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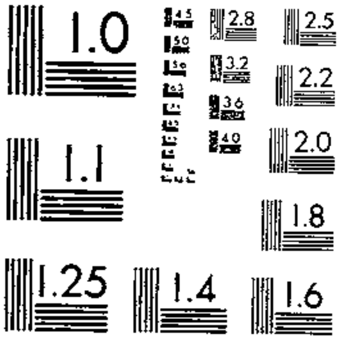

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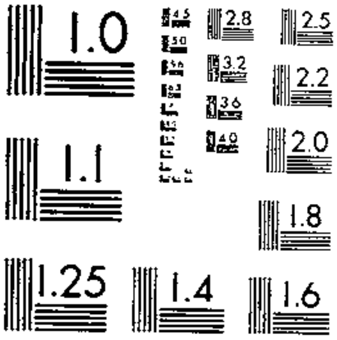

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Spread of

WHITE PINE BLISTER RUST
from
RIBES TO SUGAR PINE
IN CALIFORNIA AND OREGON

by

James W. Kimmey and Willis W. Wagener, Forest
Pathologists, Pacific Southwest Forest and Range
Experiment Station, Forest Service

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SPREAD OF WHITE PINE BLISTER RUST FROM RIBES TO SUGAR PINE IN CALIFORNIA AND OREGON

By James W. Kimmey and Willis W. Wagener, *Forest Pathologists,*[1]
Pacific Southwest Forest and Range Experiment Station,
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INTRODUCTION

When an organism causing an epiphytotic disease enters a new region, with new hosts and environmental conditions, its behavior cannot be predicted from previous experience. Its control is almost certain to present new problems.

White pine blister rust, caused by the fungus *Cronartium ribicola* Fisch., has entered such new territory in its progress southward from the place of introduction in British Columbia (*19*).[2] This rust, which alternates in its life cycle from white pines to currants and gooseberries (*Ribes* spp.), was aided in its initial spread in British Columbia by the highly favorable moisture conditions prevailing in the coastal region of that province (*21*). In its southward spread down the Pacific coast, however, the rust has not only entered the ranges of new major hosts, both pines and ribes,[3] but has also encountered a drier summer climate than is common for the western white pine region of the Pacific Northwest. The summer months become progressively drier as latitude decreases from north to south (fig. 1).

Because moisture plays a dominant role in the development of the rusts, some decrease might be expected in the capacity for damage by blister rust in the sugar pine region of Oregon and California as compared with the western white pine region of the Pacific Northwest. However, tests of the relative susceptibility of various five-needled pines exposed to the rust in British Columbia and Oregon (*6*) indicated that sugar pine (*Pinus lambertiana* Dougl.) was more susceptible to blister rust than western white pine (*P. monticola* Dougl.). Similar comparative tests on western currants and gooseberries showed that the principal associate of sugar pine in the Sierra Nevada, *Ribes roezli* Regel, was highly susceptible to the rust (*14*, *21*). A companion species, *R. nevadense* Kell., was not quite so susceptible initially but held the rust very well after infection had occurred.

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[1] Studies in Oregon were under the direction of the Portland field station, Division of Forest Pathology, United States Department of Agriculture, J. L. Bedwell in Charge; those in California were under the direction of the San Francisco field station of that Division, Willis W. Wagener in Charge. James L. Mielke and T. S. Buchanan made major contributions to fieldwork on the studies. Ten others assisted in this work at various times and places.

The senior author is now Chief, Division of Forest Disease Research at the Intermountain Forest and Range Experiment Station, Ogden, Utah.

[2] Italic numbers in parentheses refer to Literature Cited, page 59.

[3] A collective term for plants of the genus *Ribes*.

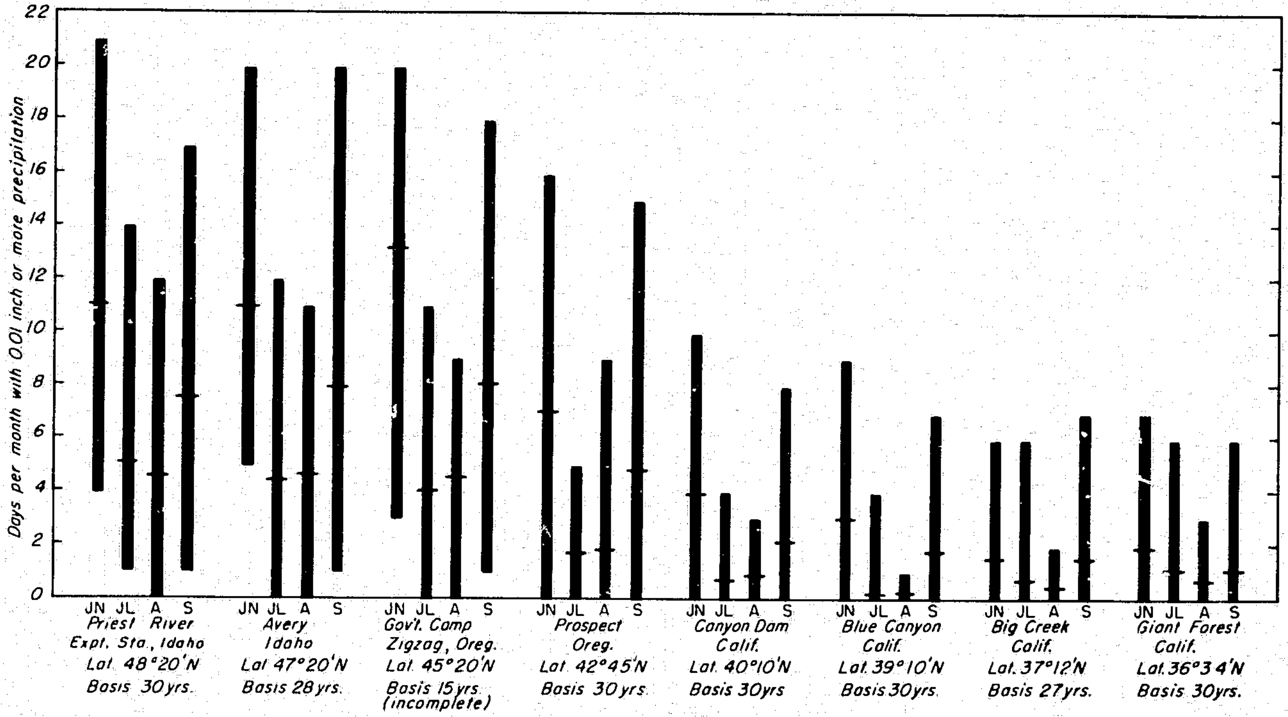

FIGURE 1.—Increase in summer dryness with decrease in latitude is indicated by the decrease in number of days per month with measurable precipitation, months of June to September, inclusive, 1926–55. Stations selected lie within white or sugar pine areas from northern Idaho to south-central California. Bars mark the maximum and minimum, and crossbars the mean number of days with precipitation for the designated month.

When the present studies were started, supervisors responsible for setting standards of ribes supression for blister rust control in sugar pine stands had to predict rust behavior from its performance in other regions. Unanswered for control areas in Oregon and California were questions on:

How much damage will result from occasional ribes missed by eradication crews?

What should be the width of protective or buffer strips around sugar pine stands delineated for protection?

Will the apparent high susceptibility of sugar pine and associated ribes be offset by the seasonally dry environment?

How do the chief ribes associated with sugar pine compare in pine-infecting potential?

To provide reliable evidence on these and related questions, the studies of ribes-to-pine spread reported here were made in Oregon (1935–42) and in California (1938–51) on a series of plots in natural stands of young sugar pine on which the spread of blister rust from a known central source could be determined.

THE STUDY

Study Areas

Methods of study, the natural occurrence pattern of sugar pine, and control policy presented difficulties and restrictions in the selection of experimental plots. The following considerations were primary:

1. The study required rust-free areas stocked with well-distributed small sugar pines, and large enough to accommodate circular plots several acres in size.
2. Sugar pine rarely occurs in pure stands, and plantations were not available.
3. Control policy was opposed to the establishment of test plots in regions south of known rust occurrence.

As the study progressed, five plot areas (table 1) were located in natural stands of sugar pine reproduction (fig. 2).

Black Rock.—Four test plots were established on the Black Rock area in 1936, after natural infections of the rust had been found on sugar pine in Oregon (*18*, *30*). A fifth plot was added in 1938. The area was within an ecological "island" of mixed sugar and ponderosa pines on the south side of Hamner Butte, Deschutes National Forest, Oreg., surrounded by an otherwise pure ponderosa pine (*Pinus ponderosa* Laws.) forest. Abundant young reproduction of both pine species, averaging about 5 feet in height, occurred underneath an open overstory of mature trees. No ribes were found within one-half mile of the plots. Abundant *Ribes cereum* Dougl. were located near the top of Hamner Butte about 2 miles distant.

Siskiyou.—A single plot was established in 1937 in a mixed Douglas-fir-sugar pine stand representative of stands in the Siskiyou Mountains of southern Oregon and northwestern California. It was located in the Siskiyou National Forest north of Selma, Oreg., in a small draw. This plot carried a dense stand of sugar pine reproduction, averaging about 7 feet high, with an admixture of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine of about

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FIGURE 2.—Sugar pine reproduction representative of test plots: *A*, Near center of Black Rock Plot No. 1, 1938; *B*, part of Big Bar Plot No. 1. 1940.

TABLE 1.—*General description of blister rust study areas in natural stands of young sugar pine, Oregon and California*

Study area, year selected	Location	Plots	Elevation	Slope and exposure	Principal associated understory plants
	Oregon	*No.*	*Ft.*		
Black Rock, 1935	Klamath Co., T24S, R7E, Sec. 1; T24S, R8E, Sec. 6 WM.	5	4, 800	Gentle, S to SE	*Arctostaphylos patula* Greene. *Ceanothus velutinus* Dougl. *Castanopsis chrysophylla* v. *minor* Benth. *Ceanothus prostratus* Benth. *Arctostaphylos uva-ursi* Spreng.
Siskiyou, 1937	Josephine Co., T37S, R8W, Sec. 14 WM.	1	2, 000	Moderate to steep, S	*Toxicodendron diversilobum* (T.&G.) Green.
	California				
Damnation, 1938	Shasta Co., T36N, R6W, Sec. 33, 34, MDBM.	3	4, 300	Gentle to moderate, NE to SE.	*Corylus cornuta* v. *californica* (A.DC.) Sharp. *Arctostaphylos* sp. *Ceanothus velutinus* *Alnus rhombifolia* Nutt. *Quercus* spp.
Deadhorse, 1938	Siskiyou Co., T39N, R2E, Sec. 6, 7; T40N, R2E, Sec. 31, MDBM.	6	4, 800	Gentle, easterly to westerly (ridgetop).	*Arctostaphylos patula* *Ceanothus velutinus* *C. cordulatus* Kell. *C. integerrimus* H.&A. *C. prostratus* *Cornus nuttallii* And.
Big Bar, 1940	Butte Co., T22N, R5E, Sec. 2, 3, 10, MDBM.	[1] 5	4, 500	Gentle, NE to SW mostly southerly.	Similar to Deadhorse plus *Pteridium aquilinum pubescens* Underw. *Ceanothus prostratus*, less common
Washington Point, 1947	Nevada Co., T17N, R10E, Sec. 3, MDBM.	1	3, 800	Gentle, easterly	*Arctostaphylos* sp. *Chamaebatia foliolosa* Benth.

[1] Plus 3 plots for special "fallen leaf" study.

the same size under an open overstory of sugar pine, white fir (*Abies concolor* (Gord. & Glend.) Lindl.), Douglas-fir, and ponderosa pine. Only 104 ribes, nearly all *Ribes cruentum* Greene, were removed in 1937 from the 250 acres of the Siskiyou area.

Damnation.—Three plots were established on the Damnation area in 1938: one in a small draw draining eastward, with moderate side slopes; the others on general southeasterly slopes. This site, on the west side of the Sacramento River drainage in northern California, was selected as representative of cutover land of high site quality in the North Coast Range Mountains. Abundant young reproduction of sugar pine and white fir, with some admixture of ponderosa pine, was present, among which were scattered older trees of Douglas-fir and incense-cedar (*Libocedrus decurrens* Torr.). A good deal of shrub growth (table 1) was interspersed among the reproduction. Rust control workers removed about 125 ribes per acre from this area in 1938 (*Ribes roezli* and *R. nevadense*). Several hundred more ribes, chiefly seedlings and root sprouts, were subsequently taken out.

Deadhorse.—Three plots were established on Deadhorse ridge in 1938, and three additional ones the next year. This area on the eastern Shasta-Trinity National Forest represented a northerly extension of the Sierra west slope mixed-conifer type and was within an established blister rust control unit. The area had a relatively good stand of young sugar pine, Douglas-fir, white fir, ponderosa pine, and incense-cedar reproduction, and an overstory of scattered mature trees, mostly white fir and incense-cedar. Small, dense patches of reproduction, predominantly sugar pine, were common in places. Shrubs were also patchy in occurrence. Mixed *Ribes roezli* and *R. nevadense* averaged about 38 plants per acre before removal in 1938.

Big Bar.—Four plots were established along Big Bar ridgetop, on the Plumas National Forest, Calif., in 1940, and a fifth in 1942. In this area, rainfall is above average for the west slope of the Sierra Nevada and temperatures are mild, providing a long growing season. Before logging between 1932 and 1936, a heavy stand of mixed conifers was present, of which scattered white firs and incense-cedars remained, along with a number of California black oaks (*Quercus kelloggii* Newb.). There was abundant reproduction of sugar pine and white fir averaging 6 to 8 feet in height when the plots were established. *Ribes roezli* and *R. nevadense* numbered about 113 plants per acre before their removal in 1940.

Three supplementary plots were established on Big Bar ridge in 1940 to test the capacity of infected and shed ribes leaves to spread rust to sugar pines, but the results did not provide trustworthy evidence. *Ribes roezli* leaves with telia were brought to the plots in large paper bags and shaken onto the ground over an area equal to that covered by a *R. roezli* plant of medium size. Leaves were left where they fell to simulate natural shedding. On one plot, established October 14, 100 leaves bearing apparently viable telia on 16 percent of the leaf surface were used; on the other two, established October 20, leaves were not counted but were numerous and all bore telia. Rain starting October 24 and continuing several days provided moist periods considered long enough for pine infection, and temperatures were mild. Yet no subsequent pine infections were found on the three plots. No following examination was made of the fallen leaves to determine whether the telia had germinated. General field experience does not indicate appreciable hazard from dropped rust-bearing leaves but, because of the propensity of *R. roezli* to shed infected foliage and the preponderance of this species in association with sugar pine, a more specific experimental determination is desirable.

Washington Point.—A single plot was established in 1947 on the gentle summit of a spur ridge projecting southeasterly toward the South Fork of Yuba River near Washington, Calif., and within the Tahoe National Forest. Well-distributed sugar pine reproduction, interspersed with about 25 percent ponderosa pine and a few white firs, had become established following logging of the area some years before. A scattered overstory of older ponderosa and sugar pines had been left at the time of logging. Near the plot center the reproduction was mostly under 5 feet in height, but on the west side of the ridgetop, thickets of saplings chiefly ponderosa pine, had reached an average height of 15 feet or more.

Ribes Tested

Ribes roezli, *R. nevadense*, and *R. cereum*, the three species used in this study, were selected because of their prevalence in sugar pine areas. The number of tests made with each was in approximate proportion to its importance in the control program.

Of the ribes commonly associated with sugar pines in California, the Sierra gooseberry (*Ribes roezli*) is the most abundant and most highly susceptible to blister rust (*14*, *15*, *21*). It is also the most difficult to suppress because of its ability to regenerate from seed stored for long periods in the soil (*23*).

The Sierra currant (*Ribes nevadense*), although not so important numerically as *R. roezli* is widely distributed and highly susceptible to rust (*14*, *15*, *21*). Control of the Sierra currant is difficult because of its layering habits and tolerance to suppression by other vegetation.

The squaw currant (*Ribes cereum*) is the most resistant to infection by blister rust (*14*) but under some conditions is capable of producing appreciable amounts of pine-infecting sporidia (*16*). This ribes occurs in large concentrations in a few valuable stands of sugar pine, and the plants often are large and costly to eradicate.

Methods and Equipment

The procedures followed were patterned on those developed for earlier tests in British Columbia (*5*) with some adaptations for local conditions. Plots established in well-distributed sugar pine reproduction were the basic experimental units for determining spread of the rust.

For each plot a center was selected after a survey of the distribution of surrounding sugar pine reproduction. If suitable ribes plants were found at a desirable center, several of them were selected as the known and only spore source and the rest removed. If no naturally established ribes could be found at a desirable center, ribes plants were moved there in pots or transplanted to it (fig. 3). Since all study areas were within the known southern limits of the rust, ribes plants other than those at the plot centers were removed from the entire study area to prevent natural spread of blister rust to the test pines from outside sources. About 250 acres or more in each area were cleared of ribes by regular eradication crews supervised by blister rust control technicians. Plot centers were spaced far enough apart to prevent spread of the rust from one study plot to another.

To permit rapid mapping and zoning of the trees on a plot, the central ribes were used as a reference hub to delimit concentric zones of variable distance from the plot center. These zones were 10 feet wide for the first 50 feet from the center and 20 feet wide beyond that distance for the Black Rock plots in Oregon, and 12.5 feet and 25 feet for similar zones on the plots in California. The zonal areas between these circles were divided into sections or "blocks" segmenting the zones into quarters for the first 25 feet, into 8ths from 25 to 75 feet, into 16ths from 75 to 150 feet, and so on. On the Oregon plots and on all plots in California except those at the Big Bar and Washington Point, areas were staked off in this manner to a radius of 150 feet (slope distance) before tests were made, or before it was determined whether pine infection had resulted. However, experience in California demonstrated that much labor could be saved by delaying staking until the extent of pine infection from the tests became evident, and this practice was followed after 1939. Furthermore this practice minimized disturbance of the stand or cover conditions before the test.

For all of the Oregon plots and those in the Damnation area, diagrams were made to show the location of each sugar pine. Crown length, crown width, and approximate number of needles[4] were then determined for each of the trees for the same years in which the central ribes were infected with rust. From these data the "target," or amount of pine foliage exposed at different distances from the central ribes, was computed in number of needles. For the other California plots, only pines that became infected were plotted and measured. All sugar pines were tallied according to size by zonal blocks or groups of two or more adjacent blocks in a single zone.

For easier visualization, the pine foliage target in the different blocks was based on a unit represented by the foliage of a standard tree rather than the million-needle unit used in the British Columbia studies (*5*). The standard tree chosen was an average sugar pine of the 5- to 10-foot height class, approximately a 7.5-foot normal tree. Such a tree was found to bear about 37,000 needles.

To infect the leaves, the central ribes were either dusted with aeciospores, using a paper bag as a bellows (*20*), or aeciospores or uredospores suspended in water were sprayed on the foliage. In California this was done under cover to minimize the possible dissemination of spores to other ribes.

In earlier studies in British Columbia and Idaho, spores were applied just before or during spring rains, which were relied on to supply the moisture for infection. Succeeding moist periods stimulated the intensification of the rust sufficiently to cause an increase through most or all of the season. In southern Oregon and in California, however, natural moist periods were too few and too erratic in occurrence to sustain rust at the plot centers. Ribes, especially *Ribes roezli*, when infected in the spring, lost many or all infected leaves

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[4] The alinement chart (*4*) for western white pine was found to apply equally well to sugar pine trees.

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FIGURE 3.—Potted *Ribes nevadense* plants at the center of Black Rock Plot 2, 1936. The pots are buried flush with the soil surface.

before the onset of autumnal rains. Heavily infected leaves of *Ribes roezli* were usually shed just before or just after rust telia were developed.

On some plots an attempt was made to overcome this difficulty by artificially exposing the ribes to the rust in moist chambers (fig. 4) two or more times during the season. On other plots a new supply of infected ribes in pots was substituted for the original plants at plot centers. After 1939 ribes were always artificially infected in late summer rather than in the spring. In all tests after 1939, therefore, no viable telia were present on the test plants before late August or early September. Even then the telia were sometimes lost before favorable weather for pine infection occurred.

Ribes roezli plants growing in place were less susceptible to premature defoliation by the rust than potted or transplanted bushes. Practically no infected leaves were prematurely dropped from *Ribes nevadense* on the one plot where natural plants of this species were growing at the center, but potted or transplanted plants of this species and of *Ribes cereum* lost considerable rust by premature defoliation even when kept well watered. Rodents and insects caused serious defoliation of test plants in some tests. In several instances wire mesh cages were used for protection from rodents. The cages were removed during moist periods to avoid interference with normal dissemination of sporidia.

Many native *Ribes roezli* plants in northern California were found to be resistant, and some almost immune to infection by the rust. One growing at the center of Deadhorse Plot 2 developed no rust in spite of repeated and heavy exposure under conditions favorable for infection. In later tests all potted *Ribes roezli* placed at plot centers were from stock from southern Sierra Nevada locations, because they were invariably found to be susceptible to the rust.

Rust retention on *Ribes roezli* has been found to be better on bushes in partial shade than on fully exposed bushes in the open (*15*). On this account lath shade frames were erected over bushes at plot centers where natural partial shade was not present. Frames were removed before rainy periods.

General notes on the development of rust on ribes at the plot centers were supplemented by detailed records of rust infection on the bushes whenever a moist period that might result in pine infection appeared

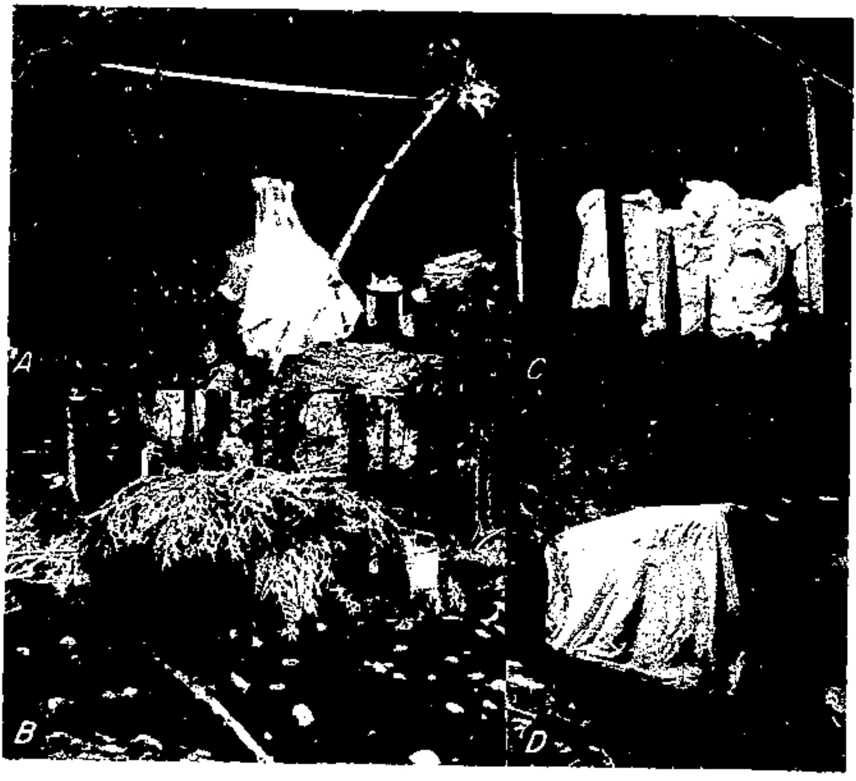

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FIGURE 4.—Types of inoculation chambers used in Oregon and California during 1938–39: *A*, Muslin chamber over wood frame at Black Rock, Plot 5; *B*, shelter over creek for infection of potted ribes at Black Rock; *C*, chambers of cotton batting on hardware cloth frames constructed over individual ribes plants; *D*, Single large chamber, of cotton batting covered with muslin over hardware cloth, enclosing a central group of ribes plants.

imminent. These records included the estimated area in square inches of leaf surface bearing apparently viable telia.

For all Oregon tests, temperature and humidity were recorded twice daily and general cloud and wind conditions daily, from the time telia first developed on the central ribes in June or July until all the leaves bearing rust had dropped in October or November; whenever rain occurred during these periods, a record was made of the time that pine foliage remained wet. On the California study areas, temperature and humidity were recorded continuously by hygrothermographs during the test seasons. Rain gages were installed, and supplemental weather data and duration of foliar moisture were recorded during and following rainstorms.

After exposure to the rust, the sugar pines on each plot were checked annually for infections. Detailed data were recorded for each canker and infected tree. On the basis of previous studies and experience with blister rust in western white pine, predictions of probable pine damage were made for each canker. To reduce the possibilities for spread of the rust to surrounding areas, all but a few cankers on two California plots were cut out before they produced aecia. The types of data for ribes and pine infections, and the methods of recording them, were essentially the same as were used for plots in British Columbia (*5*).

CONDITIONS INFLUENCING SPREAD OF RUST

Requirements for Pine Infection

In the life cycle of white pine blister rust, all spore forms initiating infection on either ribes or pines require either free moisture or a relative humidity in excess of 97 percent for germination and host infection (*11*, *12*, *32*). Over most of the sugar pine region, rain provides the chief source of free moisture for germination; rain, or rain and fog together, practically the only source sufficiently continuous for pine infection. Moisture condensed as dew is sometimes locally sufficient to cause germination of uredospores on ribes and the reinfection of the latter, because spores of the uredial stage may begin germination in 4 to 6 hours (*7*, *32*) and the resulting germ tubes make relatively rapid growth. Moisture from dew alone cannot cause pine infection, however, since dew persists too short a time for completion of the germination processes leading to infection of this host.

Each stage in the development of the rust during a season depends on the development of the preceding one. Therefore, a proper sequence of moisture, particularly in the form of rain followed by high relative humidity, is necessary for completion of the life cycle of the rust. An analysis in 1940[6] of weather records for the part of the sugar pine region within California indicated that a sequence of moisture conditions favorable for good ribes and pine infection had occurred only about one year in five. Even that frequency can be considered high for many situations; the analysis took into account only the occurrence of moisture from rain or fog and not the possible deleterious effects of high temperatures on the viability of the autumn

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[6] Zentmyer, George A., Jr., and Willis W. Wagener. California climate in relation to spread and intensification of blister rust. Unpublished report, Office of Forest Pathology, San Francisco. 20 pp. 1940.

stage of the rust. Van Arsdel and coworkers (*31, 32*) have reported that teliospore viability in Wisconsin may be adversely affected by temperatures above 68°F. This criterion, however, does not apply in California.[6] On the other hand, the 1940 analysis did not take into account the influence of dew as a source of moisture for intensification of the uredinial stage of the rust, which is a factor in some locations in California.

Teliospores in columns attached to living ribes leaves may remain viable for several months if:

- they are formed within favorable temperature levels;
- there is no intervening moisture to cause their germination;
- they are protected from appreciable exposure to direct sunlight;
- germination is not inhibited or the spores rendered sterile by high temperatures.

When in contact with free moisture in the form of rain, fog, or dew for a sufficient period to cause germination, the teliospores produce promycelia from which arise sporidia, the minute thin-walled spores capable of infecting the needles of sugar and other white pines. However, teliospores older than about 10 days require a longer exposure to moisture for germination than ones recently formed—up to twice as long depending on age (*11, 28, 29*). This requirement may be highly significant in sugar pine areas of California, where moist periods are short and infrequent before the time when ribes are defoliated in the fall.

The sporidia require a minimum of about 5 hours for germination (*11*). On moist sugar pine needles they germinate directly and produce branched germ tubes that seek entry into the needles. On other moist surfaces or in moist air, secondary or tertiary sporidia are often formed, but if these reach susceptible needle surfaces they are equally capable of causing infection.

Experimental evidence is somewhat conflicting regarding the minimum length of moist period necessary for completion of the entire pine-infection process—from the initial exposure of the teliospores to free moisture until the establishment of rust hyphae in the needles. From available published information and from field experience in the West, Mielke (*19*) concluded that abundant infection could be expected only when favorable moisture conditions prevail for a continuous period of 24 to 36 hours and that little infection could be expected from moist periods of shorter duration. Van Arsdel, Riker, and Patton (*32*) concluded from their experimental evidence that 48 hours of saturated air at temperatures under 20° C. (68°F.) are needed for completion of the entire process. This conclusion is not necessarily in conflict with evidence that pine infection has occasionally resulted in a shorter period.

Hirt (*11, 12*) showed that the germination process in teliospores and the production of sporidia may be arrested during a dry period of from an hour or so to a day and may then be resumed with only a little delay. A rain of short duration or even dew might precondition teliospores for prompt germination after the onset of a following longer moist period. Under similar circumstances promycelia might be formed that are capable of surviving moderately dry

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[6] Unpublished experiments, R. V. Bega and J. R. Parmeter. Personal communication.

conditions for a few hours and quickly producing sporidia when supplied with additional moisture. Hirt's investigations have shown that this possibility may also exist for any subsequent stage of the process leading to pine infection. Thus sporidia lodged in a protected location on sugar pine foliage may survive a short dry period, germinate promptly on the return of moist conditions, and successfully invade pine foliage in much less than 48 hours from the onset of the second moist period.

General Considerations Relating to Spore Dispersal

Dispersal in air of particles as small as rust sporidia (5 to 10 microns) after release at a single point ideally assumes the pattern of a cone with its apex at the point of origin of the particles. The angle of divergence of the conic limits varies inversely with the speed of the air stream, at least at low rates of air movement, and when particles are released near a horizontal surface the cone tends to be oval in cross section, with greater dispersion horizontally than vertically (*35*). The diffusion of particles within these limits arises from local turbulence almost always existing within a local air mass (*8*). Sporidia of white pine blister rust are so small that air movements nullify the effects of gravity. Gregory (*9*) has pointed out that sporidia may usually be regarded as being in suspension in free air.

When sporidia are released close to the ground, plants, trees, or other objects projecting from the soil surface into or through the limits of the dispersion cone not only intercept sporidia (fig. 5), but also affect air turbulence.

In the present study, sporidia were disseminated from a limited central zone occupied by the rust-bearing ribes rather than from a single point. Thus the dispersal pattern becomes one of a flattened frustum of a cone. Moreover, since free air is almost never constant in direction or velocity, the pattern shifts in direction with changes in the direction of air movement and widens and narrows in amplitude with changes in wind velocity. Close to the plot center, local turbulence in the air is likely to cause some dispersion of sporidia in all directions from the center; at greater distances the dispersal pattern is likely to show maxima in one or two directions, corresponding to the prevailing directions of air movement during the dispersal period.

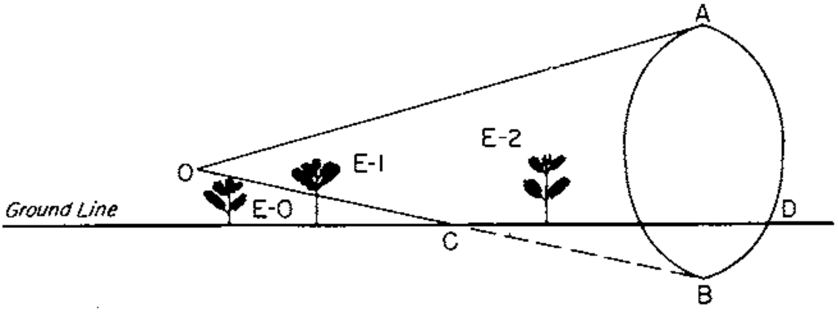

FIGURE 5.—Conic pattern of spore dispersal from a point source at a constant wind speed, and relation to interception by ground and plants: O, Spore source; OAB, cone of dispersal; C, initial point at which ground plane intercepts dispersal cone; C–D, plane of spore deposition on ground; E–0, E–1, E–2, nonintercepting, partially intercepting, and fully intercepting plants.

For conditions prevailing in the Eastern United States, Gregory (*9*) concluded that the relative absence of pine infection beyond 900 feet arose from a dilution in numbers of sporidia rather than from loss in sporidium viability. He based this conclusion on two factors: the duration of viability of sporidia of *Cronartium ribicola* as reported by Spaulding and Rathbun-Gravatt (*29*), amplified since by Hirt (*11*) and Bega (*3*), and the relatively short time required for sporidia to travel 900 feet. It is known that under favorable meteorological conditions, and with a source providing abundant sporidia, pine infection is possible beyond a mile (*1, 19, 27*). In contrast, Pennington, in tests reported by Spaulding (*26*), was unable to obtain germination of sporidia caught at distances greater than 177 feet. Nevertheless, Gregory's conclusion that dilution rather than loss of viability is the chief factor in determining the infective limits from a given spore source seems to be valid.

Dispersal into progressively greater volumes of air and interception by tree crowns and other obstacles are chief factors in the dilution. According to Spaulding (*27*), screening by vegetation is sometimes quite effective in reducing pine infection where the supply of sporidia is not large. Screening is ineffective, however, when large numbers of sporidia are produced.

Drops of rain or mist of sufficient mass to fall to earth may also intercept many sporidia. No experiments on this effect appear to have been reported, but the effectiveness with which rain clears dust or pollen from the air is well known. Rempe (*24*) observed that thundershowers reduced the pollen content of the air by half. In Russia, Shitikova-Rusakova (*25*) found a great reduction in the numbers of uredospores of rusts caught on trap slides after a rain; after prolonged rains, the catches sometimes decreased to zero. Also, as suggested by Gregory (*9*), sporidia in a very moist atmosphere may be carried out of the air by the mass of moisture condensing on them.

Free moisture in the form of rain or mist may further affect ribes-to-pine spread by washing sporidia from pine foliage before infection occurs. Even a fine mist, if continued long enough, produces sufficient runoff from plant surfaces to carry away many sporidia. For this reason, most experimenters use intermittent rather than continuous fogs or mists to prevent washing away of spores when attempting to infect host plants uniformly under cover. On sugar pine, the fact that many sporidia actually come to rest on films of water over the needle surfaces rather than on the needle surfaces themselves, facilitates the loss.

Wind Movement During Wet Weather in the Sugar Pine Region

The predominant wind movement during dispersal periods for sporidia in the sugar pine region may be anticipated from information on (1) the general pattern of air circulation associated with autumn moist periods and (2) the nighttime movement of air currents near the ground in mountainous regions.

Precipitation in California and southern Oregon is nearly always associated with normal cyclonic storm patterns in which the air movement around the center of low barometric pressure is counterclockwise. Most of the rain falls during the passage of the warm front and is accompanied by southerly winds. In general, the winds are sufficiently pronounced to maintain their southerly character regardless of local topography. Since fall rains provide practically the only source of moisture persisting long enough for germination of teliospores and subsequent pine infection, it follows that the prevailing wind direction will be southerly. Wilson and Baker (*34*) in their study of the aerial dissemination of brown rot spores in California, found that the spores responsible for blossom infection were carried chiefly in a northerly direction on south winds.

During or after rains, calm periods are apt to occur, particularly at night. Then the southerly winds characteristic of the warm front of the storm may be replaced by local air movements, in mountainous regions normally upslope during the day and downslope at night. This night movement is of particular interest, because the relative humidity is most likely to be maintained at or near the 100 percent level, favoring the production and dispersal of sporidia and subsequent pine infection. Winds move downslope at night, because air near the ground becomes heavier as it is cooled through heat loss by radiation. Downslope winds are most pronounced during fair weather, since there are greater heat losses from radiation to a clear sky than to an obscured one; but even in cloudy, calm weather, a gentle downslope drift is often noticeable in the air layer near the ground. Buchanan and Kimmey (*5*), in studies in British Columbia, found a definite downslope predominance in the number of infections resulting from sporidia originating at plot centers; the finding seems best explained by the downslope movement of air at night.

EXPERIMENTAL RESULTS

Of 56 tests, 23, or 40 percent, resulted in pine infection; 34 tests, or almost 60 percent, gave negative results even though special efforts were made to maintain rust telia at the plot centers (table 8, appendix). Six of the 23 positive tests resulted in 1 or 2 cankers only and thus were negligible in effect. Of the 34 negative tests, 9 failures could definitely be attributed to the absence of viable telia on the central ribes when moist periods occurred (moist periods are recorded in table 9). In all but one instance these ribes were *R. roezli*. The reported tendency of this species to shed heavily rust-infected leaves (*14, 15, 21*) was confirmed in these tests. Probably most of the remaining 25 failures resulted from unfavorable weather conditions. In 9 of the 25, germination of telia occurred during moist periods too brief to permit pine infection. (In some of the positive tests also, the germination of telia during short moist periods undoubtedly reduced the opportunity for subsequent pine infection.) In the remaining 16 cases the specific reasons for failure of the rust to cause pine infection are not clear.

From experience with blister rust in the sugar pine region and elsewhere, it can be assumed that the percentage of tests resulting in pine infection would have been higher if more of the test plots had been located around ravine-bottom or streamside centers rather than on slopes or ridgetops.

Under southern Wisconsin conditions, Van Arsdel[7] rated the rust hazard to pines on a scale of 13 topographic conditions (−2 to 10), the highest number representing the maximum hazard. Within this scale, he assigned a rating of 1 to slope shoulders and a rating of 5 to slopes. These basic ratings were subject to modification according to exposure, vegetative cover, and degree of slope.

Although climatic and topographic conditions in the sugar pine region of California and southern Oregon differ materially from those of southern Wisconsin, there is little doubt of the reduced rust hazard to sugar pines situated on ridgetops and slopes as compared with trees in ravine bottoms or adjacent to streams. Ravines and streamsides tend to be cooler, more subject to dew formation if not on too steep a slope, and more retentive of moisture on foliage in consequence of greater protection from sun and wind.

Of the 21 plots established, only one (Damnation Plot 1) was centered in a ravine bottom or along a stream. The others were either on slopes or along ridgetops, because these locations were the only ones where properly distributed sugar pine reproduction could be found.

The distribution of pines probably had little influence on spread of the rust to pines, with one exception. Usually the central acre on each plot was reasonably representative of stand density and size of sugar pines for the entire plot, and plot centers were selected to obtain as even a distribution of young sugar pines around them as possible. The exception occurred on one or two plots where openings formed air channels close to the centers. Under this condition, infections tended to be more numerous on trees in the path of or next to the channels, but the effect was limited to within 50 feet of the plot center.

Rust Spread on Individual Study Areas

Black Rock Plots

Figures 6, 7, and 8 depict the spread of the rust to pines on three of the four plots in the Black Rock, Oreg., area in 1936. These plots were all on a south to southeast slope, varying from moderately steep on Plot 1, to gentle on Plot 2, and very gentle on Plots 3 and 4. All pine infections on Plot 3, not shown, were in the southeast quadrant except one which was just west of the south center line. On all four plots, the greatest distance and intensity of spread was down the slope, indicating that the sporidia responsible for the infection were dispersed principally during periods of downslope air movement at night. Plot 1 (fig. 6) offers a good example of the combined effects of local air turbulence, which dispersed sporidia around the plot center, and night air movement, which carried sporidia downhill over the south-southeast octant of the plot.

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[7] Van Arsdel, E. P. Climatic factors affecting the distribution of white pine blister rust in Wisconsin. Ph. D. thesis, University of Wisconsin, Madison. 105 pp. 1954.

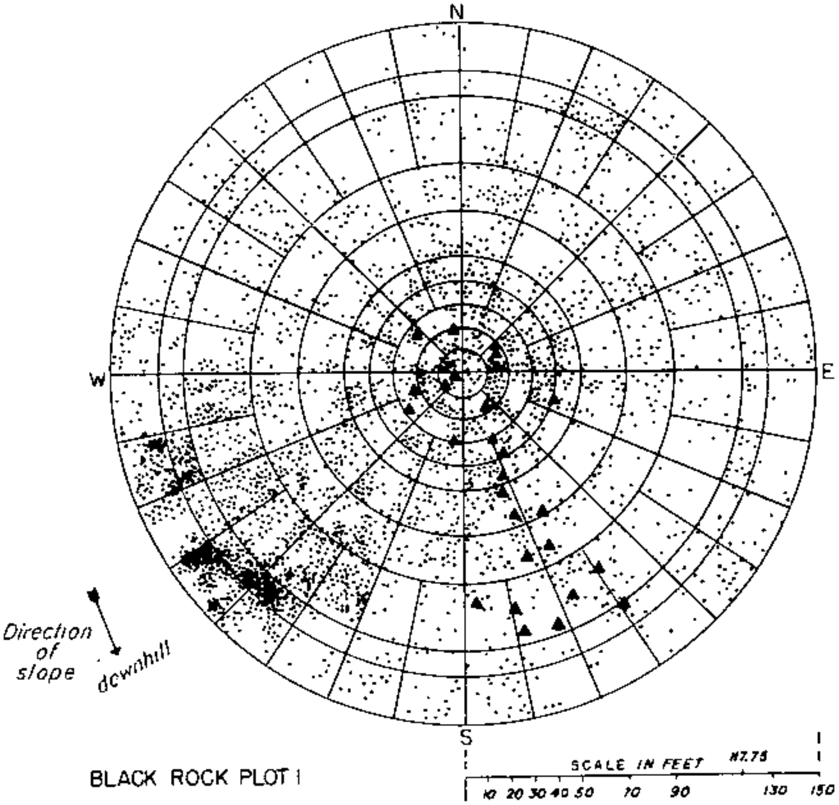

FIGURE 6.—Distribution of sugar pine trees and locations of pines with blister rust resulting from 1936 exposure on Black Rock Plot 1. Dots mark the locations of uninfected trees, and solid triangles the locations of trees with cankers originating from rust on *Ribes nevadense* at the plot center.

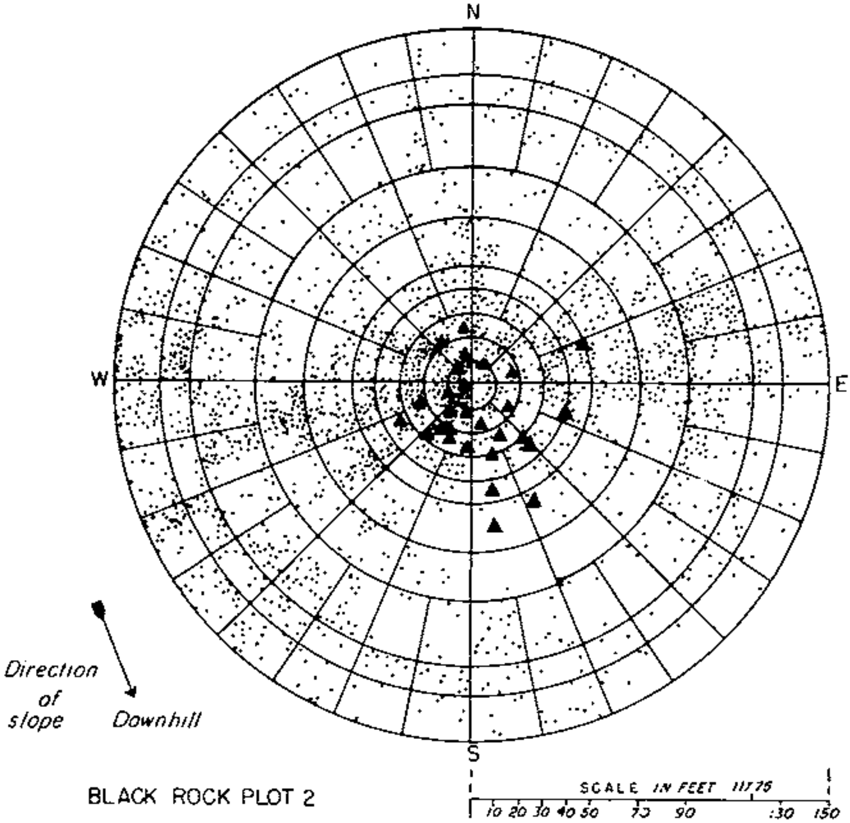

FIGURE 7.—Distribution of sugar pine trees and locations of pines with blister rust resulting from 1936 exposure on Black Rock Plot 2. Dots mark the locations of uninfected trees, and solid triangles the locations of trees with cankers originating from rust on *Ribes nevadense* at the plot center.

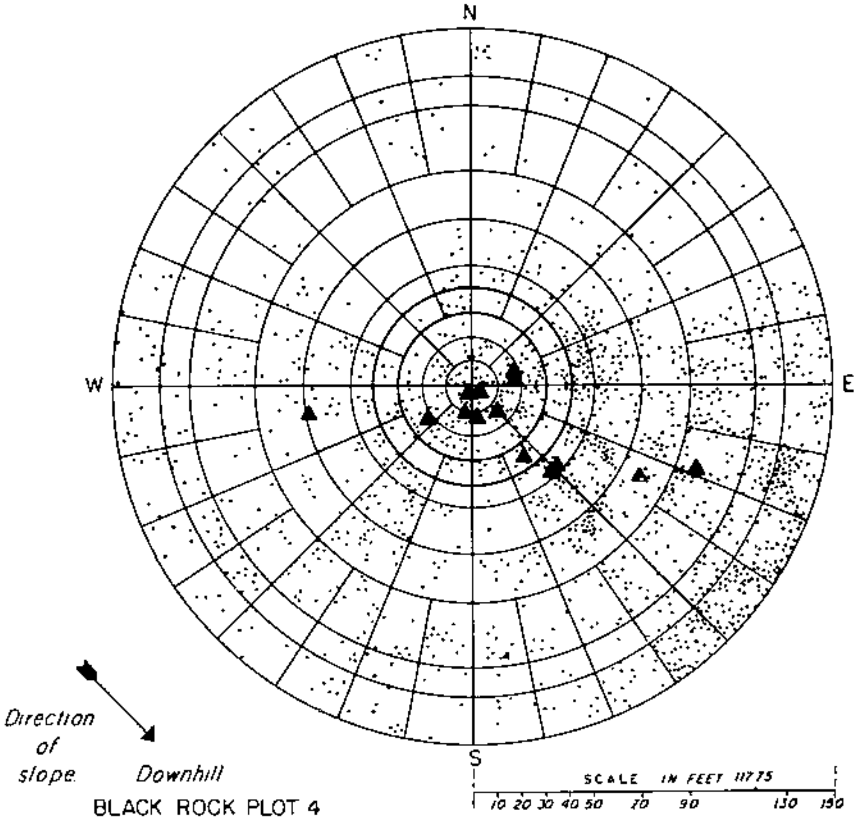

FIGURE 8.—Distribution of sugar pine trees and locations of pines with blister rust resulting from 1936 exposure on Black Rock Plot 4. Dots mark the locations of uninfected trees, and solid triangles the locations of trees with cankers originating from rust on *Ribes roezli* at the plot center.

Nearly all pine infection on the plots probably became established during the first 4 days of September. Rain began at 7:00 a.m. on September 1 and continued intermittently in small amounts through the 4th, with accompanying cloudy skies; however, daytime air humidities were often below 97 percent, so that conditions were not continuously favorable for the dissemination of sporidia or for pine infection (table 9, appendix). A small amount of pine infection may have taken place on Plot 2 in July.

An example of the data yielded by the individual plots is provided by table 2, covering the 1936 exposure of Black Rock Plot 1. The information supplements that provided by figure 6, for judging the significance of the infection. Similar tabulations were made for all tests from which appreciable pine infection was obtained, and they were used in compiling the aggregate results.

TABLE 2.—*Rust spread, infection intensity, and prospective damage to sugar pines resulting from sporidia produced on Ribes nevadense, Black Rock Plot 1,*[1] *Oreg., 1936*

Distance from central ribes plants (feet)	Pine target		Trees		Cankers		
	Foliage units	Trees	Infected	With killing-type cankers	Total	Killing-type	Per foliage unit
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
0.0-10.0	12.85	31	2	0	2	0	0.16
10.1-20.0	49.70	110	4	2	4	2	.08
20.1-30.0	71.23	108	4	4	5	5	.07
30.1-40.0	86.51	167	2	1	2	1	.02
40.1-50.0	80.54	174	3	1	3	1	.04
50.1-70.0	145.59	298	3	1	3	1	.02
70.1-90.0	208.38	431	2	1	3	1	.01
90.1-117.75	326.65	707	6	3	7	3	.02
117.76-130.0	147.85	390	1	0	1	0	.01
0.0-117.75	981.45	2,026	26	13	29	14	.03
0.0-130.0	1,129.30	2,416	27	13	30	14	.03

[1] Area=1 acre.

No pine infections resulted from the rust on *Ribes cereum* at the center of Black Rock Plot 5 in 1938 or 1940, the only two years that exposures were made on this plot. Only small amounts of telia were present on the central ribes in each test. In 1938 the telia were dissipated, because rains provided moisture over periods too brief for pine infection. In 1940 the moist periods were somewhat more favorable, but apparently they were again inadequate to permit pine infection. Only one canker resulted from the exposure on Plots 1 to 4 on the Black Rock area in 1939. This was on Plot 1. Several rains, resulting in brief moist periods in August and September, caused germination of viable telia on Plots 1 and 2 but were too short to permit pine infection. Telia on Plots 3 and 4 were lost by premature leaf cast from *R. roezli.*

Siskiyou Plot

A single canker was found on the Siskiyou plot in 1938, the only year in which a test was undertaken on this Oregon study area. September rains, which dissipated viable telia on ribes at the plot center, did not last long enough for pine infection. These rains intensified rust on the ribes, but late October precipitation fell as snow, which evidently was not favorable for pine infection although air temperatures were not excessively low.

Damnation Plots

The first tests at the Damnation area were in 1938. Weather favorable for pine infection occurred in late September and early October. At that time, *Ribes nevadense* at the Plot 1 center bore abundant viable telia, but *R. roezli* at the Plot 2 and 3 centers bore practically none. Many pine infections resulted on Plot 1, but only eight on Plot 2 and none on Plot 3. Rust was again established on the central ribes on Plots 2 and 3 in 1939 and 1940, but in each year viable telia were lacking during favorable moist periods and no pine infection resulted.

In 1941 exposures were made on all three plots. Moist periods were minimal in length for pine infection except on Plot 1, which was in a creek bottom where dews followed rains. Only two pine cankers resulted on Plot 2 and none on Plot 3. Infections undoubtedly became established on Plot 1, but they were not used in the tests because of the discovery of cankers of 1937 origin. These were from natural infection and could not be distinguished with certainty from the 1938 test infections. This fact, together with the necessity for destroying the 1937 cankers prior to sporulation, caused abandonment of the plot as a source of information on spread. It had some value, however, in indicating the hazard potential of *Ribes nevadense* in a moist ravine bottom as compared with that of *R. roezli* on open slopes.

In 1942, tests were again made on Plots 2 and 3, but no pine infection resulted. The reasons for failure are not clear.

Deadhorse Ridge Plots

On the Deadhorse Ridge study area, tests were made on three plots in 1938. Plot 1 had very few viable telia on the *Ribes roezli* at the plot center during the infection weather of September and October. Only four cankers on sugar pine resulted. Plot 2 had no viable telia present during favorable infection periods. The *R. roezli* at the center of Plot 3 had a fair amount of viable telia during favorable periods, and 32 pine cankers resulted. The greatest intensity of spread was northerly, but the greatest distance, represented by a single infected tree, was downhill to the east (fig. 9). This area had more than one apparently favorable period for pine infection in the autumn of 1938 (table 9, appendix).

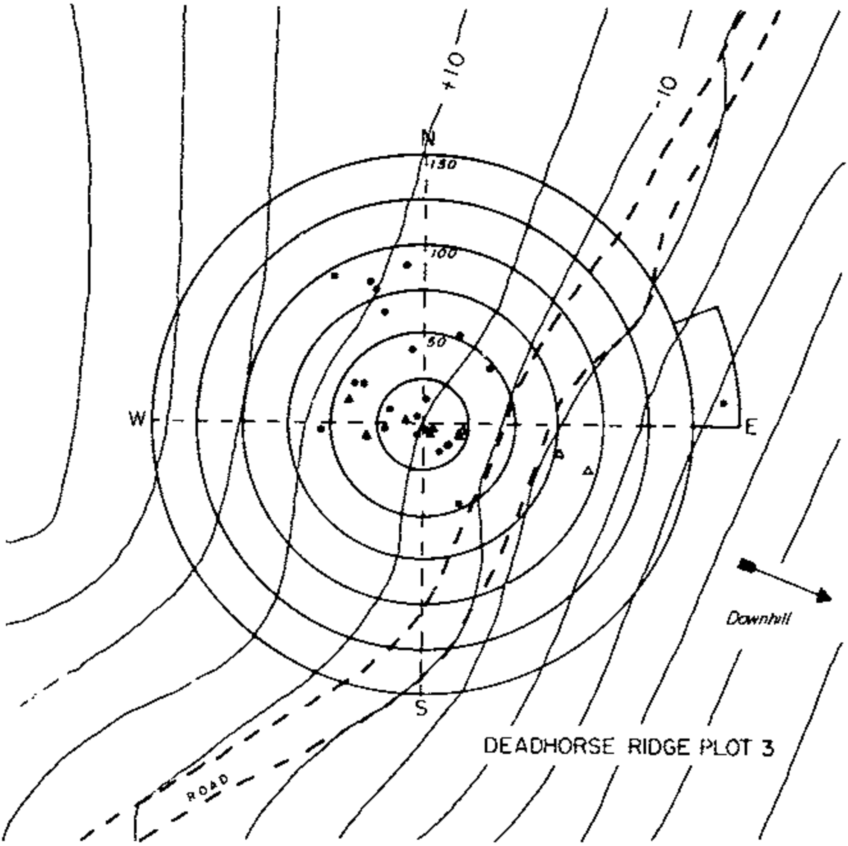

FIGURE 9.—Location of sugar pines with infection resulting from exposure to rust on the central *Ribes roezli*, Deadhorse Ridge Plot 3. Dots represent trees infected in 1938; triangles, trees infected in 1940; and solid triangles, trees infected both in 1938 and 1940. Contour interval is 10 feet.

Under the assumption that pine infection occurred on Plot 3 in 1938, the central ribes on this plot were not artificially infected the next year; those on the other five Deadhorse plots were. Limited numbers of viable telia were present on Plots 1, 2, and 4 during periods that were thought to be marginally favorable for pine infection in 1939, but no infections resulted. No infection was anticipated from the few telia present on Plots 5 and 6 and none occurred.

In 1940, only Plots 3, 5, and 6 were used for tests, because previous pine infection was suspected on the other three plots. Although abundant telia were present on the central ribes of these three plots in 1940, the moist periods were generally so short and intermittent that relatively little pine infection resulted. Eleven cankers on Plot 3, 6 cankers on Plot 6, and none on Plot 5 resulted from the 1940 exposure. Although there was some spread to the west on Plot 3, the greatest intensity and distance of spread was downhill (fig. 9). Plot 6 had been selected for study of rust spread from a few feet of ribes live stem, equivalent to a medium sized *Ribes roezli*, typical of those sometimes missed in eradication work on brushy hillsides. The pines on the plot were scattered among a dense stand of tall *Ceanothus velutinus*, and the plot center was located in the midst of the dense brush cover with a small opening in the immediate vicinity of the ribes. The resulting pine infection, all down the slope to the east of the center, was very light but extended 170 feet from the central ribes (fig. 10).

The central ribes on Deadhorse Plots 1, 2, and 4 were infected with rust again in 1941, but the lack of favorable moist periods prevented pine infection except for one canker on Plot 1.

In 1942, tests were made on all six of the plots on this study area, but no pines became infected even though enough telia were present and the weather seemed favorable.

Big Bar Plots

Of the four plots established in the Big Bar study area in 1940, all but Plot 4 had abundant viable telia when rains occurred in September and October, but the moist periods were relatively short for pine infection. A fair amount of pine infection did occur on Plots 1 and 2, but the infections were confined almost entirely to pines

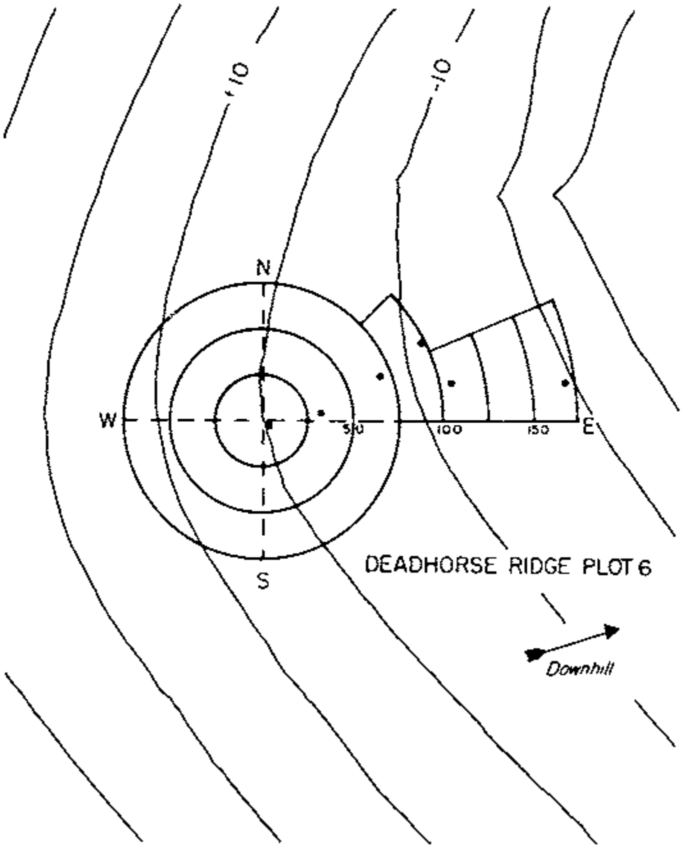

FIGURE 10.—Location of sugar pines with infection resulting from exposure to rust on *Ribes roezli* on Deadhorse Plot 6 in 1940. Dots represent infected trees. Contour interval is 10 feet.

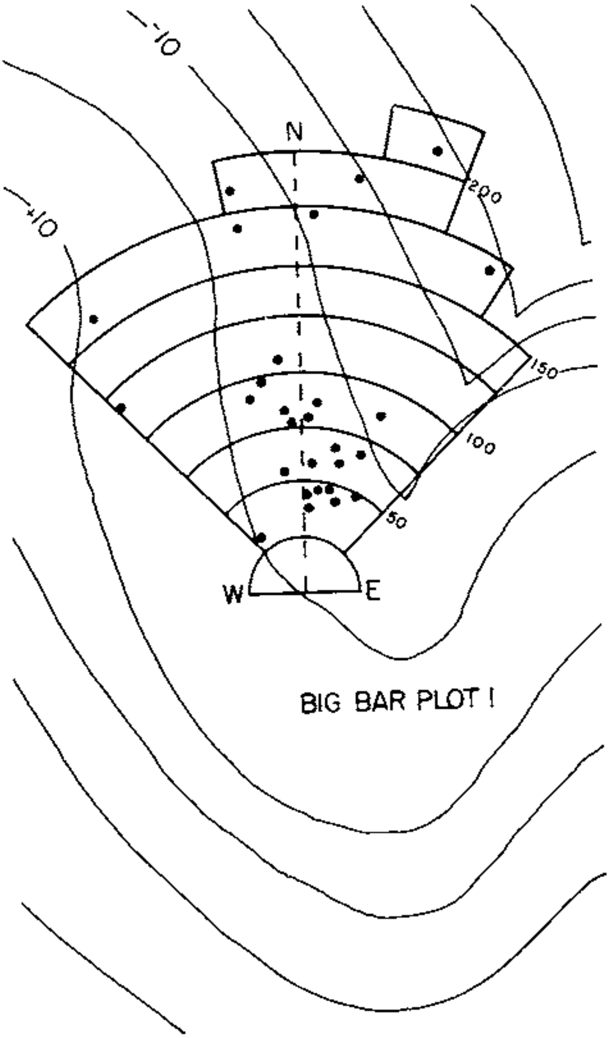

FIGURE 11.—Location of sugar pines with infection resulting from exposure to rust on *Ribes roezli* on Big Bar Plot 1 in 1940. Dots represent infected trees. Contour interval is 10 feet.

in dense thickets with young white firs, where the pine foliage undoubtedly held moisture much longer than in less dense stands. (The periods of wet pine foliage given in table 9, appendix, are based on average conditions that existed on the study areas; no observations were made on moisture retention in the dense thickets.)

The entire spread of rust to pines was in a northerly direction on Plot 1, and it spread to more than 200 feet from the central *Ribes roezli* (fig. 11). This restricted spread pattern suggests that effective dissemination of sporidia occurred over a relatively short period. There were dense thickets of pines in all directions from the central ribes, and those to the north were farthest away. During a long period, air turbulence would have resulted in a more generalized spread. This spread pattern indicates also that, during the effective dissemination, air movement was entirely from the south. Although the greatest distance of spread was somewhat downhill, it seems evident that the general direction of air movement influenced this spread more than did the slope.

In contrast, the spread on Plot 2 in 1940 was in all directions from the central *Ribes roezli* plants, and confined mostly within a 50-foot radius (fig. 12). Although the farthest spread was to the north, spread downslope to the west was practically as far. Very likely, air movement from the south was less pronounced and effective sporidial dissemination continued over a longer period than on Plot 1. The pine infections resulting from the 1940 exposure were confined

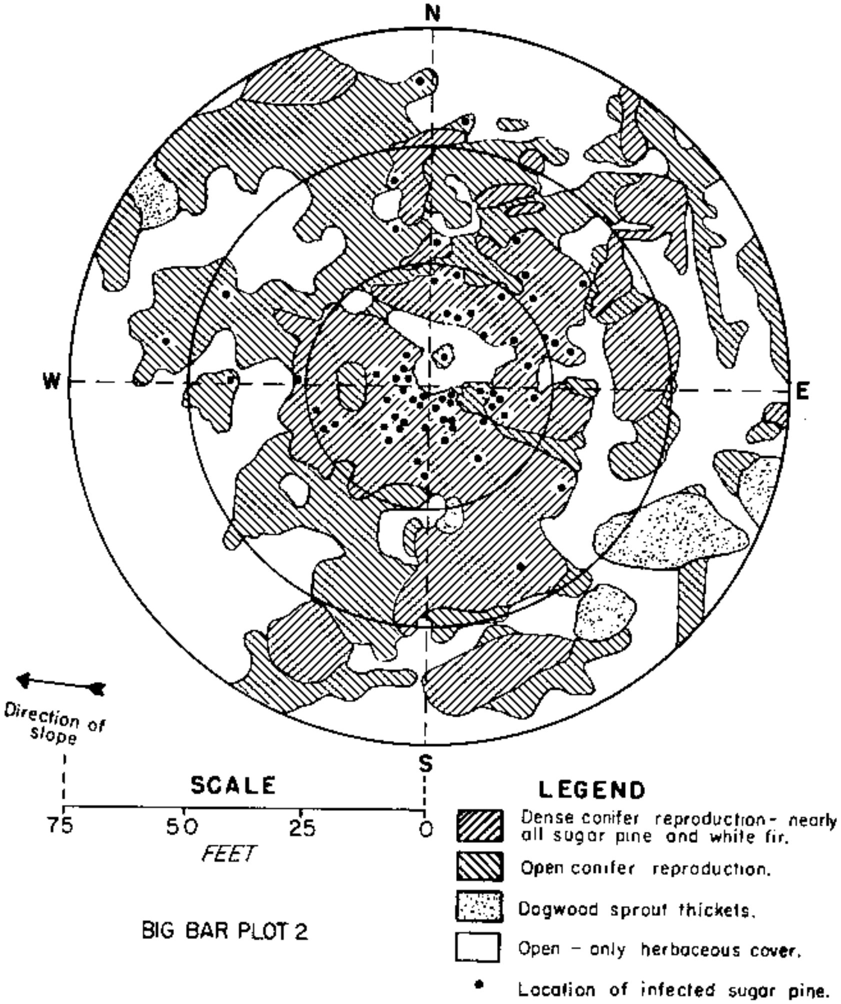

FIGURE 12.—Location of sugar pine trees with infection resulting from exposure to rust on *Ribes roezli* on Big Bar Plot 2 in 1940, in relation to vegetative ground cover.

almost entirely to dense thickets of white fir and sugar pine reproduction (fig. 12). Hundreds of small white firs were cut out of these thickets in 1943 to facilitate examination of the associated sugar pines. This plot also had a sparse overstory of large conifers which the other plots on this area lacked. The shelter provided by these trees may have aided in the retention of moisture on understory foliage. Viable telia were abundant on Plot 3 in 1940 at the time pine infection occurred on Plots 1 and 2, but no pines became infected. The several *Ribes roezli* at the plot center were in the open where they were subject to drying by the sun and wind, and no germination of telia occurred.

On Plot 4, no viable telia remained on the one *Ribes roezli* growing at the plot center during the moist periods in September and on October 2. Three telia-bearing *Ribes roezli* in pots were placed at the center on October 7, but there were no periods favorable for pine infection before these plants became defoliated.

In August 1941, the *Ribes roezli* growing in situ at the centers of the four plots on the Big Bar study area were exposed to rust in moist chambers. However, heavy defoliation of the plants from anthracnose occurred before the blister rust infection produced telia. The ribes at the centers of Plots 2 and 4 were so badly defoliated that they became valueless as sources of telia. Accordingly they were cut flush with the ground, and potted *Ribes nevadense* bearing abundant viable telia were substituted in September. On October 19 a rain of short duration caused germination of telia on the *Ribes nevadense* on Plots 2 and 4 but none on the *Ribes roezli* on Plots 1 and 3. At the time it was assumed that no ungerminated teliosphores remained in the columns on Plots 2 and 4, but this assumption was undoubtedly erroneous; Bega (*2*) has recently shown that a much longer moist period than occurred on October 19 is required to exhaust the production of sporidia by telial columns, even at nearly optimum germination temperatures. From rains later in October, further germination of telia occurred on the central ribes of Plot 3 (and undoubtedly on Plots 2 and 4), but accompanying temperatures averaged about 40° F. and no appreciable pine infection was anticipated.

Plot 2 had 1,565 cankers on 307 sugar pines as a result of the 1941 exposure. Although there was considerable spread down the slope, as in 1940, the greatest distance of spread was to the north (fig. 13).

On Plot 3 nearly all effective sporidial dissemination was in the northwest quadrant, and only a single canker was found down the slope southeast of the central ribes (fig. 14), although pines were considerably more numerous to the southeast. There were no sugar pines within 25 feet of the central ribes on the uphill side of the plot.

The spread pattern on Plot 4 in 1941 (fig. 15) shows a strong tendency for downhill spread, but the greatest distance of spread was up slope to the northwest, in the opposite direction. Chances are that air movement during part of the period of sporidial dissemination was from the southeast, and downslope spread took place at night during a period of calm.

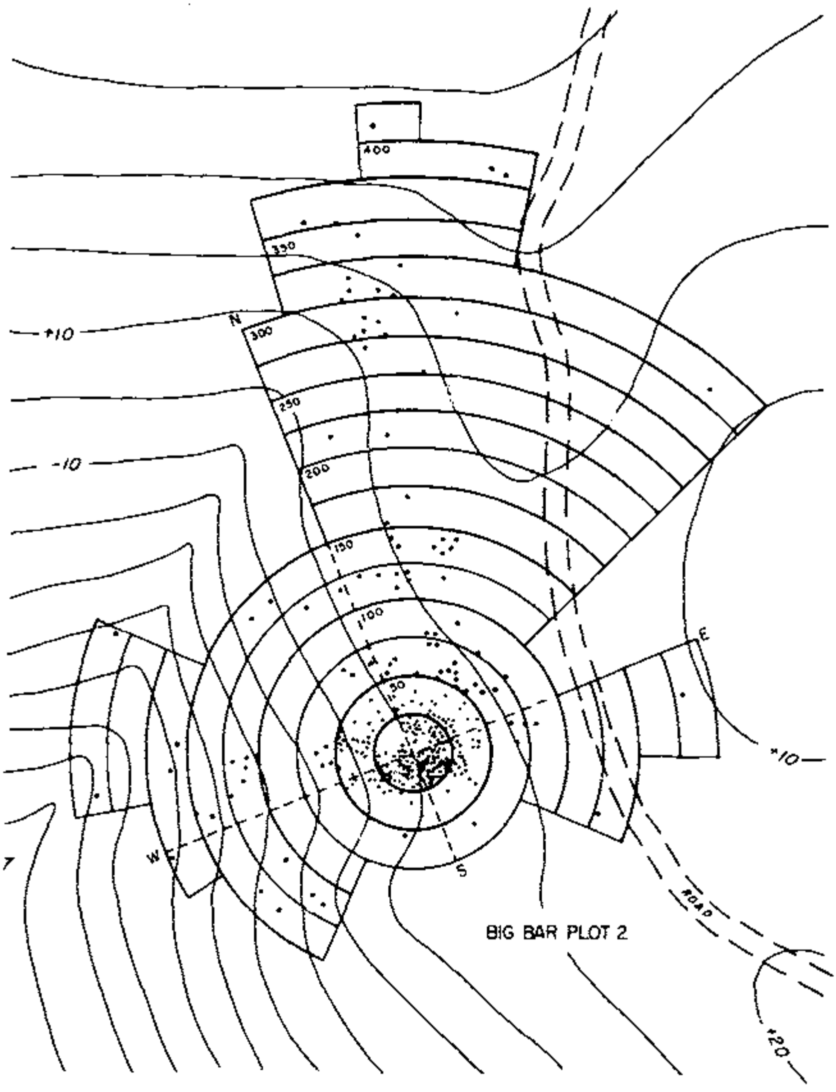

FIGURE 13.—Location of sugar pines with infection resulting from exposure to rust on *Ribes nevadense* on Big Bar Plot 2 in 1941. Each dot represents an infected tree. Contour interval is 10 feet.

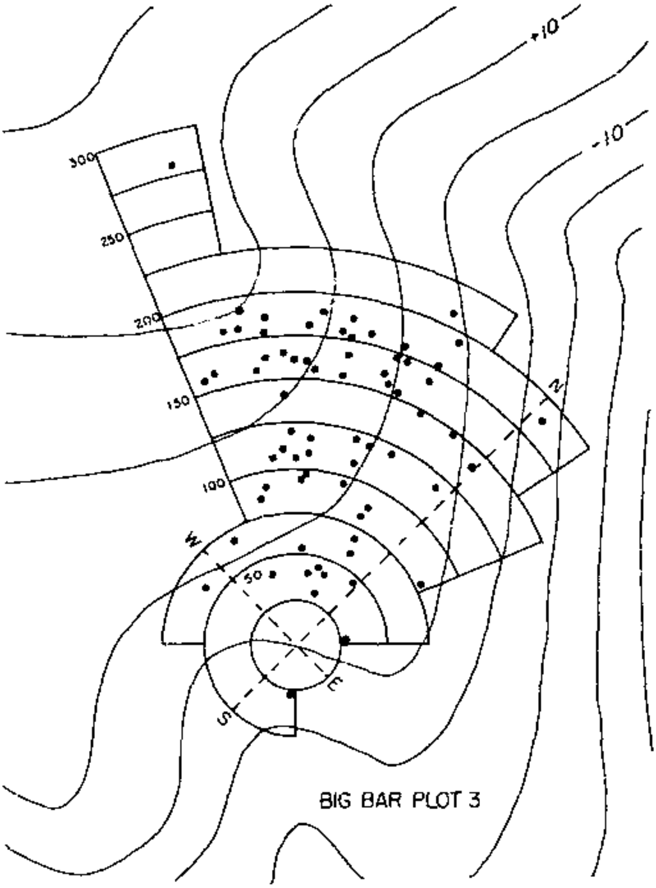

FIGURE 14.—Location of sugar pines with infection resulting from exposure to rust on *Ribes roezli* on Big Bar Plot 3 in 1941. Each dot represents an infected tree. Contour interval is 10 feet.

Because the weather conditions in 1941 were believed to have been unfavorable for pine infection, the *Ribes roezli* plants growing at the plot centers were infected again in August 1942. Abundant viable telia were present at all 4 centers, and considerable viable telia were present on the 10 potted *R. cereum* at the center of a fifth plot, when rains were of a nature and duration that were considered favorable for pine infection. However, only four cankers of definite 1942 origin were found on the plots in subsequent pine examinations. Two of these cankers were found on Plot 1 and the other two on Plot 3.

Washington Point Plot

No cankers resulted from the single season of exposure on the Washington Point plot in 1947, even though several rains in October kept pine foliage continuously wet for periods of 38 to 47 hours when rust was present on the central ribes. However, temperatures during these periods averaged only about 45°F. At this temperature level

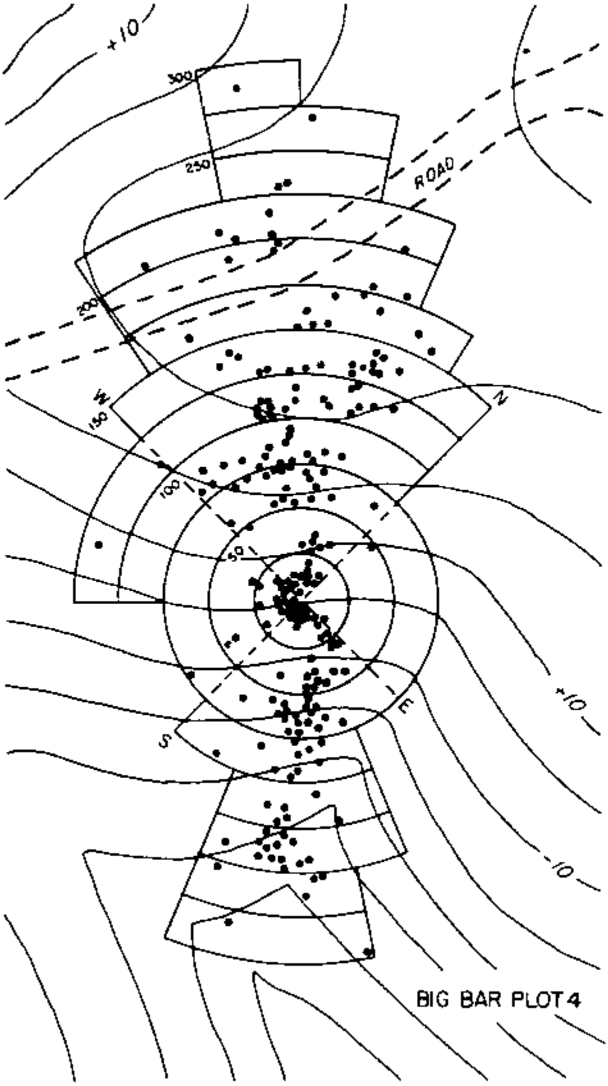

FIGURE 15.—Location of sugar pines, with infection resulting from exposure to rust on *Ribes nevadense* on Big Bar Plot 4 in 1941. Each dot represents an infected tree. Contour interval is 10 feet.

the germination of teliospores or sporidia and the growth of germ tubes proceeds slowly (*11*), and the moist periods may not have been long enough to permit infection. Morever, the rains were quite heavy and may have removed many sporidia from pine foliage.

Relation of Weather to Pine Infections

The marginal nature of weather conditions for pine infection is indicated by the different results sometimes obtained within a single season on one area. Such was the case in 1940 on three plots in the Big Bar area, where pine became infected on two plots but not on a third although adequate telia were present on the ribes at the centers of all three.

Infection on Big Bar Plots 1 and 2 evidently occurred during some period in the latter half of September or the first few days of October. The first rain after telia were formed was a light shower (0.05 inch rain) on September 15, followed by a heavy downpour (0.40 inch rain and hail) on September 18. Light showers occurred on September 26 and October 2. The rains were all of short duration, the temperatures ranged from 38° to 55°F., and the relative humidity was fairly low between rains.

Although some telia germinated following the heavy shower on September 18, no pine infection would have resulted under usual conditions on open cutover land, as evidenced on Plot 3. On Plots 1 and 2, however, the combination of aspect, shade, and protection from wind apparently provided conditions for the maintenance of moisture on protected foliage for a sufficient time to permit pine infection. No further moist periods occurred on the area up to October 20 when the limited remaining telia were removed from the plots. It was therefore impossible for pine infection to have occurred subsequent to that date in 1940.

Although the weather in the autumn of 1941 at the Big Bar area was considered at the time to be unfavorable for pine infection, heavy infection occurred on Plots 2, 3, and 4. No infection occurred on Plot 1 as a result of the slight germination of telia there late in October.

After telia were formed in 1941, the first rain was gentle and began about 3:30 on the afternoon of September 18. The following morning the rain gage showed 0.42 inch of rain, and the hygrothermograph had registered 100 percent humidity for a continuous period of 14 hours. There was only a trace of teliospore germination, and it is believed that the period of wet pine foliage was too short for pine infection.

On October 12 a shower of 0.05 inch of rain about 9:30 a.m. resulted in a relative humidity of 100 percent for less than 3 hours. Following a week of warm weather and low humidity, a 3-day period starting about 3:00 p.m. on October 19 provided moisture that may have resulted in some pine infection on Plots 2 and 4 (fig. 16). This consisted of a shower of 0.15 inch rain on October 19 and 0.03 inch of rain and fog on October 21 with accompanying 100 percent humidities. Unfortunately almost 18 hours of hygrothermograph record are missing for October 20 and 21 because of a clock stoppage, but in auxiliary notes a light drizzle on October 21 was recorded as starting about 7:30 a.m.

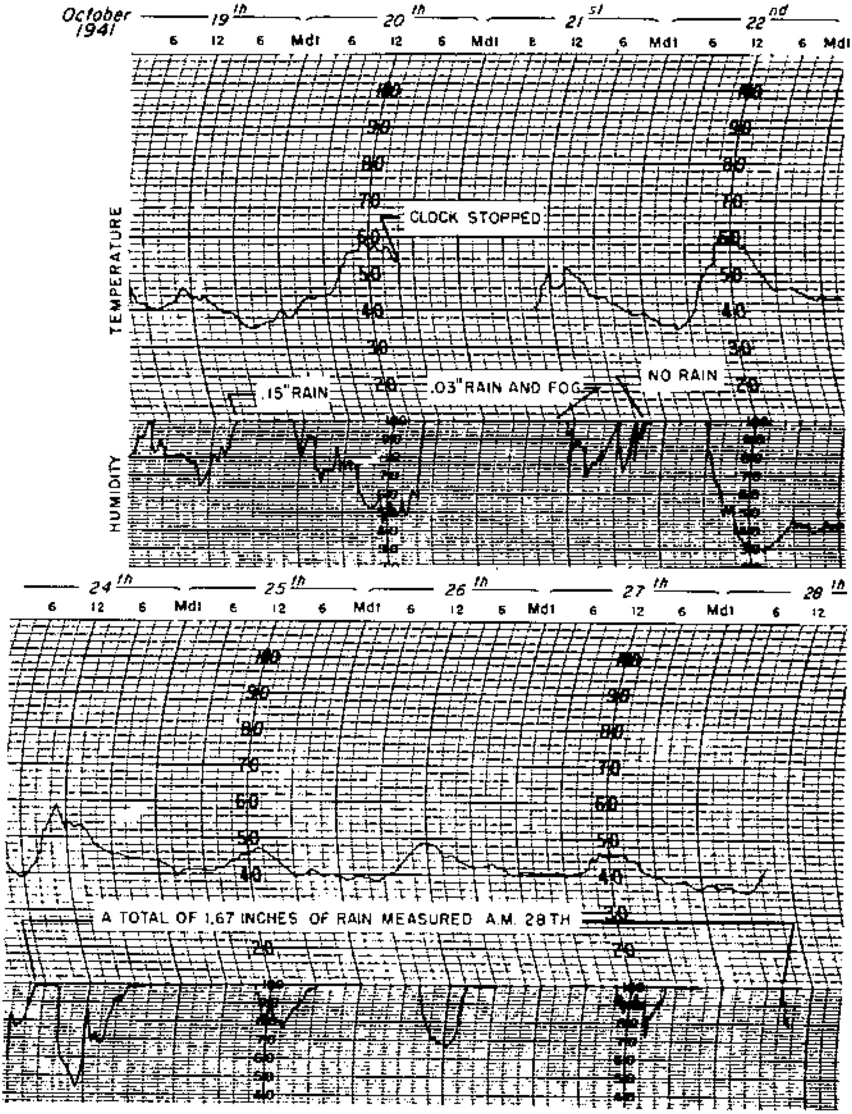

FIGURE 16.—Hygrothermograph record for October 19 to 22, inclusive, and 24 to 27, inclusive, 1941, on the Big Bar area.

On October 21 all telia on the *Ribes nevadense* on Plots 2 and 4 gave evidence of good germination, but telia on Plots 1 and 3 had not germinated. It should be noted that the ribes on Plots 2 and 4 were shaded by surrounding trees, whereas those at the Plot 1 and Plot 3 centers were not.

Intermittent showers totaling 1.67 inches of rain and snow fell from October 24 to 28. Germination of telia occurred on the central *Ribes roezli* on Plot 3 during this period, and also probably on the *R. nevadense* on Plots 2 and 4. For the latter plots, the amount of germination could not be judged visually because of previous germination from the same telial columns on October 19 to 21. It is believed that most of the pine infections of 1941 origin on Plots 2, 3, and 4 occurred during this latter 3-day period, even though temperatures were low.

When the tests were made in 1942 on 13 plots in California, there appeared to be enough telia for pine infection on all plots during favorable periods of moisture from October 10 to 14. At this time temperatures were low but adequate for telial germination. Some pine infections were expected on all plots and abundant infections on most of them, especially on the Big Bar plots. Two cankers resulted on each of 2 plots on the Big Bar area, and none on the other 11 California plots.

At Big Bar, relative humidities of 100 percent or nearly so prevailed for 32 hours (fig. 17)—longer than the continuous periods that probably resulted in infection in 1940 and 1941 at Big Bar. Pine foliage was wet for 52 hours, which should have made infection possible. However, temperatures were below 50°F. for the entire moist period and dropped below 40° for 13 hours.

The reason for the scarcity of pine infection in 1942 is not certain. The most probable hypothesis is that germination and infection processes were retarded by the low temperatures prevailing during the moist period October 10 to 12, and that the time interval was insufficient for more than minimal infection to take place. Temperatures on the Big Bar area were under 50° F. for the first 36 hours when foliage was wet, and they dropped below 40° for the next 13 hours (fig. 17). Temperatures on the Damnation and Deadhorse areas were similar in pattern but averaged 2° to 4° lower than at Big Bar. According to tests by Hirt (*11*), germination at these temperatures should require several hours longer to start than germination at temperatures in the mid-50° range. Proportionately, infection processes would have been retarded much more because of the temperature drop during the latter part of the moist period. Moreover, on the Damnation area the moist period was not continuous, and some drying of foliage probably occurred.

Most of the telia on ribes at the plot centers were formed during the latter part of September and should have been viable on October 10, although delay in germination could be expected because of age (*11*). Two 3-day periods with maximum temperatures of 83° to 85° F. occurred after September 14 on the Big Bar area, and temperatures reached 95° on the Damnation area. According to recent experimental evidence,[5] however, these temperatures would not impair via-

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[5] Bega, R. V. and J. R. Parmeter. Personal communication.

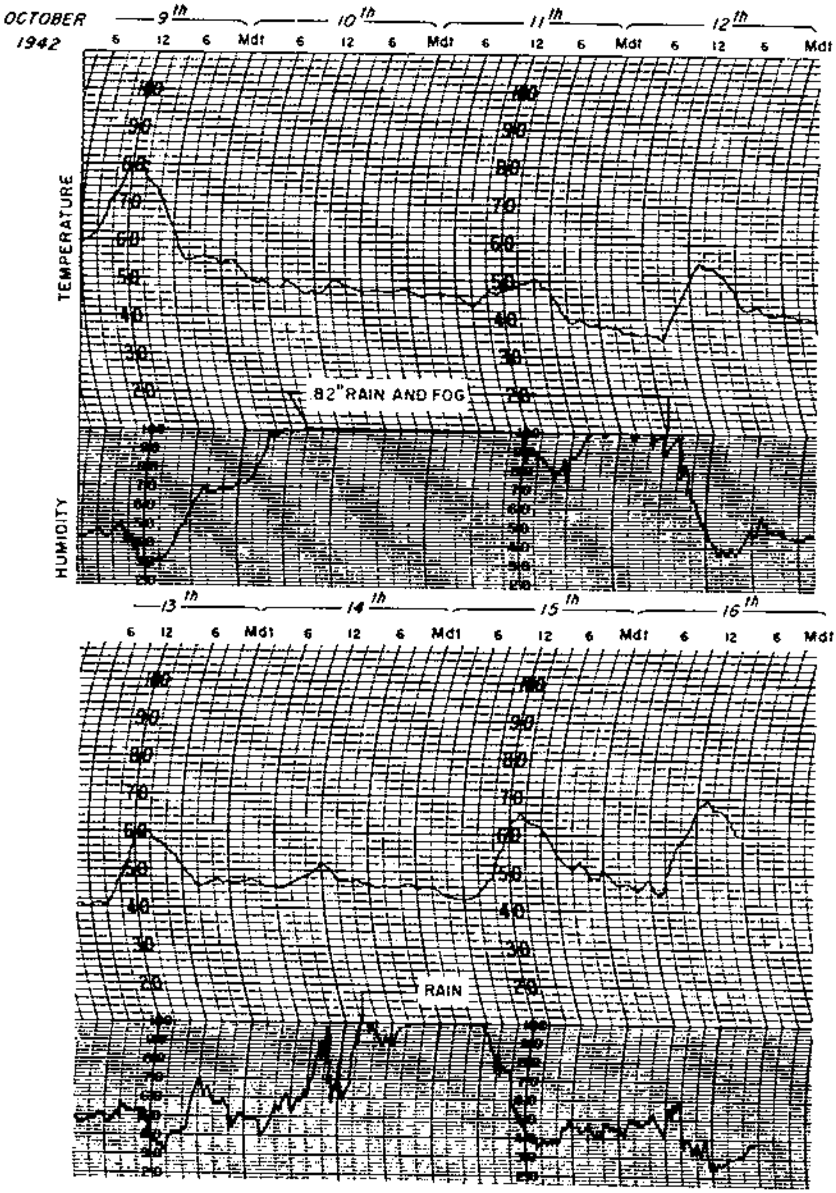

FIGURE 17.—Hygrothermograph record for October 9 to 16, inclusive, 1942, on Big Bar area.

bility under California conditions, although reported to do so in Wisconsin (*32*).

The examples cited illustrate that the influence of weather as a determinant of pine infection in the sugar pine region is complex in action, as well as subject to modification by local environment and the physiological condition of the rust pathogen.

Distance of Spread and Associated Infection Intensities

In regions where rains are frequent and high humidities prevail, the pine infection pattern from a single ribes center for any one season is likely to be the composite result of the dispersal of several to many waves of sporidia. Since the infection pattern and gradations of infection intensity are largely determined by wind movement during dissemination periods, and since both direction and velocity of the wind are apt to vary from period to period, the differences tend to be blended in the seasonal result. Over a number of seasons under such conditions, infections occur to some degree in all directions from a plot center, as indicated by infection data obtained by Posey and Ford (*22*) on a plot at Kittery Point, Maine.

The present tests, however, show that in most of the sugar pine region infection patterns for a single season are usually the consequence of dissemination of sporidia during only one or two favorable moist periods. Since air movement during any one moist period is apt to be limited to one or two major directions, the dissemination patterns produced are likely to be much less uniform than if they resulted from numerous dissemination waves. The usual uneven-aged and patchy character of sugar pine reproduction also contributes to irregularity in the infection pattern.

On the other hand the physical laws governing particle dispersion in air are basically uniform in effect and impart some degree of similarity to infection patterns. As a result, infections generally decrease in number with distance from the dissemination center even though the gradient of decrease may not be uniform.

Intensity of pine infection may be expressed either by area or by infection gradient. Control supervisors usually appraise intensity of infection by number of cankers or infected trees per acre. Ordinarily in such appraisals the source of infection is uncertain or multiple. In the British Columbia tests reported by Buchanan and Kimmey (*5*) on spread of white pine blister rust from single rust centers on ribes to surrounding western white pines, intensities were expressed as numbers of cankers per million host needles for concentric zones around the centers. Since the computations were by entire zones, this amounted to a disease gradient determined on an areal basis rather than by the line-sample method, the one probably most commonly employed in obtaining such determinations (*9*, *35*). Gradients based on full concentric zones provide satisfactory averages where dissemination has taken place in substantially all directions from a center, but when it has been primarily in one or two directions, as in part of the California tests reported here, such gradients do not satisfactorily represent actual effects over the exposed areas. Gradients based on segments over which dissemination has been concentrated are much more significant.

For entire distance zones, the number of cankers per foliage unit by zones decreased with distance but not at a consistent rate (tables 3 and 4). The principal cause of irregularity was undoubtedly the uneven distribution of the sugar pine target trees, particularly in zones close to the plot centers. Contributory influences were the individual differences in susceptibility of the trees to rust and differences in local shelter affecting the retention of moisture on foliage.

Big Bar Plot 1 offers a good example of the effects of tree distribution and shelter and probably also of differences in tree susceptibility in disrupting the pattern of an even infection gradient. All infection on this plot in 1940 occurred in a northerly direction (fig. 11). The infected north quadrant for that year had only three trees within the first 25-foot zone around the central ribes, and these were in fully open positions and not directly in the line of the observed infection pattern. The highest number of cankers per foliage unit occurred in the 50.1 to 75.0 foot zone (table 5). However, 9 of the 12 cankers found in this zone were on 2 out of 20 trees present. The concentration of cankers on these two trees can be attributed most readily to high susceptibility and unusually good shielding from sun and wind. Similar sources of irregularity were operative on practically all plots.

TABLE 3.—*Total blister rust cankers and number of cankers per foliage unit*[1] *by distance zones from central ribes for Plots 1 to 4. Black Rock Area, Oreg., 1936 exposure*

Distance from central ribes (feet)	Plot 1		Plot 2		Plot 3		Plot 4	
	Total	Per foliage unit	Total	Per foliage unit	Total	Per foliage unit	Total	Per foliage unit
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
0.0–10.0	2	0.16	9	0.52	0	0.00	5	0.33
10.1–20.0	4	.08	10	.20	0	.00	5	.30
20.1–30.0	5	.07	13	.18	6	.24	1	.04
30.1–40.0	2	.02	4	.03	2	.09	1	.04
40.1–50.0	3	.04	3	.03	0	.00	2	.05
50.1–70.0	3	.02	4	.03	1	.01	1	.01
70.1–90.0	3	.01	------	------	0	.00	1	.01
90.1–117.5	7	.02	------	------	0	.00	1	.004
117.6–130.0	1	.01	------	------	1	.01	------	------
Total	30	------	43	------	10	------	17	------

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[1] Foliage unit adopted as standard for this study—the amount of foliage on an average pine of 5- to 10-foot height class.

TABLE 4.—*Total blister rust cankers and number of cankers per foliage unit*[1] *by distance zones from central ribes for Deadhorse Area Plot 3 and central part of Big Bar Plot 2, Calif.*

Distance from central ribes (feet)	Deadhorse Plot 3—1938		Deadhorse Plot 3—1940		Big Bar Plot 2—1940		Big Bar Plot 2—1941[2]	
	Total	Per foliage unit	Total	Per foliage unit	Total	Per foliage unit	Total	Per foliage unit
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
0.0–12.5	11	2.66	3	0.64	142	9.66	493	27.42
12.6–25.0	7	.27	2	.07	27	.50	542	8.54
25.1–37.5	1	.07	1	.06	16	.24	242	2.89
37.6–50.0	5	.12	2	.04	10	.18	92	1.37
50.1–75.0	3	.03	0	.00	4	.06	91	1.07
75.1–100.0	4	.04	3	.03				
100.1–125.0	0	.00						
125.1–150.0	0	.00						
150.1–175.0	1	.004						
Total	32		11		199		1,460	

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[1] Foliage unit adopted as standard for this study—the amount of foliage on an average pine of 5- to 10-foot height class.

[2] First 75 feet of plot only.

Table 5.—*Total blister rust cankers and number of cankers per foliage unit*[1] *by sectors of distance zones for various California plots and years of exposure*

Distance from central ribes (feet)	Deadhorse Plot 6, 1940, S45° of NE quadrant		Big Bar Plot									
			1, 1940, N90° quadrant		2, 1941, W45° of NE quadrant		3, 1941, N67° 30′ W–N22°30′ E quadrant		4, 1941, NW quadrant		4, 1941, mid. 45°, SE quadrant	
	Total	Per foliage unit	Total	Per foliage unit	Total	Per foliage unit	Total	Per foliage unit	Total	Per foliage unit	Total	Per foliage unit
	No.	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
0.0–12.5	[2] 1	4. 35	0	0	81	36. 00	0	0	265	56. 03	74	20. 73
12.6–25.0	0	. 00			130	13. 50			81	73. 63	5	4. 67
25.1–37.5	1	. 80	10	1. 07	57	5. 59	90	8. 47	57	15. 41	4	1. 28
37.6–50.0	0	. 00			4	. 85			1	. 72	10	1. 46
50.1–75.0	1	. 13	12	2. 00	19	1. 44	5	. 71	115	5. 99	30	1. 41
75.1–100.0	1	. 19	15	. 80	7	1. 16	36	2. 30	54	1. 87	11	. 59
100.1–125.0	1	. 04	3	. 15	12	2. 53	24	. 98	41	. 77	8	. 19
125.1–150.0	0	. 00	0	. 00	9	. 26	8	. 27	36	. 42	15	. 19
150.1–175.0	1	. 09	4	. 06	2	. 05	22	. 21	19	. 19	5	. 13
175.1–200.0	------	------	2	. 05	0	. 00	20	. 13	6	. 14	2	. 37
200.1–225.0	------	------	1	. 02	3	. 85	1	. 05	6	. 25	------	------
225.1–250.0	------	------	------	------	1	. 24	0	. 00	2	. 02	------	------
250.1–275.0	------	------	------	------	2	. 09	0	. 00	1	. 006	------	------
275.1–300.0	------	------	------	------	9	. 19	1	. 01	1	. 008	------	------
300.1–325.0	------	------	------	------	8	. 10	------	------	------	------	------	------
325.1–350.0	------	------	------	------	1	. 05	------	------	------	------	------	------
350.1–375.0	------	------	------	------	2	. 09	------	------	------	------	------	------
375.1–400.0	------	------	------	------	2	. 08	------	------	------	------	------	------
400.1–425.0	------	------	------	------	1	. 02	------	------	------	------	------	------
Total	6	------	47	------	350	------	207	------	685	------	164	------

[1] Foliage unit adopted as standard for this study—the amount of foliage on an average pine of 5- to 10-foot height class.

[2] Canker just outside sector but counted as in.

At Big Bar Plot 2, ribes species at the plot center differed in 1940 and 1941, as did the amount of telium-bearing leaf surface present at the time of sporidial dissemination, but it is evident that differences in weather during dissemination and afterward must have been responsible for most of the difference in intensities and gradients for the two seasons. For the 1941 exposures the intensity of infection, measured either as cankers per foliage unit (fig. 18) or cankers per acre (table 6), was somewhat under 3 times as great as for 1940 exposures in the central 12.5 circle of the plot, whereas it was 9 to 22 times greater in the zones beyond.

Undoubtedly one cause for the lower 1941 canker intensity close to center at Big Bar Plot 2 was the pruning out in 1942 of 1940 infections to prevent their sporulation. In the process, many 1941 infections on the same twigs or branches that had not developed far enough to be visible must have been removed from the central area of the plot. Another contributory cause probably was the greater directional trend of sporidial drift toward the northeast in 1941. In this direction there was less pine foilage target near the plot center than toward the west and south (see fig. 12, p. 25) where much of the 1940 infection occurred.

TABLE 6.—*Infection by zones within 75 feet of center, Big Bar Plot 2, 1940 and 1941, expressed as cankers per acre*

Zone (feet)	Area	Cankers in—		Cankers per acre	
		1940	1941	1940	1941
	Acre	*Number*	*Number*	*Number*	*Number*
0.0–12.5	0. 011	142	493	12, 909	44, 818
12.6–25.0	. 034	27	542	794	15, 941
25.1–37.5	. 056	16	242	286	4, 321
37.6–50.0	. 079	10	92	127	1, 165
50.1–75.0	. 225	4	91	18	409
0–75.0	. 406	199	1, 460	490	3, 596

Table 6 shows that, on the commonly used per acre basis, canker numbers from the presence of but a few small ribes can run high as the result of only one or two moist periods. If the bushes had been larger and scattered, as often happens in nature, resultant numbers of cankers could have been extremely high.

Infections resulting from the 1941 exposure on three Big Bar plots undoubtedly occurred on all those plots during the same moist period and as a result of the dissemination of sporidia during the same phase of northerly wind movement. Logarithmic curves of the infection gradients are quite similar in shape, although the one for Plot 2 sector tapers off less rapidly beyond 100 feet than those for the sectors of the other plots (fig. 19.) The amounts of viable telia differed on the plots, but this difference is reflected chiefly in the intensities per foliage unit for any one zone rather than in the shape of the gradient curve. A curve for the gradient of infection

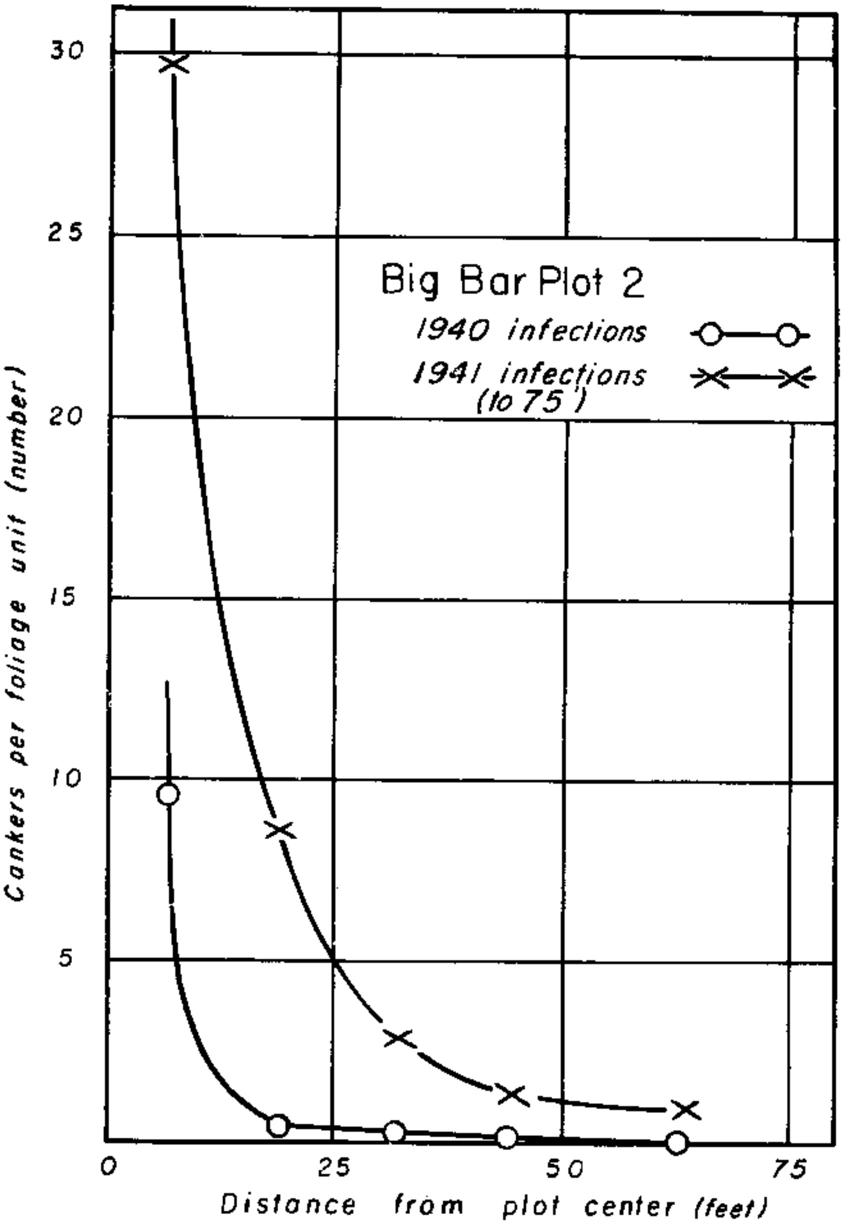

FIGURE 18.—Infection gradient curves for 1940 and 1941 infections on Big Bar Plot 2 expressed as cankers per foliage unit for different distance zones from the plot center.

resulting from the downslope drift of sporidia on Big Bar Plot 4 in 1941 (fig. 20) differs somewhat in form from the northerly gradient on this plot (fig. 19).

In general, the intensity of pine infection should be proportional to the effective spore supply on ribes at the spore source. If the supply of viable spores at a plot center were doubled, the resulting pine infection at any given distance from the central ribes should be doubled under the same infection conditions. The distance of spread, however, does not show this relationship to increased spore supply since infection tends to decrease inversely as the square of the distance from the spore source (*26*). This relation is best clarified by a mathematical equation that fits the particular disease gradient on a plot.

Wilson and Baker (*35*) have developed an equation to express the infection gradient of brown rot blossom blight from *Sclerotinia laxa* Ader & Ruh. spores at a single source to apricot trees in orchard plantings. Their equation was found to express reasonably well the gradients in this study; the equation is

$$Y=\frac{100(1+a)^2}{(X+a)^2}$$

where Y is the intensity of infection, X the distance from the plot center, and a is a constant. The value of a, which determines the slope of the curve, is influenced by the environmental conditions controlling infection and by the location of the initial distance, X_1, with respect to the source. As a criterion for the determination of a, Wilson and Baker propose the condition that the sum of the differences between the observed and derived values should equal zero. The value of a may be calculated according to the following equation:

$$\int_{x_2-\frac{1}{2}\Delta x}^{xn+\frac{1}{2}\Delta x}\frac{100(1+a)^2}{(x+a)^2}\,dx=\sum_{1=2}^{M} yi\Delta x$$

where Yi's are the observed percentages infected and Δx is the interval between x's. Or, a may be obtained by trial and error following a preliminary estimate of a probable near value.

For the curved values of the disease gradient obtained on Big Bar Plot 2 as a result of 1940 exposure (fig. 18), a value for a of 0.05 gave the closest fit; for the gradient on the west 45° of the NE quadrant of this plot resulting from 1941 exposure, a value for a of 0.33 was closest. A 10-foot interval from the plot center was used for X values for the 1940 exposure and a 25-foot interval for the 1941 exposure. For each the intensity of infection, expressed as number of cankers per foliage unit, was considered to be 100 at the first station where $X=1$ and as percentages of 100 at the subsequent stations. For the 1941 exposure the observed value, after curving, at 25 feet (X_1) was 8.5 cankers per foliage unit. With this as the 100 percent value, that for Y at X_2 (50 feet), derived by formula, would be 32.58 percent of 8.5 or 2.77 cankers per foliage unit. Curves for the observed and derived values for the 1941 gradient are shown

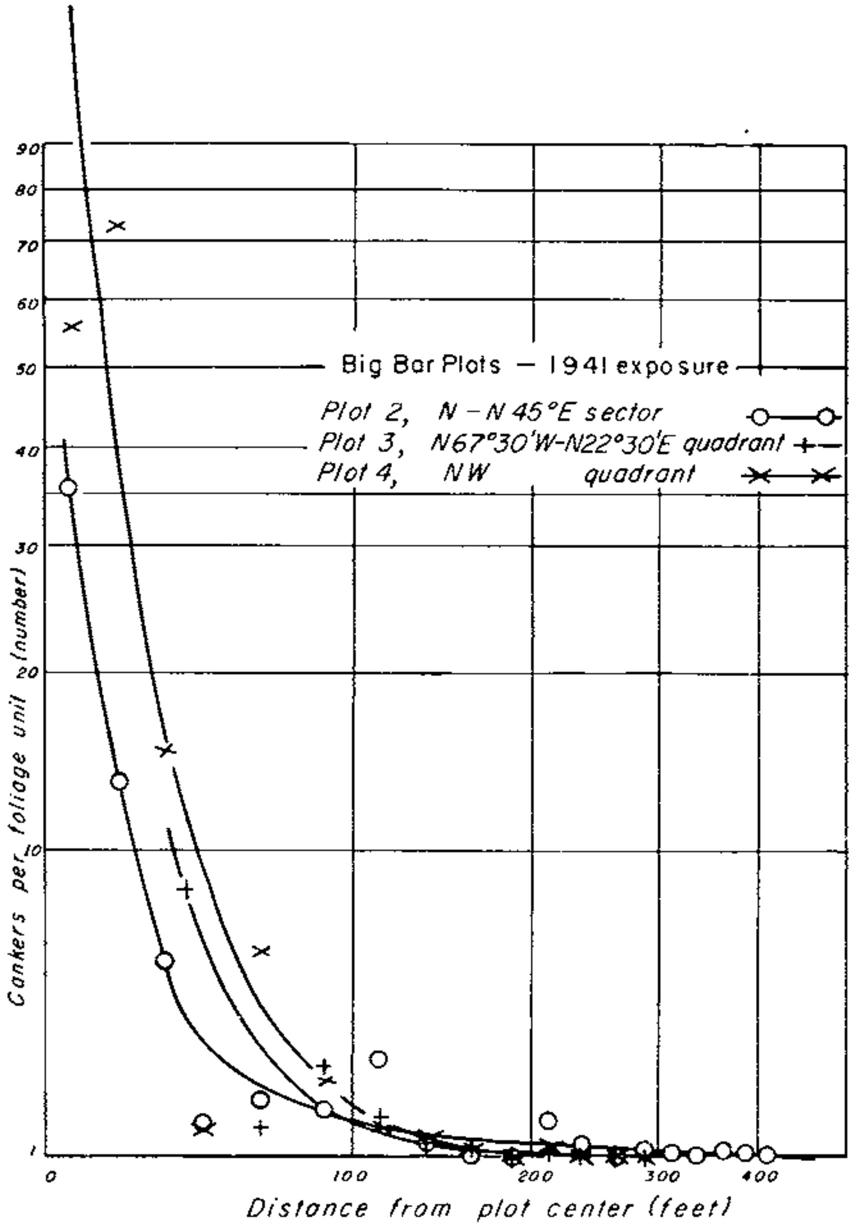

FIGURE 19.—Gradient curves for cankers resulting from northerly drift of sporidia on Big Bar Plots 2, 3, and 4 as a result of 1941 exposure. Curves represent cankers per foliage unit plotted over distance from the plot centers on plot sectors over which the northerly drift occurred.

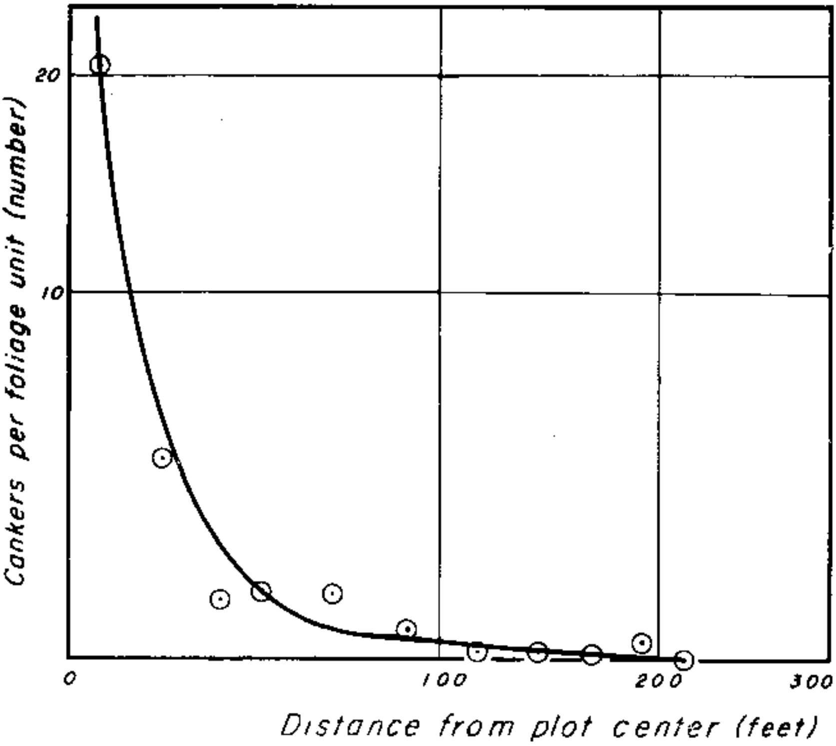

FIGURE 20.—Downslope gradient of cankers per foliage unit on 45° sector, southeast quadrant, Big Bar Plot 4, 1941 exposure.

in figure 21. Both in these and in the curves for the 1940 gradient, not shown, observed gradients terminate more abruptly than the theoretical ones derived from the equations. Wilson and Baker (*35*) have noted this difference in gradients for other diseases.

The observed gradient for 1941 (curve *A*, fig. 21) reaches zero at approximately 425 feet, but the equation (curve *B*) gives an intensity of 0.05 cankers per foliage unit at this distance because of the change in slope as it approaches zero. Accordingly, for determining the approximate limits of infection at other initial intensities by use of the equation, the zero point was considered to be at the distance where the calculated value of cankers per foliage unit reached 0.05. By doubling the intensity at X_1 the equation gives a value of 0.05 at about 575 feet, or 150 feet farther than the limit on the observed curve. For an increase of 10 times in the intensity at the first station, equivalent to increasing the effective spore supply at the plot center 10 times, the 0.05 value would be extended to 1,350 feet. For a steeper gradient, as represented by the infections from the 1940 exposure, increasing the intensity by 2- and 10-fold would increase the limits from approximately 72 feet to 120 and 260 feet respectively. As already noted, actual infection limits can be expected to terminate more abruptly than limits calculated by formula. Thus the outermost infection from the 1940 exposure on Big Bar Plot 2 was approximately 63 feet from the plot center instead of at the 72-foot limit determined by formula.

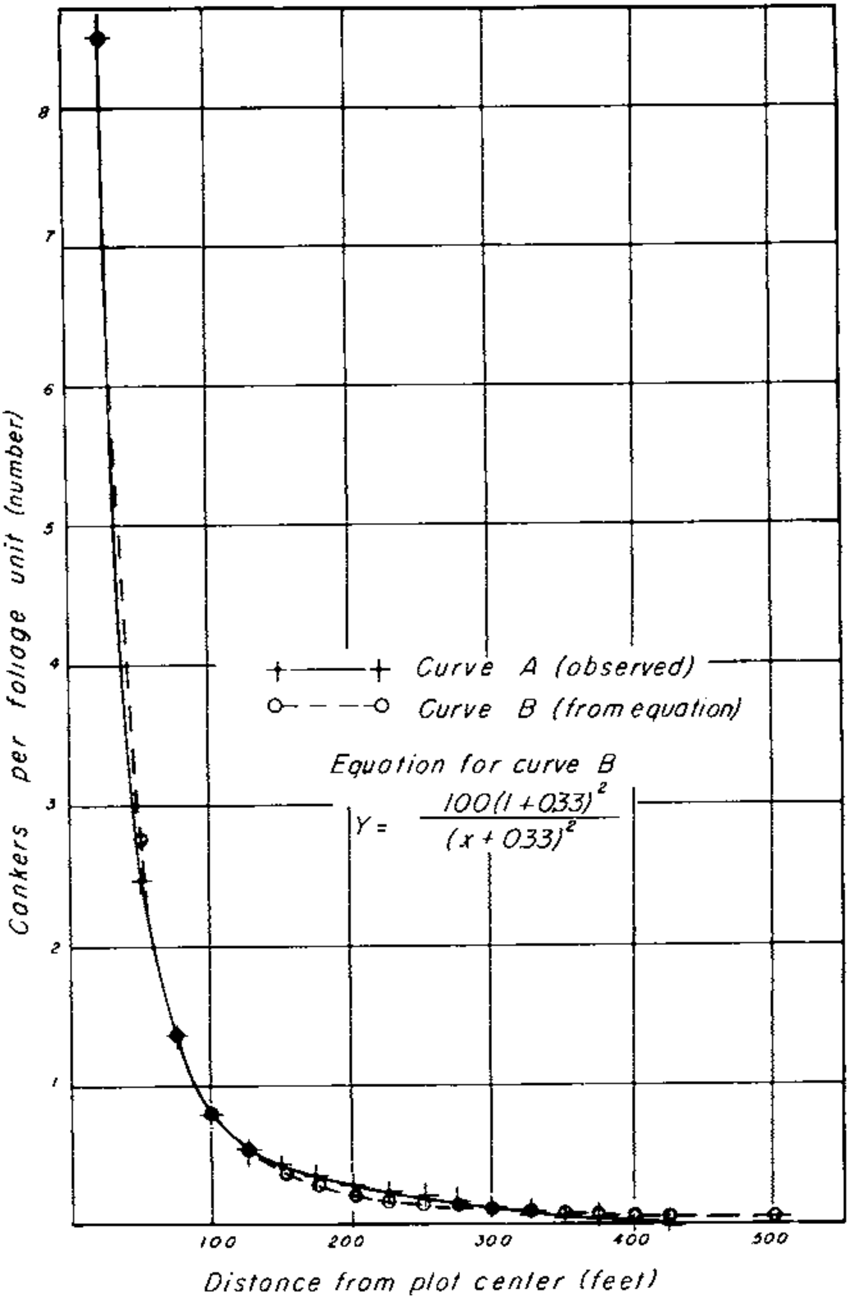

FIGURE 21.—Number of cankers per foliage unit at different distances from the plot center on the sector of Big Bar Plot 2, 1941 exposure. Curve *A* represents values from curve of observed canker numbers, and curve *B* the values derived by means of the Wilson and Baker formula, using a 25-foot interval for x and a determined value of 0.33 for a.

When considering anticipated damage, the extreme limits of infection are usually of less concern than the distance to which appreciable numbers of infections extend. Thus on Big Bar Plot 3 (fig. 14) the most distant infection resulting from the 1941 exposure was at about 280 feet, but the limits of significant infection were in the 175.1 to 200-foot zone where 20 cankers were found, or 0.13 per foliage unit (table 5). In the part of this zone over which infections were found (fig. 14), established cankers were at the rate of 134 per acre on 100 trees per acre—a rate of prospective damage too high to be tolerated, although in the zones beyond the rate of damage was negligible.

Pine Damage

The greatest number of cankers from one year's exposure on a single tree was 90 of 1941 origin on a tree about 10 feet northwest of the center of Big Bar Plot 4. This tree was 5.7 feet tall. Three other trees nearby, but farther from the center, developed 46, 56, and 69 cankers (fig. 22). A tree with a crown length of 3.5 feet, located about 10 feet from the center of Big Bar Plot 2, bore 19 cankers of 1940 origin and 82 of 1941 origin. Infections per tree decreased rapidly with distance from the plot centers. On the Big Bar plots, most infected trees farther than 125 feet from centers bore but one canker each. Exceptions to the general relationship on Plot 2 were traced to a small opening near the ground that provided an air channel through the dense vegetation around the plot center. One small procumbent tree nearly 60 feet from the center along this channel had 30 cankers of 1941 origin.

Most sugar pines on the plots were under 10 feet in height, and most cankers were on lower branches or in heavily shaded or well-protected places where moisture favorable to infection was retained longer than on exposed foliage. Near the plot centers, nearly all cankers were less than 5 feet from the ground. At greater distances from the centers, the average height from the ground tended to increase although not in any regular relationship with distance. About 85 percent of all cankers were within 5 feet of the ground, and less than 1 percent were more than 10 feet above ground. The highest canker was 25 feet from the ground in a tree 175 feet from the plot center. No figures were obtained on the percentage of foliage target at the different heights.

Because so many of the cankers were on the lower and longer branches, which are liable to early suppression, nearly half of all cankers formed were rated as nonkilling. These judgments on probable mortality were based almost entirely on experience with the rust in western white pine, because no similar basis of experience was available for sugar pine. Although field observations since then indicate that too few cankers were rated as the killing type, the ratings should suffice for comparisons. Even as originally rated, the percentages of killing cankers in these sugar pine tests are much higher than those reported by Buchanan and Kimmey (*5*) for western white pine in British Columbia.

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FIGURE 22.—Sugar pine 3.9 feet tall about 17 feet northwest of the center of Big Bar Plot 4 in 1943. Tags mark locations of 69 cankers from the 1941 exposure.

The sugar pine ratings show that plots in the same area and for the same season may differ widely in the percentage of killing-type cankers developed. For example, Black Rock Plots 2 and 4 in 1936 had 35 and 71 percent of killing cankers, respectively; Big Bar Plots 1 and 2 in 1940 had 85 and 43 percent, respectively (table 7). In these instances the influence of weather can be dismissed as a source of difference between two plots in the same area, since weather must have been similar on both. The source must be looked for in either the character of the exposed pines on the respective plots or the density of the plant communities in which the pines grew.

The relatively low percentage of killing cankers on Big Bar Plot 2 in 1940, for example, is attributable to the concentration of infections on lower branches around the plot center where most of the sugar pines occurred in dense thickets. In these thickets the small lower branches were subject to rapid suppression and as a result many of them were very slender, with living foliage only at the tips. Many of the cankers originating in this foliage were expected to die with the branches before the rust could grow into the main stems. In contrast, Plot 1 was very open around the center; thickets in the path of the drifting sporidia beyond the central opening were less dense, and the individual tree branches more thrifty. The difference in percent of killing-type cankers between Black Rock Plots 2 and 4 is also traceable to the greater prevalence of suppressed branches on pines near the plot center on Plot 2.

In general, the greater the distance from the plot center, the larger the percentage of killing cankers, as illustrated by the percentages for the Deadhorse-Big Bar group of plots (fig. 23). For the Black Rock group of plots, the increase in percentage of killing cankers with distance from the plot center was less pronounced.

TABLE 7.—*Total and killing-type blister rust cankers developed from 12 exposure tests, 1936–41, as judged when tallied 2 to 3 years later*

Study area and plot number	Year of test	Total cankers produced	Total killing-type cankers produced [1]	Killing-type cankers produced [1]
		Number	*Number*	*Percent*
Black Rock:				
1	1936	30	14	47
2	1936	43	15	35
3	1936	10	5	50
4	1936	17	12	71
Deadhorse:				
3	1938	32	18	56
4	1940	11	6	55
6	1940	6	3	50
Big Bar:				
1	1940	47	40	85
2	1940	199	86	43
2	1941	1, 565	811	52
3	1941	211	183	87
4	1941	1, 143	544	48
Total and mean percent		3, 314	1, 737	52
Mean of plot percents				57

[1] Field observations after the ratings on these cankers were made indicate that the numbers rated "killing type" were probably too low. The mean percent of killing-type cankers probably should have been about 76 instead of 52 percent.

Both vegetation density and weather may influence the number of killing cankers. Moisture tends to be retained longer on foliage of pines in dense thickets than in open stands. When moist periods are marginal in duration for pine infection, most infections take place in the dense thickets and few in the open stands. Part of those in the dense thickets die before entering the main stem, but the number of killing cankers remaining is still higher in the thickets than in the open. Longer moist periods permit infection in the open as well as in thickets, and a higher overall percentage of killing cankers results. For an individual canker, the higher its point of establishment on a tree, the greater its likelihood to be a killing canker.

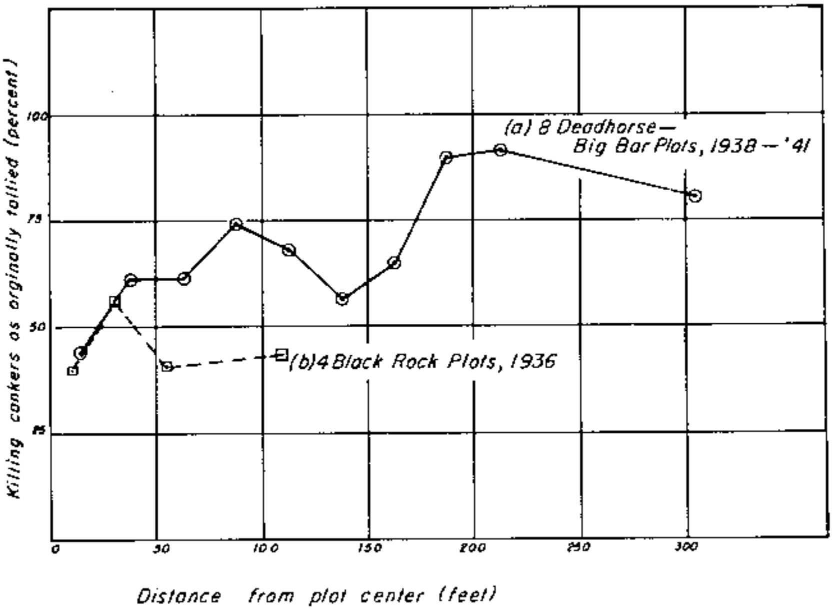

FIGURE 23.—Trends of killing-type cankers at different distances from plot centers for (*a*) 8 Deadhorse-Big Bar plots, 1938–41; (*b*) 4 Black Rock Plots, 1936.

Nonkilling cankers should not be classed as harmless, because most of them produce aeciospores before their death, thus aiding in perpetuation and spread of the rust.

The number of nonkilling cankers on the Big Bar area would have been greater had it not been for the exceptionally rapid canker growth that occurred there. Some branch cankers were 6 inches or more in length, and some stem cankers 8 inches or more, when cut out the second year after their origin. Most of the cankers were in "incipient" or "juvenile" stage the first year after infection, and nearly all of them produced pycniospores the second year. This rate of development is much faster than that at most locations in the West where canker growth has been observed. Usually the "juvenile" stage occurs the second year, and the pycnial stage occurs the third year following pine infection. Rapid canker growth and development readily permitted the separation of cankers of 1940 origin from those of 1941 origin in Big Bar Plot 2. On Damnation Plot 1, on the other hand, the growth and development of cankers was slower, and cankers of 1937 origin could not be readily distinguished from those of 1938 origin.

Omitting the infections on Damnation Plot 1, 826 trees were infected in all the tests, of which at least 85 percent, by revised estimates, would have been killed; 452 trees, or well over half of the total number of trees infected had but one canker each. Of these, over 75 percent would eventually have been killed.

The greatest damage possible from the cankers established around any one plot center in a single season would have been the killing of about 280 trees from infections established in 1941 on Big Bar Plot 2.

Although this damaging infection resulted from rust on four very small *Ribes nevadense* with but 7 feet of live stem, their leaf area was the equivalent of that on about 20 feet of normal live stem. These plants were replacements that had been grown for a time in the greenhouse before being moved out of doors, and their concentration of foliage was not typical of plants in the open. Also, they had been artifically infected in a moist chamber in late summer at a relatively cool location and had produced teliospore columns of nearly uniform age and apparently in prime germinative condition at the time of the October moist period. Abundant germination of the teliospores resulted. The resultant pine infection, therefore, is probably close to the maximum likely to be suffered from an equivalent footage of normal live stem of rust-bearing *R. nevadense* under natural conditions in California.

For not more than two effective moist periods and only a limited footage of ribes at a plot center, this amount of kill is high; if it represented effective damage to the stand, it would indeed have serious implications. Meinecke (*17*), in a discussion of the evaluation of loss in stands of reproduction attacked by rust, pointed out that only where losses of trees bring about a reduction in desirable stocking can the effect on a stand be regarded as damaging. But the nature of the thinning brought about by the rust should be taken into account. The killing of trees in thickets does not always result in thinning of a desirable type. Ideally, only the weaker trees should be removed, leaving most of the dominants as crop trees. When rust attacks a dense stand, cankers that become established in the most vigorous trees are the ones most likely to persist until they become killing. Thus, the rust would leave an undesirably high percentage of suppressed trees to form the future stand.

In a more open stand with a high percentage of dominants, even a moderate degree of future loss from cankers established during a single season, if repeated at intervals of a few years, might well reduce sugar pine stocking to an uneconomic level (*33*) before the trees could reach merchantable size.

Disregarding Damnation Plot 1, 20 tests resulted in the formation of one to many cankers. On these test plots an average of 820 sugar pines was present on the central acre. However, a central circular acre does not provide a reliable measure of damage per acre from a single source in the sugar pine region, because patterns of spread, as judged by the distribution of infections, are seldom circular.

To obtain an acreage figure corresponding more closely to actual patterns of spread, the acreages covered by the actual distribution of infected trees in eight tests, as diagrammed in figures 9 to 15 were calculated. The limits of sporidial drift usually follow a rounded outline rather than the angular patterns shown on the diagrams. By rounding off these patterns, it was concluded that on the average about 20 percent should be added to the derived acreages to approximate the probable effective dispersal limits. The addition resulted in exposed acreages for the different tests ranging from 0.28 acre for Deadhorse Plot 6 in 1940 to 3.56 acres for Big Bar Plot 2 in 1941. The average for the eight tests was 1.11 acres on which the revised expected mortality in the sugar pine reproduction averaged about 10 percent per acre from 28 feet of live stem or its equivalent at the plot centers. This loss is entirely too high to be tolerated, even though occurring only at intervals of several years or longer; it would eventually result in the virtual elimination of the sugar pine in the exposed area.

Of 11 tests with *Ribes nevadense*, only 2 gave negative results. Three of the positive tests (all on Damnation Plot 1) were unusable. In the other 6 tests, 587 pines were infected from a total of 61 feet of live stem, the estimated equivalent of 87 feet on normal bushes. This would be about six trees infected for each foot of normal live stem present for a single year of exposure. Pines were infected to a maximum distance of 410 feet from the central ribes.

Of 43 tests with *Ribes roezli*, 29 were negative. In the 14 positive tests, a total of 239 pines were infected from 325 feet of live stem, or less than 1 tree for each foot of live stem present, during a single year of exposure. Maximum spread to pines was 285 feet. These results are in accord with previous conclusions regarding the relative pine-infecting potentialities of equal units of these two ribes in the presence of an aeciospore supply adequate for initial infection (*15*).

The negative results on the plots with *Ribes cereum* at the center support previous evidence (*13*, *16*) that the form of this species in the northern part of the sugar pine region will not ordinarily present much hazard to associated sugar pines. Kimmey and Miekle (*16*) have shown, however, that the species may be somewhat less resistant in the southern Sierra Nevada.

Although the present studies confirm earlier observations that *Ribes nevadense* can cause much more damage per unit of live stem than *R. roezli*, the prevalence of *R. roezli* renders it the more important host plant regionwide. In unprotected stands in northern California, rust damage to date has been almost entirely from *R. roezli* or its near relative *R. cruentum* and only a minor part from *R. nevadense*.

DISCUSSION

Pine infection in the northern part of the sugar pine region, as demonstrated by the plots, was erratic even when special efforts were made to provide a supply of viable telia at the plot centers. If infection methods at the centers had been as uncertain as methods approximating natural exposure of ribes used in British Columbia and Oregon tests (*5*, *13*, *21*), pine infection would have been still more limited and erratic. Where infection resulted, it was sometimes under quite marginal conditions, as demonstrated in 1940 on the Deadhorse and Big Bar areas where infection occurred on only two out of three plots although telia were present at three plot centers on each area.

Nevertheless, numerous cankers developed on Big Bar Plots 2, 3, and 4 from the 1941 tests with small amounts of rust-bearing ribes live stem. The high susceptibility of sugar pine is a significant factor in these variable results. Thus the potential for heavy damage to sugar pine is present wherever susceptible ribes and pine grow in situations comparable to those on the test plots. The uncertainty lies in how frequently serious damage may occur.

Frequency of Infection Weather in the Sugar Pine Region

Among the eight stations whose weather records were studied (fig. 1), five—beginning with Prospect, Oreg.—are within the sugar pine region. A decrease can be noted among these stations from north to south in the incidence of days with measurable precipitation during the months June to September inclusive, at least for as far south as the Big Creek Powerhouse station in the southern Sierra Nevada. The difference in incidence between the Prospect, Oreg., station and the California stations is particularly noticeable.

Although these records provide some measure of the possibilities for the intensification of rust on ribes from rains in the sugar pine region during the summer, they are not well adapted for judging the chances for pine infection. Field scouting experience in the sugar pine region and published observations such as those by Kimmey (*15*) at northern California locations have demonstrated that few telia are formed on infected ribes before August 1 south of the summit of the Siskiyou Mountains, roughly paralleling the Oregon-California border. North of this summit, telium formation may begin a little earlier; in some years moderate numbers may be formed during July although even in such seasons most of the telia appear later. Infrequently a limited amount of pine infection may take place during July in favorable locations in the Siskiyous and northward, but for the sugar pine region as a whole pine infection before August is not significant.

The quantity of telia present normally reaches a peak during August (*15*), but August is often the driest month of the year (fig. 1). Chances for pine infection then are extremely small, even without considering the possible limiting influence of temperature on teliospore viability at that time of year. Nevertheless, August 1 can be considered the beginning of the season for pine infection in most of the sugar pine region even though the probability for it at that time is low.

The end of the infection season depends on temperatures and on the ribes species concerned. *Ribes roezli*, which makes up about 90 percent of the ribes population associated with sugar pine in the Sierra Nevada, loses nearly all of its telium-bearing leaves by late October. On *R. nevadense*, the other principal species associated with sugar pine, telium-bearing leaves persist later in the season, but after October 20 temperatures accompanying moist periods are likely to be low, often with part of the precipitation falling as snow. At these low temperature levels, moist periods seldom last long enough to permit pine infection. Not only does *R. nevadense* occur in less than one-tenth the numbers of *R. roezli*, but it is very much more limited ecologically in occurrence, being confined largely to moist locations. Moreover, in districts frequented by livestock it is often heavily grazed, whereas *R. roezli* is ordinarily not touched. Thus *R. nevadense* offers a hazard to a very much smaller percentage of the sugar pine population than does *R. roezli*. Several other wild currant species that occur as associates of sugar pine in limited portions of the region hold telium-bearing leaves in a manner comparable to *R. nevadense* and may be included with it with respect to the duration of the season of infection.

The infection season for the sugar pine region as a whole, then, may be regarded as August 1 to October 20. In localized parts of the region the season may extend to the end of October. As nearly as could be judged, most of the infection obtained on the test plots became established during September or the first half of October.

No infection appeared to have occurred in August. However, in the occasional years when favorable moist periods do occur during August, pine damage can be heavy if preceding conditions for rust intensification on ribes have been good (*15*).

Because pine infection depends on so much more than the daily amounts of precipitation, it has generally been conceded that precipitation records alone are insufficient for judging the incidence of periods favorable for pine infection (*19*). However, where precipitation is as infrequent as it is during the early fall in the sugar pine region, the records of its occurrence as reported in the Climatological Data sections by the United States Weather Bureau can yield useful comparisons. The comparisons may be based either on the incidence of periods during which infection might be possible or on seasons so dry that no probability of infection exists.

The incidence of favorable periods over the 30 years 1927–56 was compared for six selected Weather Bureau stations at different latitudes within the sugar pine region (fig. 24). The criterion selected was periods when rain falling on 2 successive days aggregated 0.30 inch or more. This criterion probably represents minimum conditions for pine infection. The requirements of rain on 2 successive days was adopted to eliminate the occurrence of moisture from rapidly moving cold-front storms and thunderstorms; neither type is likely to produce high air humidities for periods long enough to permit pine infection.

If the soil has been wet by previous rain, it is sometimes possible for infection to occur with less than 0.30 inch of rain, as may have happened on Big Bar Plots 2 and 4 in 1941, but such occurrences will be offset by periods in which more than 0.30 inch falls without producing infection or only an occasional canker, as happened in 1942. Each 2-day period with the requisite rainfall was tallied separately. Thus 4 successive days with rain of more than 0.30 inch for each pair of days were tallied as two periods, whereas from an infection standpoint they would constitute only a single long period. Few cases of this sort were encountered.

The incidence of possible favorable periods was much higher at the Prospect, Oreg., station than at any of the California stations, and the incidence decreased with latitude within California (fig. 24). Also of note is the higher incidence of favorable periods during the last decade at Prospect and Mount Shasta than during previous decades. The opposite relationship existed at Giant Forest. The relative dryness of the 1947–56 decade in the southern Sierra may help to explain the lack of known extension of the rust southward in the Sierra Nevada in recent years. In figure 24, it must be kept in mind that the criterion of comparison represented probably minimum conditions for infection: actual favorable periods would be almost certain to occur less frequently than indicated in the graph.

The selected stations may also be compared as to number of seasons in which no pine infection could be expected to become established owing to unfavorable moisture conditions. Below are listed the number of seasons in which no periods of 2 consecutive days with 0.30 inch or more of rain occurred between August 1 and October 20 inclusive:

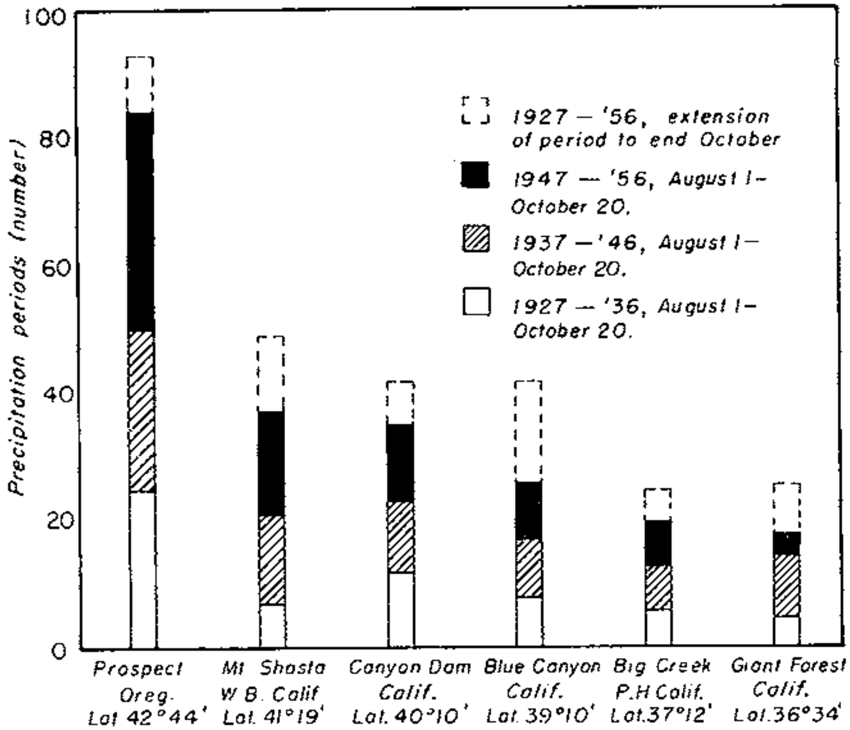

FIGURE 24.—Periods by decades, 1927–56, at 6 stations in the sugar pine region, for season August 1–October 20, inclusive, when precipitation for two successive days aggregated 0.30 inch or more. Column extensions show total periods if season is lengthened to the end of October. Stations are in north to south order.

Station	*Seasons (number)*
Prospect, Oreg.	0
Mt. Shasta W. B., Calif.	10
Canyon Dam, Calif.	12
Blue Canyon, Calif.	13
Big Creek Powerhouse, Calif.	16
Giant Forest, Calif.	18

In other words, at Giant Forest 18 seasons out of 30 were too dry to allow any possibility of pine infection until after October 20, whereas at Prospect, Oreg., no such dry seasons occurred in the same 30 years. This statement applies to moisture conditions for pine infection only. Some seasons in the sugar pine region will be unfavorable for the establishment and intensification of blister rust on ribes even though they occur in years when fall moisture conditions would favor pine infection. The number of seasons at each station in which pine infection is unlikely will thus be greater than suggested by the tabulation.

The chief purpose of these comparisons is not to provide a basis for estimating the probable number of seasons in which pine infections could be expected to occur. Rather, the comparisons indicate that the probabilities decrease with latitude within the sugar pine region and that this trend has been especially marked within the 1947–56 decade.

The comparisons likewise do not reflect local differences in blister rust hazard at any particular latitude within the region—differences referable to host susceptibility or to the influence of altitude, topography, distance from the coast, and soil moisture. These conditions may have a strong effect locally on hazard. From these combined effects and that of latitude it is safe to say that as great and perhaps even greater diversity in blister rust hazard may be expected within the sugar pine region than within the commercial range of any other species in the white pine group in North America. The existence of this diversity is already being borne out by actual field developments in rust infection within the region.

Application to Control

Mention has been made of the difficulties encountered in establishing and maintaining a supply of rust at the plot centers in these tests. Experience gained in the study, coupled with field observations to date, strongly indicate that the rust hazard for any particular season or location in the sugar pine region will depend greatly on opportunities for the maintenance and intensification of rust on ribes during summer and early fall. For sugar pine stands in general, this factor is probably more important in determining the rust hazard for any particular year than the occurrence of fall rains suitable for pine infection.

Intensification depends on moisture in some form. Summer rain is so uncommon and erratic in the California part of the sugar pine region that only occasional seasons provide much opportunity for rust intensification on ribes from it. Summer fogs are practically nonexistent. In seasons when rainfall is lacking, the rust hazard is restricted to locations where dews or spray from turbulent mountain streams have provided free moisture on ribes leaves.

Field evidence is accumulating that dew is a key factor in determining the degree of rust hazard in California. The generally low humidities prevailing favor high heat losses through radiation at night, which in turn promote the formation of dew on open, low ground where the cold air tends to accumulate. It may be expected around meadows, in stream bottoms, or on flats, and can cause heavy rust intensification on ribes even in the complete absence of summer rain.

The effect of dew in maintaining rust should be distinguished from the influence of soil moisture. Locations with higher than average soil moisture, such as along streams and around springs, seeps, and the edges of meadows have long been recognized as areas of high rust hazard. Moist soil favors ribes regeneration and strong growth, the retention of foliage in a vigorous condition, and, for species such as *Ribes roezli* that continue growth through the season under favorable conditions, the continued production of new foliage. It also favors the presence of moisture-loving species, such as *R. nevadense*. Evaporation from moist soils and from plants on them causes an appreciable cooling of contiguous air layers immediately above (*8*). This cooling not only favors dew formation at night, but also tends to reduce maximum daytime temperatures during hot spells, which aids in the retention of teliospore viability. Moist spots usually occur in the same locations that favor dew formation, and so soil moisture and dew work together to enhance the rust hazard.

The years covered by the tests apparently did not include any in which climatic conditions were exceptionally favorable for rust on the test areas. On the basis of the Zentmyer-Wagener climatic comparison already mentioned, 1925 was apparently a highly favorable year over most of the sugar pine region, although field confirmation was impossible since the rust was not then present in sporulating condition on pine in California or southern Oregon. No equally favorable season seems to have occurred since 1925. Accordingly there has been no opportunity to learn what such a season might produce in the way of pine damage in the region. Years with rains more frequent than usual during the dry season probably cannot be expected more often than years of extreme drought, but their recurrence at wide intervals can be expected. Considering the high average susceptibility of sugar pine and ribes hosts, such a year might result in widespread damage to pine where ribes are present in nonprotected pine stands.

The tests failed to provide a sound basis for judging the frequency and extent of pine damage on ridgetops, upper slopes, and under an overstory of larger trees even though most of the test plots represented such sites. Conditions for dew formation are less favorable in such locations than on open low ground, and rust intensification on ribes is more dependent on other forms of moisture. The plots provided evidence that heavy pine damage may result on ridges if viable rust is present on ribes at the time of fall rains, but it seems doubtful whether any material pine infection would have occurred on them under natural conditions for rust development on ribes in the test years.

Results on the Big Bar plots in particular demonstrate the strong influence that stand density of young sugar pines may have on infection probabilities by influencing water retention by the foliage. Any other local environmental niches where the evaporative effects of sun and wind are minimized should be rated as places of higher infection hazard than average for the stand as a whole. Narrow ravines and well-protected and shaded north banks fall in this category.

The spread patterns obtained on the plots indicate that in the sugar pine region the infection pattern from a central source of sporidia will almost always be irregular and that in California the chief movement of rust sporidia from infected ribes will be either in a northerly direction or downslope. However, local air turbulence may cause some dispersal to a short distance in all directions from the place of origin. Downslope drift is more certain to take place than carriage northward by southerly storm winds, but when northerly movement occurs it will ordinarily provide effective dissemination of sporidia to a greater distance than down the slope in cases where the respective directions for each do not coincide. These conclusions have application in decisions regarding the location and width of protective strips around sugar pine stands.

Four questions were listed in the introduction as examples for which answers were needed at the time that these studies were begun. From what has been presented, it should be evident that the test results have provided no single simple answers for most of the questions and that any such answers that might be deduced would be of limited usefulness.

On the question of rust hazard to surrounding pines presented by a ribes bush missed by eradication crews, it seems certain that the hazard offered will depend very much less on the feet of live stem present than on the location of the bush—geographical, altitudinal, topographical, and environmental. Because of climatic differences, a bush in southern Oregon presents a greater hazard than one in the central Sierra Nevada; one at 5,000 feet elevation more than one at 3,500 feet; one in a stream bottom or on a meadow edge more than one a ridgetop or slope; one in half shade more than one in full sun; one on a north slope more than one on a south slope. Even soil type and local competition for moisture influence the hazard. On the basis of the minimum criterion for infection used in figure 24, about 40 percent of possibly favorable periods occur before October 1 at the California stations, and many of these periods come during the last week in September. It follows that bushes that lose their leaves before October, as a result of either dry soil conditions or cold, offer very little rust hazard, especially since infected leaves are among the first to be shed.

In the tests *Ribes nevadense* caused approximately six times as much pine damage per foot of live stem as *R. roezli*, but this ratio would not be likely to hold for bushes of the two species missed in control operations. *R. nevadense* does not become infected as readily from a distant aeciospore source as *R. roezli*. Heavy infection on *R. nevadense* usually occurs only when it is close to an abundant spore source on pines. Bushes missed in a control unit would not ordinarily be close to such a source, and the chances for becoming infected would thus be less for *R. nevadense* than for *R. roezli*. This difference in susceptibility could well offset the difference in potential hazard offered by heavily infected bushes of the two species.

Through 1958, the most southerly location where blister rust on pine had been found in the sugar pine region was on the Stanislaus National Forest at approximately latitude 38°10′.[10] No farther southward spread has been discovered in several years, nor had any appreciable local extension of the rust occurred around the most southerly infection centers up to the time of their discovery.

Progress of the rust southward since 1945 has been much slower than originally anticipated; some control workers have suggested that this status may continue, with prospects that sugar pines in the southern Sierra may indefinitely escape damage. From the records of moisture conditions summarized in figure 24, we can expect that chances for infection will be less frequent in the southern part of the sugar pine region than farther north. Aside from the less frequent possibilities for infection, however, there is nothing in this analysis to suggest that conditions will not occasionally be favorable for pine infection in the southern Sierra Nevada. The analysis indicates only that progress of the rust southward from its current limits, and local intensification after establishment there, can be expected to be slow and irregular.

A single control standard for the entire region—whether in terms of ribes live stem per acre, width of protective zone, or other reason—does not seem possible, for several reasons: the wide differences from north to south within the sugar pine region in the incidence of climatic conditions favorable for white pine blister rust, the irregular occur-

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[10] MacGregor, Neil J. Annual report on the control of white pine blister rust in California for the calendar year 1958. U.S. Dept. Agr., Forest Serv., California Region, 9 pp. 1958.

rence of these favorable conditions, the pronounced local differences in hazard potential, and the narrow line between conditions producing no damage and those resulting in heavy damage. This has already become evident in actual protection experience within the parts of the region already invaded by the rust. In consequence a series of control standards has been set up corresponding to the hazard judged to be present on the tract to be protected.

In other regions where blister rust is a threat to five-needled pines, it has been recognized that infection obtained during an average year climatically is of only minor value in indicating the degree of control that will be required for satisfactory protection. It is the occasional "bad" year that determines control requirements. The indications are that this principle will apply with even greater force in the sugar pine region because of the low frequency of years exceptionally favorable for the rust. Accordingly, many years may elapse before we can be certain what the ultimate control requirements will be for all parts of the region.

So far as can be seen, destruction of ribes will continue to be a keystone of blister rust control in sugar pine even if other control treatments, such as by the use of antibiotics, prove feasible. However, evidence now available suggests that greater economy in control can probably be achieved by fitting ribes control measures to the local environment with greater selectivity in application than in the past. The unit-area concept of Dunning (*10*) for the silvicultural treatment of pine and mixed-conifer stands in California may prove useful in an adapted form in the application of such measures.

SUMMARY

Rains become less frequent and the summer dry period more pronounced with decrease in latitude in the white and sugar pine regions of the Pacific Slope. To provide an index of the pattern and distance of spread of white pine blister rust from principal ribes hosts to sugar pine, field tests were conducted between 1935 and 1950 at two locations in southern Oregon and four in California. A total of 56 tests were made on 21 plots at these locations from rust developed on *Ribes roezli*, *R. nevadense*, and *R. cereum*. Three tests were also made during one season of the infective potential of rust on fallen leaves of *R. roezli*. Plot observations were continued until all resulting pine infection had had an opportunity to develop.

Even though special efforts were made to retain rust on ribes at the plot centers, no pine infections resulted in 34 tests, or 60 percent of the total. Most of these failures were attributable to lack of favorable moisture conditions or to the premature shedding of infected leaves from *Ribes roezli*. In about one-third of the total negative tests, the reasons for the failure of pine infection to occur were not evident: low temperatures during moist periods may have been involved.

Of the 43 tests with *Ribes roezli*, pine infections resulted in only 14, whereas out of 11 tests with *R. nevadense* 9 were positive, of which 6 were usable to determine spread. All three tests with *R. cereum* were negative, as were the three with fallen, rust-bearing leaves of *R. roezli*. In the 14 positive tests with *R. roezli* 239 pines became infected from 325 feet of live stem, or less than 1 pine infected per foot of live stem. In the 6 usable tests with *R. nevadense*, the total number of pines infected was 587 from an equivalent of 87 feet of live stem, or over 6 infected trees per foot of normal live stem. This represents average infection for a single year of exposure.

Infection patterns from a single source of sporidia in the sugar pine region are almost always irregular. The most prevalent directional trend in the tests was downslope, probably from drift during the night hours. In four tests in California, however, pronounced spread occurred in a northerly direction, indicating carriage of sporidia by the south winds usually prevailing during storm periods. Northerly spread was to greater distances than the spread downslope.

The maxium intensity of infection obtained, expressed as number of cankers per acre, was 3,596 within a 75-foot radius of the plot center. Intensities expressed as cankers per foliage unit were variable, depending on the amount of viable rust at the plot center and more particularly on the character and duration of the moist period permitting infection. When plotted according to distance from the plot center, however, the infection gradients produced curves of similar form that could be closely represented by formula. Gradients in the direction of storm winds were less steep than downslope gradients. The maximum probable distance of infection for any given volume of rust at a center under a particular set of weather conditions may be approximated by a suggested formula.

Because of irregular infection patterns, circular plots are not satisfactorily adapted for gaging damage from white pine blister rust on an areal basis in the sugar pine region. Areas over which infection actually occurred, plus a 20-percent border allowance, averaged 1.11 acres per test for eight tests. On these areas expected pine mortality was about 10 percent, too high a loss to be tolerated periodically in the growing of sugar pine.

Ribes roezli sheds infected leaves prematurely, and in the northern Sierra Nevada it shows great variability in susceptibility to blister rust. *R. nevadense* holds infected leaves well; its susceptibility to rust, although only moderate in degree, is quite uniform. *R. nevadense* proved to be 5 to 10 times as potentially dangerous per unit of live stem as *R. roezli* as a source of pine damage. However, the prevalence of *R. roezli* in the region makes it the more important of the two with respect to hazard to sugar pine. To date it has been the source of almost all natural pine infection found in the Sierra Nevada.

Moisture conditions considered to be a probable minimum for pine infection—rain aggregating 0.30 inch over a 2-day period—were compared for the 30 years 1927–56 at six selected stations in the sugar pine region. The number of favorable periods decrease with latitude, from 84 at Prospect, Oreg., to 18 at Giant Forest, Calif. Years which provided no such favorable periods for pine infection increased in incidence at the selected stations from none out of 30 at Prospect to 18 out of 30 at Giant Forest.

Because of the wide differences in environmental conditions within the sugar pine region, the ultimate economy in control will probably be achieved by fitting control measures to the local environment.

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APPENDIX

TABLE 8.—*A summary of all ribes-to-pine spread tests and their resultant pine infection, Oregon and California, 1936–47*

Study area and plot number	Ribes at plot center				Sugar pines on central acre		Resultant pine infection			
	Species	Live stem	Plants		Trees	Foliage units [1]	Cankers	Maximum spread to pines	Pines infected	Pines expected to be killed
			No.	Type						
1936										
Black Rock:		*Ft.*			*No.*	*No.*	*No.*	*Ft.*	*No.*	*No.*
1	*nevadense*	5	2	Potted	2,026	981	30	119	27	13
2	do	10	4	do	1,447	895	43	60	30	12
3	*roezli*	10	4	do	1,472	534	10	138	8	4
4	do	4	2	do	960	613	17	100	14	10
1938										
Black Rock:										
5	*cereum*	18	3	Planted	2,323	1,379	0			
Siskiyou:										
1	*roezli*	11	6	Potted	1,079	983	1	18	1	1
Damnation:										
1	*nevadense*	72	3	In situ	73	120	(2)	(2)	(2)	(2)
2	*roezli*	23	6	Planted	698	(3)	8	120	8	7
3	do	23	6	do	1,706	(3)	0			
Deadhorse:										
1	do	15	5	do	465	(3)	4	35	3	2
2	do	(4)	(4)		534	(5)				
3	do	14	4	Planted	385	351	32	165	23	16

1939

Black Rock:										
1	*nevadense*	15	3	Potted	2, 013	1, 368	1	88	1	1
2	do	30	4	do	1, 443	1, 275	0	------	------	------
3	*roezli*	14	5	do	1, 469	748	0	------	------	------
4	do	6	3	do	954	865	0	------	------	------
Damnation:										
2	*roezli*	31	7	6-planted 1-potted	698	(3)	0	------	------	------
3	do	35	7	6-planted 1-potted	1, 705	(3)	0	------	------	------
Deadhorse:										
1	do	23	5	Planted	465	723	0	------	------	------
2	do	23	5	1-in situ 2-planted 2-potted	534	345	0	------	------	------
4	do	40	5	Planted	401	279	0	------	------	------
5	do	41	4	do	578	562	0	------	------	------
6	do	22	4	do	249	273	0	------	------	------

1940

Black Rock:										
5	*cereum*	86	8	Planted	2, 323	(5)	0	------	------	------
Damnation:										
1	*nevadense*	------	3	In situ	73	(5)	(2)	(2)	(2)	(2)
2	*roezli*	31	7	6-planted 1-potted.	698	(5)	0	------	------	------
Deadhorse:										
3	do	41	7	2-planted 5-potted.	385	400	11	92	9	6
5	do	36	7	Potted	578	(5)	0	------	------	------
6	do	45	7	1-planted 6-potted.	249	292	6	170	6	3
Big Bar:										
1	do	30	2	In situ	436	190	47	210	28	25
2	do	35	3	1-in situ 2-planted.	743	398	199	65	65	35
3	do	15	2	In situ	375	(5)	0	------	------	------
4	do	25	4	1-in situ 3-potted.	947	(5)	0	------	------	------

See footnotes at end of table.

TABLE 8.—*A summary of all ribes-to-pine spread tests and their resultant pine infection, Oregon and California, 1936–47*—Continued

1941

Study area and plot number	Ribes at plot center				Sugar pines on central acre		Resultant pine infection			
	Species	Live stem	Plants		Trees	Foliage units [1]	Cankers	Maximum spread to pines	Pines infected	Pines expected to be killed
			No.	Type						
		Ft.			*No.*	*No.*	*No.*	*Ft.*	*No.*	*No.*
Damnation:										
1	*nevadense*	60	4	3-in situ 1-potted	70	(5)	(2)	(2)	(2)	(2)
2	*roezli*	9	4	Planted	698	(5)	2	150	2	1
3	do	12	3	do	1,697	(5)	0			
Deadhorse:										
1	do	24	5	do	465	(5)	1	28	1	1
2	do	(4)	(4)		533	(5)	0			
4	do	(4)	(4)		401	(5)	0			
Big Bar:										
1	do	35	2	In situ	436	(5)	0			
2	*nevadense*	7 [6] 20	4	Potted	743	475	1,565	410	307	255
3	*roezli*	24	3	In situ	375	299	211	285	69	60
4	*nevadense*	7 [6] 20	4	Potted	947	374	1,143	285	220	178

1942										
Damnation:										
2	*nevadense*	10	5	Potted	698	(5)	0			
3	*roezli*	11	4	1-planted 3-potted	1, 697	(5)	0			
Deadhorse:										
1	do.	21	5	4-planted 1-potted	465	(5)	0			
2	do.	18	5	1-in situ 2-planted 2-potted	533	(5)	0			
3	do.	18	4	1-planted 3-potted	354	(5)	0			
4	do.	19	3	Planted	401	(5)	0			
5	do.	20	3	1-planted 2-potted	578	(5)	0			
6	do.	19	3	1-planted 2-potted	249	(5)	0			
Big Bar:										
1	do.	40	2	In situ	436	(5)	2	65	2	1
2	do.	44	3	1-in situ 2-planted	743	(5)	0			
3	*nevadense*	17	6	Potted	375	(5)	2	110	2	2
4	*roezli*	11	2	do.	947	(5)	0			
5	*cereum*	36	10	do.	(5)	(5)	0			
1947										
Washington Point:										
1	*roezli*	19	5	Potted	(5)	(5)	0			

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[1] A foliage unit equals the amount of foliage, approximately 37,000 needles, on a normal, average sugar pine of the 5–10 foot height class.

[2] By 1941 it was apparent that numerous blister rust infections had become established on the plot area in 1937 before the plot was laid out or the native ribes removed. It was found impossible to distinguish between these cankers and those resulting from the 1938 plot exposure. So much pine foliage was sacrificed in removing the cankers that the plot was rendered unusable for subsequent tests.

[3] Not computed.

[4] There were no viable telia on planted or potted ribes at the plot center when rains occurred.

[5] No data.

[6] Because the plotted plants used were grown in a greenhouse and bore an unusual concentration of large leaves for the amount of live stem present, the 7 feet of actual live stem present was equivalent to about 20 feet for normal plants in nature.

TABLE 9.—*Dates and amounts of rainfall during seasons when blister rust telia were present, number of hours over which pine foliage remained continuously wet, and areas of viable telia present on leaves of central ribes on observed dates for all Oregon and California study areas, 1936–47* [1]

BLACK ROCK, OREG.

Date		Rainfall	Time foliage wet	Area of viable telia on plot number—					
				1	2	3	4	5	6
		In.	*Hrs.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*
1936:									
July	8	0.02	72	0.0	1.5	0.0	0.0	------	------
	9	.30		------	------	------	------	------	------
	10	.08		------	------	------	------	------	------
	11	.04		------	------	------	------	------	------
Aug.	13	.00	0	4.4	2.7	.0	.0	------	------
	31	.00	0	14.0	21.2	12.9	6.4	------	------
Sept.	1	.13	99						
	2	.12							
	3	.05		------	------	------	------	------	------
	4	.14							
	5	.00							
	12	[2] .08	45	2.4	5.1	.1	.2	------	------
	13	.02		------	------	------	------	------	------
Oct.	3	(3)	13	21.3	42.5	5.5	.0	------	------
	4	.04		------	------	------	------	------	------
	13	.00	0	.0	.0	.0	.0	------	------
1938:									
July	27	.18	18	------	------	------	------	.0	------
	28	.00		------	------	------	------	------	------
Sept.	5	.08	18	------	------	------	------	.1	------
	7	[4] .23	30	------	------	------	------	------	------
	8	[4] .02							
	18	.10	20	------	------	------	------	------	------
	19	.00		------	------	------	------	1.2	------
	24	.03	20	------	------	------	------	------	------
	25	.00							
	28	.22	13	------	------	------	------	------	------
Sept.	29	[5] .03	14	------	------	------	------	------	------
	30	.02	25	------	------	------	------	------	------
Oct.	1	(3)	------	------	------	------	------	------	------
	2	.09	47	------	------	------	------	------	------
	3	.12		------	------	------	------	------	------
	4	.19		------	------	------	------	.0	------
1939:									
July	3	.12	8	.0	.0	5.7	2.3	------	------
	10	.08	4 and 3	.3	.4	2.6	.6	------	------
	27	.01	1	------	------	------	------	------	------
Aug.	24	.01	1	------	------	------	------	------	------
Aug.	31	.05	16	------	------	------	------	------	------
Sept.	1			89.9	17.8	.0	.0	------	------
	11	.10	29	41.9	7.3	.0	.0	------	------
	12	.01		------	------	------	------	------	------
	13	.68	13	------	------	------	------	------	------
	20	.10	19	.0	.1	.0	.0	------	------
	21			------	------	------	------	------	------

See footnotes at end of table.

TABLE 9.—*Dates and amounts of rainfall during seasons when blister rust telia were present, etc.*—Continued

BLACK ROCK, OREG.—Continued

Date	Rainfall	Time foliage wet	Area of viable telia on plot number—					
			1	2	3	4	5	6
	In.	*Hrs.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*
Sept. 30	[6].14	36	.0	.0	.0	.0		
Oct. 1								
2	.13							
1940:								
Aug. 26							1.7	
Sept. 2	(3)	[7]2						
3	.29	[7]36						
4	.01							
7	.19	[7]18						
9	.10	[7]18						
12	.06	[7]48						
13	.15							
14	(3)	[7]10						
15	.21	[7]60						
16	.05							
17	.42							
25							2.2	

SISKIYOU, OREG.

Date	Rainfall	Time foliage wet	1	2	3	4	5	6
1938:								
June 16	0.00	0	0.4					
17	.01	2						
Sept. 4	[5].00	6						
5	.04	8						
7	.08	9	.1					
23	.00	16						
24	.07							
25	(3)	6						
28	.03	13						
29	.22	26	1.3					
Oct. 3	.43	45						
4	.00							
23	[9].04	35	3.9					
24	.12							
27	.03	21						
28	(4)							
29	.44	185+						
30	.17							
31	.08							
Nov. 1	1.11							
2	.73							
3	.33							
4	.34+							

See footnotes at end of table.

TABLE 9.—*Dates and amounts of rainfall during seasons when blister rust telia were present, etc.*—Continued

DAMNATION, CALIF.

Date	Rainfall	Time foliage wet	Area of viable telia on plot number—					
			1	2	3	4	5	6
	In.	*Hrs.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*
1938:								
Sept. 26	0.00	0	95.5	0.0	0.0	------	------	------
27	2.12	60+	------	------	------	------	------	------
28								
29								
Oct. 2	3.44	55	------	------	------	------	------	------
3								
Nov. 1	.00	0	1.3	.3	.2	------	------	------
1939:								
June 15	.22	36	------	.2	.2	------	------	------
16								
30	.00	0	------	.1	.1	------	------	------
July 3	.07	8	------	------	------	------	------	------
8	.00	0	------	.1	.4	------	------	------
10	.05	12	------	------	------	------	------	------
Aug. 6	.00	0	------	.0	.0	------	------	------
Sept. 11	.03	10	------	.0	.0	------	------	------
12	.70	41	------	------	------	------	------	------
13								
25	.50	84	------	.0	.0	------	------	------
26			------	------	------	------	------	------
27	.00							
30	[10] .35	13	------	------	------	------	------	------
Oct. 5		36	------	------	------	------	------	------
6	[10] .85	------	------	------	------	------	------	------
7		18	------	.0	.8	------	------	------
24	[2] .30	8	------	------	------	------	------	------
27	.00	0	------	.0	.0	------	------	------
1940:								
Sept. 12	.36	10	------	------	------	------	------	------
14	------	------	(11)	(11)	------	------	------	------
16	.05	12	------	------	------	------	------	------
18	(3)	4	------	------	------	------	------	------
26	.52	18	------	------	------	------	------	------
Oct. 2	.28	22	------	------	------	------	------	------
20	.03	16	------	------	------	------	------	------
21	------	------	(11)	(11)	------	------	------	------
1941:								
Sept. 1	.40	16	------	------	------	------	------	------
3	------	------	164.4	12.1	5.6	------	------	------
18	.05	8	60.0	------	------	------	------	------
Oct. 12 [12]	.46	18	------	------	------	------	------	------
13	------	------	(3)	3.0	3.7	------	------	------
1942:								
Sept. 8	.10	20	------	8.3	------	------	------	------
Oct. 10	.81	54	------	24.7	6.6	------	------	------
11	.45							
12								
13								
14		27	------	------	------	------	------	------
15	------							

See footnotes at end of table.

TABLE 9.—*Dates and amounts of rainfall during seasons when blister rust telia were present, etc.*—Continued

DEADHORSE, CALIF.

Date	Rainfall	Time foliage wet	Area of viable telia on plot number—					
			1	2	3	4	5	6
	In.	*Hrs.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*
1938:								
July 13	0.61	10	(3)	0.0	(3)	------	------	------
Sept. 7	.21	27	(3)	.0	0.5	------	------	------
28	.47	35	0.3	.0	1.5	------	------	------
29	.32		------	------	------	------	------	------
Oct. 1	1.26	48+						
2			------	------	------	------	------	------
5	.08	5	------	------	------	------	------	------
14	.41	36						
15			------	------	------	------	------	------
28	2.26	80+	.0	.0	6.5	------	------	------
29			------	------	------	------	------	------
30			------	------	------	------	------	------
31			------	------	------	------	------	------
1939:								
June 15	.11	36	------	------	------	------	------	------
16			.0	.0	------	0.0	0.0	0.0
July 3	.61	24	.0	.0	------	.0	.0	(3)
6	------	------	------	------	------	------	.3	------
10	.11	12	(3)	.1	------	.1	------	.5
29	.02	8	------	------	------	------	------	------
Aug. 4	------	------	.3	.0	------	.1	.0	.4
Sept. 11	.81	41						
12			------	------	------	------	------	------
13								
14	------	------	.7	.4	------	3.2	.1	.1
20	.02	2	------	------	------	------	------	------
25	.10	5	------	------	------	------	------	------
26	[13].00	48						
27			------	------	------	------	------	------
28								
Oct. 4	.21	5	------	------	------	------	------	------
5	(14)	32						
6			------	------	------	------	------	------
9	------	------	2.3	1.5	------	1.6	.0	2.9
24	(9, 14)	32	.0	.0	------	.0	.0	.0
1940:								
Sept. 6	------	------	------	------	7.2	------	136.2	74.7
12	.16	16	------	------	------	------	------	------
13	------	------	------	------	13.4	------	------	------
15	.13	8	------	------	------	------	------	------
16		5	------	------	------	------	------	------
17	.49	17	------	------	------	------	------	------
18			------	------	------	------	------	------
19		18	------	------	28.3	------	138.3	102.9
26	.24	15	------	------	------	------	------	------
27			------	------	------	------	------	------

See footnotes at end of table.

TABLE 9.—*Dates and amounts of rainfall during seasons when blister rust telia were present, etc.*—Continued

DEADHORSE, CALIF.—Continued

Date		Rainfall	Time foliage wet	Area of viable telia on plot number—					
				1	2	3	4	5	6
		In.	*Hrs.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*
Oct.	2	.04	20	------	------	------	------	------	------
	8	------	------	------	------	(15)	------	(15)	16.6
	20	.02	13	------	------	------	------	------	------
	22	------	------	------	------	(15)	------	(3)	(15)
1941:									
Sept.	12	.08	4	------	------	------	------	------	------
	19	.39	10	------	------	------	------	------	------
	20		14	------	------	------	------	------	------
	21			(15)	(15)	------	(15)	------	------
Oct.	12[16]	.55	28	(15)	(15)	------	(15)	------	------
1942:									
Sept.	8	.26	14	------	------	------	------	------	------
	9								
	10	.02	22	.0	74.5	39.9	0.0	61.3	33.9
Oct.	10	.50	48	------	------	------	------	------	------
	11			------	------	------	------	------	------
	12			16.3	11.9	11.2	14.0	8.0	21.0
	13	(3)	------	------	------	------	------	------	------
	14	.05	26	------	------	------	------	------	------
	15	------							

BIG BAR, CALIF.

Date		Rainfall	Time foliage wet	1	2	3	4	5	6
1940:									
Sept.	15	.05	2	------	------	------	------	------	------
	18	.40	20	105.7	29.3	(15)	(15)	------	------
	26	.10	14	------	------	------	------	------	------
Oct.	2	.17	18	(15)	(15)	(15)	(3)	------	------
1941:									
Sept.	18	.42	14	(15)	(15)	(15)	(15)	------	------
Oct.	12	.05	6	------	------	------	------	------	------
	19	.15	18	(15)	199.0	(15)	199.0	------	------
	21	.03	4	------	------	------	------	------	------
	24[19]	1.67	6	------	------	------	------	------	------
	28		88	(17)	(18)	16.2	(18)	------	------
1942:									
Sept.	8	.11	45	19.1	------	------	------	------	------
	10	------							
Oct.	10	.82	52	233.1	29.0	72.3	21.4	6.5	------
	11			------	------	------	------	------	------
	12			------	------	------	------	------	------
	14	(20)	16	------	------	------	------	------	------
	15	------							
	23	------	------	75.3	4.8	2.0	6.3	.0	------
	25	(3)	14	------	------	------	------	------	------
	26	(3)	16	------	------	------	------	------	------
	31	------	------	(3)	------	(3)	------	------	------

See footnotes at end of table.

TABLE 9.—*Dates and amounts of rainfall during seasons when blister rust telia were present, etc.*—Continued

WASHINGTON POINT, CALIF.

Date	Rain-fall	Time foli-age wet	Area of viable telia on plot number—					
			1	2	3	4	5	6
	In.	*Hrs.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*	*Sq. in.*
1947:								
Oct. 7	1.00	23						
8			10.1					
9	1.10	47						
10	.65							
11								
15	2.95	38						
16			1.8					
20	.78	26						
21			1.1					
28	1.85	46						
29								
30			.4					

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[1] The number of plots established differed at the different locations; also at each location the number of plots exposed to blister rust often differed from year to year.

[2] Snow and rain.

[3] Trace.

[4] Cold.

[5] Mostly mist.

[6] Part snow.

[7] Estimated from Crescent Ranger Station records.

[8] Fog in a.m.

[9] Snow.

[10] Estimated from record at Vollmers; total for period was accurate.

[11] Some telia present Sept. 14 to Oct. 22, 1940.

[12] Temperatures very low.

[13] Patchy fog.

[14] No record.

[15] Viable telia present but not measured. No germination.

[16] Temperatures 32°–44°F.

[17] Small amount of viable telia but not measured.

[18] Viable telia undoubtedly present but amount not determinable because of previous germination.

[19] Temperatures 38°–48°F.

[20] Light rain; no record of amount.

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END