imperfect stage showing several pycnidial cavities on one stroma. Approximately $\times$ 30.

Fig. 2. Median longitudinal section of a single pycnidium. Approximately $\times$ 30.

Fig. 3. Conidiophore with immature conidia attached. Approximately $\times$ 1,000.

Fig. 4. Mature conidia. Approximately $\times$ 2,000.

Fig. 5. Median longitudinal section of an apothecium of the perfect stage. Approximately $\times$ 30.

Fig. 6. Asci and paraphyses. Note the innumerable small secondary ascospores in both asci and the two large primary ascospores very indistinct in the ascus on the right. Approximately $\times$ 700.

Fig. 7. Ruptured ascus with free secondary ascospores. Approximately $\times$ 700.

Fig. 8. Secondary ascospores. Approximately $\times$ 2,000.

Fig. 9. Primary ascospores. Approximately $\times$ 1,000.

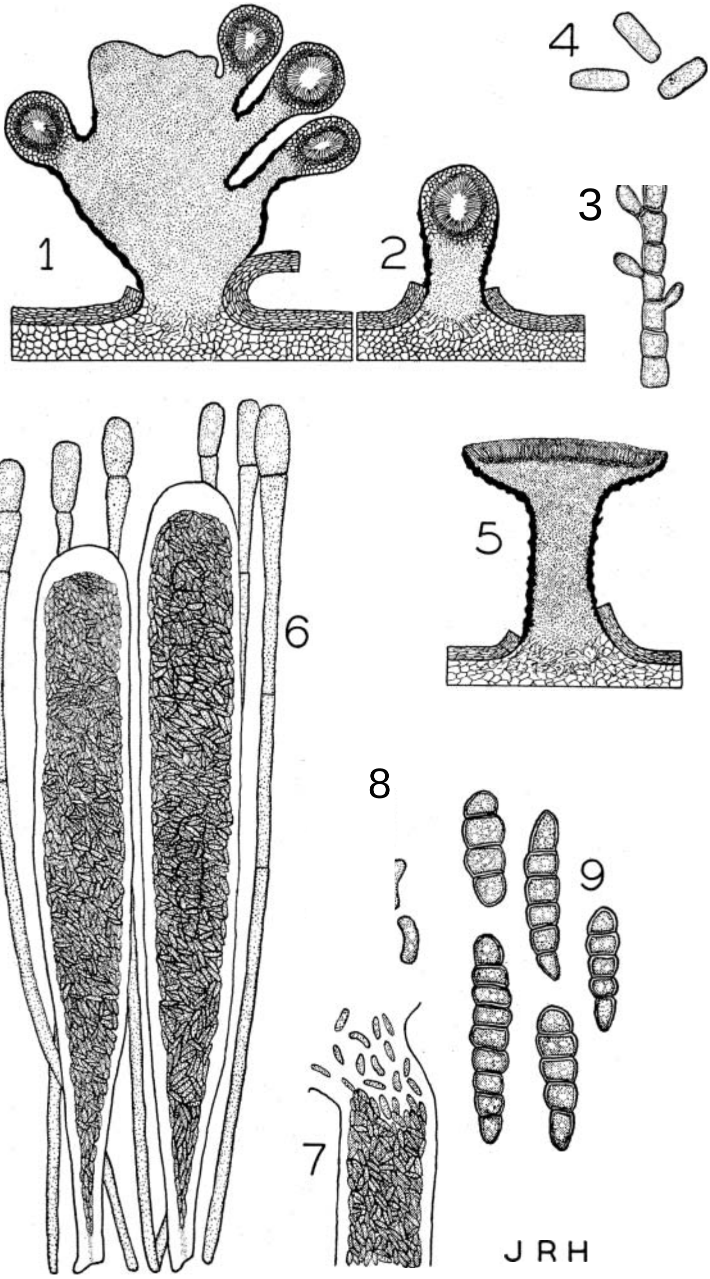
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PLATE X

PHOTOMICROGRAPHS of *Tympanis sp.* on red pine.

Fig. 1. Median longitudinal section of apothecium. Approximately × 100.

Fig. 2. Median longitudinal section of two pycnidia on stromatic tissue. Approximately × 100.

Fig. 3. Mature ascus filled with secondary ascospores. Approximately × 400.

Fig. 4. Younger ascus with one primary ascospore near base. Approximately × 400. Note the thick ascal wall here as compared to that in Figure 3.

Figs. 5, 6, and 7. Stages in the germination of a secondary ascospore, 36, 48, and 72 hours, respectively, after sowing. Approximately × 600. Note the conidia being budded off the mycelium in Figure 7.

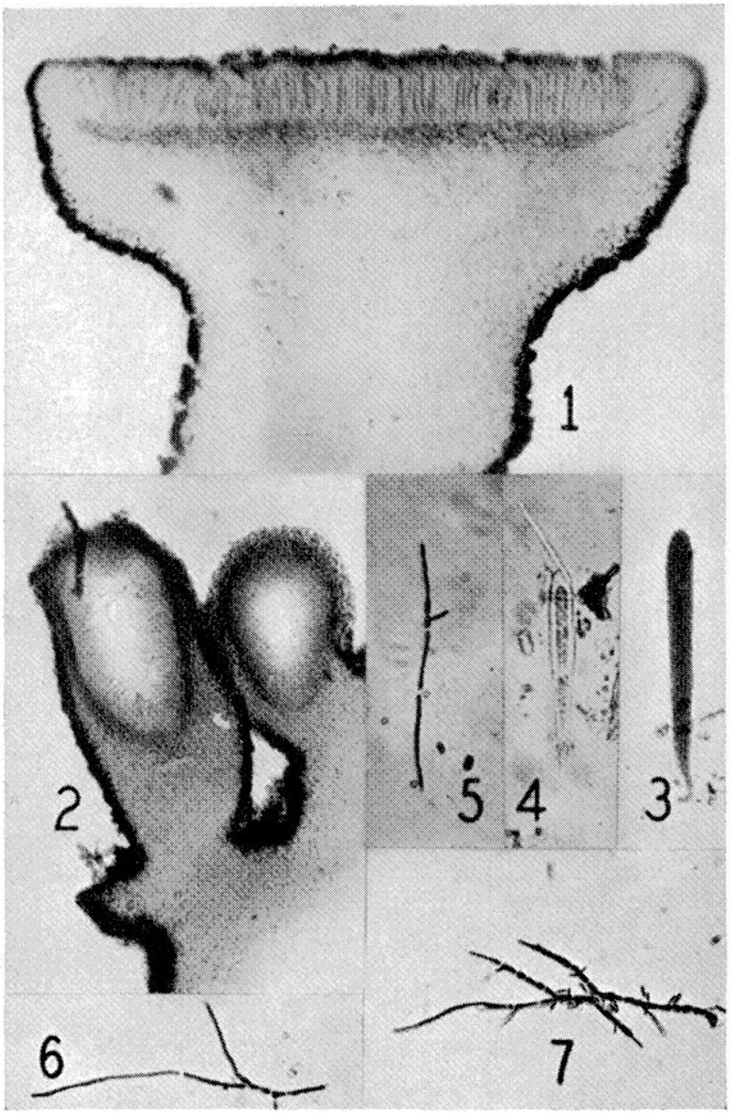
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PLATE XI

INJURIOUS effects of the disease on red pine trees.

Fig. 1. Group of dead and dying diseased trees in southern Connecticut. Note the fallen trees.

Fig. 2. A single diseased tree in southern Connecticut. The weakened stem is broken at the cankered node.


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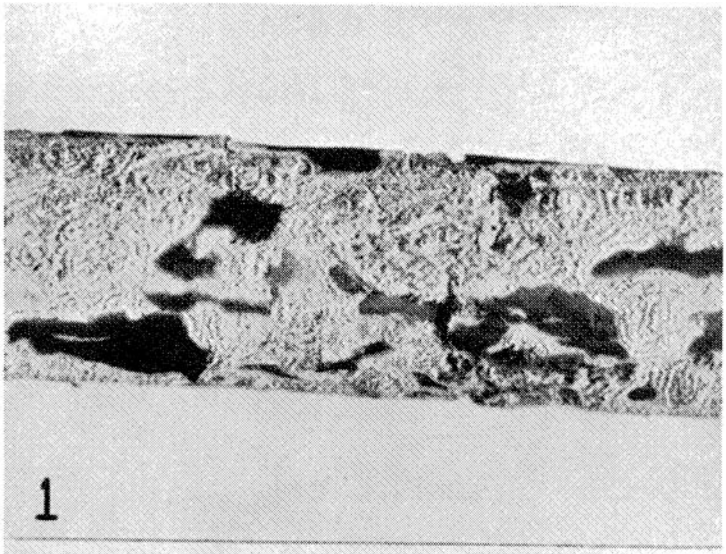
PLATE XII

FUNGI causing secondary decay in cankered living red pines.

Fig. 1. *Radulum spathulatum*. Note the irregularly toothed structure and the somewhat concentrically ringed formation of the fruiting body. The color is a light buff. Approximately × 2.

Fig. 2. *Poria versipora*. Note the variation in size and shape of the pores. The color is also a light buff. Approximately × 2.



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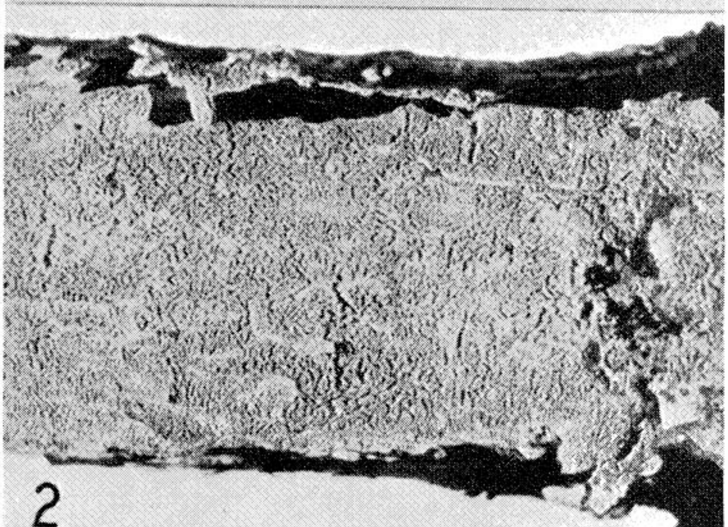

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