1943

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J. L. Mielke
United States Department of Agriculture

Recommended Citation

Mielke, J. L., "White Pine Blister Rust in Western North America" (1943). *Yale School of Forestry & Environmental Studies Bulletin Series*. 56.
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YALE UNIVERSITY · SCHOOL OF FORESTRY

Bulletin No. 52

WHITE PINE BLISTER RUST IN WESTERN NORTH AMERICA

BY

J. L. MIELKE, B.S.F., M.S., PH.D.

Associate Pathologist, Division of
Forest Pathology, Bureau of Plant Industry,
Soils, and Agricultural Engineering,
Agricultural Research Administration,
United States Department of Agriculture

NEW HAVEN
Yale University
1943

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2012

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The publication of the results of this investigation was made possible by the Charles Lathrop Pack Foundation at Yale University.

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

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INTRODUCTION

WHITE pine blister rust *(Cronartium ribicola,* Fischer) needs no introduction to American plant pathologists and foresters. Aided by the developed forms of transportation of man and by his constant urge for new and better forms of plant life, the fungus was enabled to escape from its native Asian home and to establish itself first in Europe and then in America. The new hosts with which it was brought in contact proved congenial and from obscurity and a relatively innocuous endemism it emerged to assume the status of a virulent parasite of a group of our important forest trees.

The complex nature of the blister rust organism with its five types of spores maturing at different times during the growing season, its dependence, for epidemic development, on two different hosts (pines and ribes)[1] and the interaction of a number of environmental factors operating in proper sequence over the period that the spores are produced, combine to make the disease quite intricate. Nevertheless, as a result of extensive investigations over a period of many years, most of the basic factors governing the spread and intensification of the rust are now known.

Because of the reasonable certainty that the rust in western North America is all from a single point of introduction, even though its limits now extend over hundreds of thousands of square miles, and because the records obtained as a result of field work by the investigative and control forces provide a relatively accurate history of its progress from year to year, it has offered an unusual opportunity forepiphytological analysis; one probably not previously equaled for any tree disease in the history of phytopathology.

The epidemic development of blister rust is affected by so many factors that consideration, at least to some degree, must be given to nearly everything known about the life history of the fungus or the habits of the disease. A number of these factors have been determined as

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[1] The common name "ribes" and the generic name "*Ribes*" are used herein to indicate both currants and gooseberries.

a result of eastern studies that have not been duplicated in the West.[2] Reference to some of these investigations has therefore been necessary for a better understanding of the epiphytology of the rust in the West.

Although studies on the blister-rust epidemic in western North America were inaugurated in 1922 (Pennington 1925) and are still in progress, published results of blister-rust investigations have not covered the subject. It has therefore been attempted to synthesize into one report the various epiphytological phases having a bearing on the behavior of the rust under the new host and environmental conditions prevailing in the West. Particular consideration has been given to the method and possible limits of seasonal spread and the factors influencing this.

Investigations to date have by no means provided answers to all the problems of epiphytology created by the rust, particularly in some of the regions more recently invaded. Even in regions early invaded some of the weather influences are not yet well understood. Accordingly the present contribution should be regarded as a summary of evidence so far obtained on the subject rather than a completed record.

ORIGIN OF WHITE PINE BLISTER RUST

IT is generally supposed that northern Asia is the native habitat of white pine blister rust and that *Pinus cembra* L., a tree of wide distribution there, is the original pine host (Moir 1924; Spaulding 1922a, 1929; Tubeuf 1936). Moir (1924), and particularly Spaulding (1922a; 1929), have devoted considerable attention to this question including reviews of pertinent literature and reports of their own observations and findings. In their publications the known history of the origin of *Cronartium ribicola* and its spread over Europe is quite thoroughly dealt with. Regarded as noteworthy from their writings are the facts that in 1854 Dietrich found the first known specimens of the fungus on ribes and pine in the Baltic Provinces of Russia; that by about 1900 it was widespread over northern and most of western Europe; and that forest-tree nurseries were responsible in a large measure for this rapid and extensive spread of *C. ribicola* especially by their distribution of diseased eastern white

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[2] Throughout this paper the term "the West" is used synonymously with "western North America" and refers to the part of the Continent lying west of the Great Plains.

pine *(P. strobus* L.),[3] a tree then in generally high favor for reforestation purposes in many of the European countries.

INTRODUCTION TO NORTH AMERICA

EASTERN NORTH AMERICA

THE most detailed accounts available covering the history of the introduction of blister rust to eastern North America are those by Spaulding (1911; 1922a; 1929), and the following brief review has been prepared chiefly from his publications.

Cronartium ribicola has been definitely known in America since 1906 when it was found on ribes at Geneva, New York, but later findings indicated it was present in the northeastern States as early as 1898, if not a few years prior to that date. Evidence has been presented indicating that the fungus may have been first discovered in this country in 1905 when a diseased *Pinus strobus,* presumably infected with blister rust, was found near Philadelphia (Pierce 1917). Definite discovery of the rust on pines occurred in 1909, and subsequent investigations revealed the disease present in seven eastern States that year. There had occurred small-scale importations of nursery stock from Europe for many years, but from about 1900 to 1910, and particularly between 1907 and 1909, millions of eastern white pine seedlings were shipped in to supply the suddenly increased demand occasioned by a general reforestation movement in the East, which the local nurseries were not able to meet. The majority of these seedlings came from one nursery in Germany and it was discovered that diseased white pines had been shipped to well over 200 localities in eastern North America. Thus C. *ribicola* became widely distributed throughout the northeastern States, the Lake States, and eastern Canada in a relatively short time.

WESTERN NORTH AMERICA

In western North America the rust was unknown until September 1921, when it was discovered at Vancouver, British Columbia, on the

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[3] The common names of all American forest trees and ribes are in accordance with Standardized Plant Names (American Joint Committee on Horticultural Nomenclature 1942), and the scientific names are in accordance with the International Rules of Botanical Nomenclature.

European black currant *(Ribes nigrum* L.) (Eastham 1922). Further search for the fungus that fall revealed its presence on a few young exotic white pines at two places in Vancouver and on *R.nigrum* over a considerable area in the Lower Fraser Valley and at three places on Vancouver Island. Negative results were obtained from a limited amount of scouting in the Kootenay District in the southeastern part of the Province.

United States authorities, upon notification of the discovery by the Canadian officials, inaugurated a scouting program in northwestern Washington adjacent to the infected area in British Columbia, and as a result the rust was found near the International Boundary on European black currants at Sumas, Mt. Vernon, Beverley Park, and Port Townsend, and on two planted white pines in a nursery at Mt. Vernon (Bethel 1921; Posey 1922). The search, however, was conducted late in the fall after most of the ribes were defoliated and under adverse weather conditions, consequently it was considered that the actual extent of the infection area still remained to be determined. Also, the few diseased white pines found that fall in British Columbia and Washington were regarded as bearing secondary infections, the primary source of which was unknown.

Scouting by officials of both countries was resumed the following spring as soon as weather conditions permitted and by the end of the season the rust was found to be widely distributed on western white pine *(Pinus monticola* Doug!. ex Lamb.) and ribes in British Columbia (Davidson 1922), and mainly on ribes in the State of Washington west of the summit of the Cascade Mountains. In addition to other pertinent investigations by the Canadian officials, inspection was made of all existing white pine plantings originating from importations[4] into British Columbia during the years 1904 to 1914, inclusive (Davidson 1922; 19.24). This procedure resulted in the finding of but one lot of rust-infected trees, which were growing in a nursery on Point Grey near Vancouver. In 1910 the owner had imported 1,000 *P. strobus* seedlings from a nursery in Ussy, France. After being set out the plantation was largely neglected owing to the World War and at the time of the inspection in 1922 out of the original total only 180 trees remained, 68 of which were diseased. The oldest canker found was a stem infection on the growth of 1910. Since infected white pines are known to have been

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[4] White pines have not been imported or grown to any extent by western nurserymen.

shipped from Ussy that year (Spaulding 1911: 36) it is highly probable some of the trees in question were diseased prior to importation.

Substantiating this probability is the fact that nowhere else in western North America have there ever been found white pines regarded as having been infected with blister rust in 1910 or earlier, nor is there any evidence to date that *Cronartium ribicola* has ever been introduced at any place in the West other than at Point Grey. Also, no evidence has been obtained indicating that any pines were ever shipped from the Point Grey nursery. Considering the fact that investigations in British Columbia were continued for more than ten years after the discovery there, that the systematic inspection, beginning in 1916 and continuing for several years, of planted white pines and of ribes shipped into the Rocky Mountain and Pacific Coast States prior to the establishment of the Federal Quarantine resulted negatively (Bur. PI. Ind. 1918; 1920), and that scouting for the rust in these states has been continued to a greater or lesser degree ever since, it seems highly improbable that any other source for the rust could have escaped detection.

Accordingly, the present known distribution of *Cronartium ribicola* in western North America is regarded as being traceable to a single place of introduction, Point Grey near Vancouver, B.C., from which it has spread by natural means. This circumstance has made it possible to determine facts pertaining to the epiphytology of the fungus in the West that could not be ascertained in the East where, as previously mentioned, the disease spread more or less simultaneously from a large number of introduction points scattered over a wide area.

WHITE PINES OF WESTERN NORTH AMERICA

NATIVE to western North America there are seven species of white pines exclusive of the pinon pines. Their names, together with the ranges of each, are as follows:[5]

Pinus monticola Dougi. ex Lamb. Western white pine.

Range: Occurring in two rather widely separated belts, which may be designated as "coastal" and "interior." The coastal belt extends from southwestern British Columbia

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[5] The ranges of these trees in British Columbia are those outlined by Whitford and Craig (1918) and in the remainder of western North America by Munns (1938) and Sudworth (1917; 1927).

southward through western Washington and Oregon to the southern portion of the Sierra Nevada in California and in extreme western Nevada. The interior belt is situated in northern Idaho, northeastern Oregon, northeastern and southeastern Washington, western Montana, and adjacent southeastern British Columbia. This tree is most abundant in northern Idaho and adjacent northeastern Washington and western Montana. In the coastal belt it is generally of scattered or patchy occurrence.

Pinus lambertiana Doug!. Sugar pine.

Range: Western Oregon southward through California to northern Lower California in Mexico and of very limited occurrence in extreme western Nevada. Most abundant in the Sierra Nevada of California.

Pinus albicaulis Engelm. Whitebark pine.

Range: In alpine country generally near timberline from British Columbia southward to southern California and eastward to western Alberta, central Montana, northwestern Wyoming, and northern Utah. Next to the most widely distributed of western white pines but usually scattered or patchy in occurrence.

Pinus flexilis James. Limber pine.

Range: The most widely distributed of the western white pines and reported from all western States except Washington. Occurring generally at high elevations from the southern Rocky Mountain region of British Columbia and Alberta southward to southern California and northern Mexico and eastward to western South Dakota, Nebraska, and Texas. The species is of much more frequent occurrence in the Rocky Mountain region than the Pacific region.

Pinus balfouriana A. Murray. Foxtail pine.

Range: Confined to California, occurring at high elevations, and limited to two relatively small and widely separated regions-one in the northern Coast Range and the other in the southern Sierra Nevada. Reports of its occurrence in southern Oregon and the southern Coast Range of California are questionable.

Pinus aristata Engelm. Bristlecone pine.

Range: High mountainous country from east central California eastward through Nevada, Utah, and northern Arizona to central Colorado and northern New Mexico. Probably of greatest abundance in Colorado.

Pinus ayacahuite Ehren. Mexican white pine.

Range: Southeastern Arizona, southwestern New Mexico, western Texas, and southward through Mexico and Guatemala.

The present known distribution of the rust on pines within their natural stand is) with but few exceptions) confined within portions of the range limits of *Pinus monticola* and ***P.*** *lambertiana.* The limits of distribution of these two species are shown in Figure 1. Composite range limits of all white pine species in western Canada and in most of the western States are shown later on the maps outlining the spread of the rust on ribes.

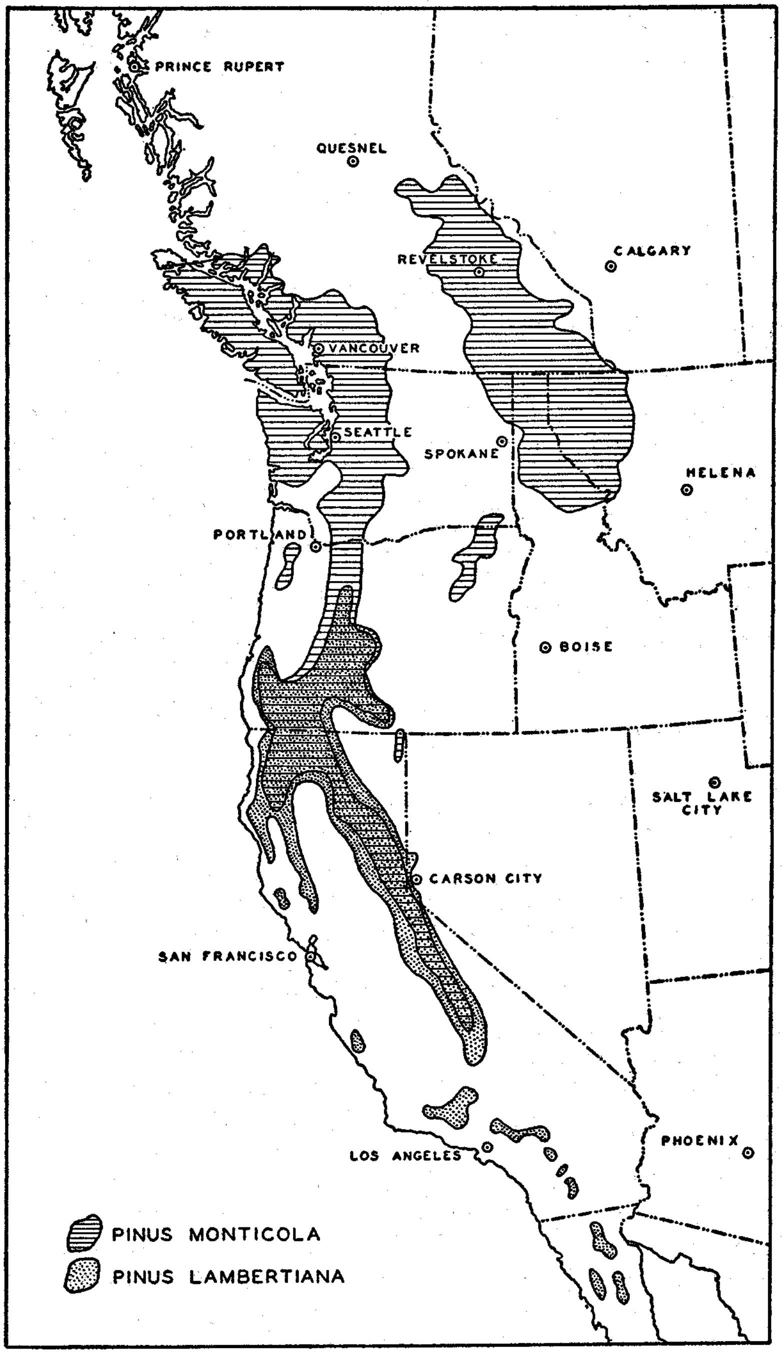

FIGURE 1
Range limits of western white pine (*Pinus monticola*) and sugar pine (*P. lambertiana*).

THE RUST ON PINES

RELATIVE SUSCEPTIBILITY OF WESTERN WHITE PINES

ALL species of the western white pines have been planted in various parts of eastern United States and Europe for many years, and mainly as a result of the plantings on the latter continent they were there first exposed to *Cronartium ribicola.* According to information accumulated by Moir (1924) and Spaulding (1922a; 1929), naturally infected individuals of all species except *Pinus albicaulis* had been noted in Europe prior to the discovery of the rust in western North America, hence they were previously known to be susceptible. These investigators also found that a considerable difference in degree of susceptibility existed between some of the species.

Within their native stands only three (*Pinus monticola*, *P. lambertiana*, and *P. albicaulis*) of the seven western species are known up to the present time to have become naturally infected with *Cronartium ribicola.* As a consequence, the relative susceptibility relationships of these three species are reasonably well known, while for the others only comparatively meager information of this nature exists. Extensive tests of all the species are now in progress. A reliable rating of the degree of susceptibility of all western species is accordingly not available at the present time.

Tentative relative susceptibility ratings, which were regarded as liable to revision, of all white pines in the world were published by Spaulding (1922a; 1925; 1929). As additional information gradually accumulated it was found that some changes in this ranking of the species could be made, and it seems entirely possible that future rearrangements will be necessary.

The destructive nature of the rust in native stands of *Pinus monticola* has amply demonstrated the high degree of susceptibility of this species, and in comparison it is regarded as more susceptible than *P. strobus*, which has been severely attacked both in eastern United States and Europe (Spaulding 1925; 1929). Results of preliminary tests (Lachmund and Hansbrough 1932), substantiated by observations on naturally infected trees (Mielke 1938), strongly indicate that *P. lambertiana* is considerably more susceptible than *P. monticola.* A study conducted in a mixed stand in British Columbia showed a susceptibility approximately seven to ten times greater in *P. albicaulis* than in *P. monticola* (Lachmund 1938), and later *P. albicaulis* was reported to be by far the most susceptible of numerous species tested (Childs et al. 1938). As a result of recent studies in mixed stands on eight different areas in three of the northwestern States it Was found that the average number of cankers per tree was from a little less than three times to more than thirty times as great on *P. albicaulis* as on *P. monticola* (Bedwell and Childs 1941). Infection experiments (Bedwell 1937; Myers 1934; Pennington et al. 1921) and observations (Moir 1924; Spaulding 1929) outside its native habitat show *P. flexilis* to be very susceptible and possibly the species may therefore be rated about equal with *P. monticola*. Moir (1924) observed *P. ayacabuite* heavily infected in Belgium and England and concluded that it was readily susceptible, while Spaulding (1929) ranks it close to *P. lambertiana*. Birt (1940), who conducted tests in the East on small planted trees, found *P. monticola* and *P.flexilis* more susceptible than *P. strobus* while *P. ayacabuite* and *P. aristata* were less so.

Based on the above information plus preliminary results of tests still under way by the Division of Forest Pathology (Bedwell 1937), the following tentative order of susceptibility of the western white pines appears probable: *Pinus albicaulis, P. lambertiana, P. monticola, P. flexilis, P. ayacabuite, P. aristata*, and *P. balfouriana*. Such a rating does not give the true relationships between species, however, for *P. albicaulis* apparently is considerably more susceptible than any of the others; *P. lambertiana* evidently is much more susceptible than *P. monticola; P. flexilis, P. ayacabuite*, and *P. monticola* appear to be of about equal rating; and *P. aristata* and *P. balfouriana* are regarded as resistant in comparison with the others.

Of all the white pines in the world *P. albicaulis, P. lambertiana, P. monticola, P.flexilis*, and possibly *P. ayacabuite* are the most susceptible according to present knowledge. On this basis the potentialities for spread and intensification of the ruSt may be considered greater in the West than anywhere else. This has already been amply demonstrated in the case of *P. monticola* and to a certain degree for *P. lambertiana* and *P. albicaulis*, in the respective stands of which the rust has not been present for so long a period of time as has been the case with *P. monticola*.

DEVELOPMENT OF THE RUST ON PINES

Mode of infection

Pine infection practically always takes place through the needles (Clinton and McCormick 1919; Birt 1938, 1939a; Lachmund 1933a, 1933b; McCubbin 1917; Spaulding 1929). It is considered possible that the rust may sometimes infect young bark directly or through wounds (Clinton and McCormick 1919; Spaulding 1929), but these modes of infection apparently may be regarded as of slight if any importance because of the almost total lack of infection in this manner.

Following penetration of the needle by the germ-tube of the sporidium a compact mass of hyphae develops near the point of infection before hyphal growth begins downward through the vascular bundle and into the bark (Chapman 1934b; Clinton and McCormick 1919). Generally the first visible evidence of the presence of the fungus in the bark is a small yellowish to orange-colored spot roughly circular in outline around the base of a needle fascicle and commonly referred to as an incipient canker. Chapman (1934b) found that the bark at the base of an infected needle does not become discolored until about four weeks after the mycelium has reached the base of the needle sheath.

Incubation period

The time from infection of the needle to appearance of the discoloration of the bark is herein regarded as the incubation period. This is in accord with the definition given by Lachmund (1933c) who found, in studies on *Pinus monticola* conducted mainly in British Columbia, that for trees more than 3 feet high and 8 years old most of the incipient cankers make their appearance in the second year after the infection year and practically all of the remainder in the third year, but for smaller and younger trees they generally appeared in the year following infection. Considered on a monthly basis, he calculated that for the older trees the incubation period commonly ranges from about 20 to 26 months, is generally not less than 16 months, but in extreme cases the minimum might be as little as 9½ months and the maximum 41 months. For younger trees the period was calculated to be generally about 12 months less than the older trees or 8 to 14 months with a possible minimum of 6 months. The writer has observed a similar length of incubation in seedlings of *P. lambertiana* and *P. albicaulis* growing in test plots in British Columbia.

Length of growing season, character of the seasonal weather, locality, and altitude are some of the factors that may affect to some extent the length of the incubation period. Since it is generally accepted that temperature affects the rate of growth of the fungus, incubation should require a longer period of time in northern latitudes and in high elevations than in southern latitudes and in low elevations because of the differences in length of growing season normally occurring between them. At any altitude, however, length of the growing season as affected by character of the seasonal weather may vary more or less from year to year thus influencing to some extent the length of the period. In some years character of the weather may be of considerable importance and this appears to have been the case in the Pacific Northwest particularly during the winter of 1933-34, when, in general, temperatures were considerably above normal over much of the range of blister rust in the West. At Portland, Oregon, for example, according to U.S. Weather Bureau records, the temperature did not fall to the freezing point at any time during the winter, with the months of December, January, February, March, and April, respectively, the mildest of record, the mean temperature being 7.3° F. above normal for the 5-month period. At various other places over the region the temperatures for October were generally about normal, but for November at most places they were considerably above normal.

The effect on incubation of the mild weather during the winter of 1933-34 was manifest at several places in the West where western white pine was studied. E. L. Joy of the Division of Plant Disease Control, Bureau of Entomology and Plant Quarantine, has furnished the writer with data from British Columbia, Oregon, and Montana showing that on trees more than 3 feet high and 8 years old relatively large numbers of incipient cankers having their inception in 1932 were in evidence by late fall (November) of 1933. Additional data from him concerned potted western white pines used in controlled tests in Idaho. On 34 such trees 6 to 8 years old exposed to infected ribes from September 3 to October 11, 1933, incipient cankers were found as early as April 2, 1934, or approximately 6 to 7 months after exposure and they continued to form until October 2, or approximately until 13 to 14 months after infection. Another group of 30 similar-aged pines exposed from July 11 to August 11, 1934, had visible cankers on May 21, 1935, or approximately 10 to 11 months after infection occurred. The minimum incubation period of 6 to 7 months in the former test as compared with 10 to 11 months for the latter would seem strong evidence of the effects of the mild winter of 1933-34 as contrasted with the colder winter of 1934-35, during which temperatures were fairly close to normal.

Chapman (1934b), in studies of potted *Pinus monticola* 6 to 8 years old kept out-of-doors at Moscow, Idaho, found that the mycelium of the rust in the needles continued to be active therein and grow downwards toward the bark when the trees were in winter dormancy. His work was done, however, during the exceptionally mild winter of 1933-34. Consequently, it would seem desirable to conduct similar experiments during a more normal winter to determine if such activity of the fungus might regularly be expected. Nevertheless his findings would seem to question the tenability of considering incubation period on a basis of active and inactive months such as was done by Lachmund (1933c).

The time of year in which pine infection occurs, i.e., early summer or fall, may also affect the length of the incubation period. **In** this regard, the species of ribes in association with the pine may also be of importance for on at least one common and widely distributed western species-the prickly currant *Ribes lacustre* (Pers.) Poir.-the majority of the telia may form considerably earlier in the season than on some of the other species. The time of teliospore formation on some western ribes will be discussed later.

Chapman (1934a), in studies on *Pinus monticola,* found evidence indicating that the distance of a needle spot, i.e., the point of infection, from the bark influences to some extent the length of the incubation period.. The same relationship was found in *P. strobus* by Hirt (1939a), and there seems no reason to believe that it would not hold true for other white pine species.

Pinus monticola is the only one of the seven species of white pines in the West for which the incubation period is relatively well known. A limited amount of field evidence indicates, however, that the schedule of development of the rust in sugar pine may be similar to that for western white pine. A knowledge of this period is of considerable value in working out the history of infection on pines in new localities, the relation of this to intensification of the rust, and in anticipating probable rate of rust development in new regions.

Pycnial production

The pycniospores, which probably have a sexual function (Pierson 1933), always precede the aeciospores on the identical area by at least one season. Their production, which apparently is strongly influenced by temperature, usually begins in June, or shortly after the main aecial period, is most active during the warm summer months, and in some seasons may continue into October and November (Lachmund 1933c;

Mielke and Kimmey 1935). The earliest that pycnial drops have been noted in the West is April 21 (Mielke and Kimmey 1935).

Pycnia have seldom been observed on cankers until after the latter have attained a length of about an inch. According to Lachmund (1933c), who conducted studies on *Pinus monticola* in British Columbia, the period required for the production of pycnia after formation of the incipient cankers may vary from about a month to as high as 10 months, depending upon altitude, seasonal conditions, and the time of year the cankers form. Results of his studies also showed that for those cankers appearing in the second year after infection, the percentage producing pycnia during that year varies according to the time at which the cankers form during the season, the average being about 70 per cent. Of the cankers that appear in the third year after infection an average of about 90 per cent produce pycnia the same year, and practically all that form too late in the season to bear pycnia that year produce pycnia the next year.

The pycniospores are produced in sticky, light amber-colored droplets of fluid that exude from the infected bark. In time, the areas on the bark where pycnia are formed change color from a honey yellow to dark brown or bluish black. These dark-colored and irregularly shaped spots, which are termed "pycnial scars," are of diagnostic value.

Limited studies and observations on *Pinus lambertiana* indicate that pycnia and pycnial scars may not always be as prominent on this species as on *P. monticola,* and that the season of pycnial production in some instances may not be as long (Mielke 1933a; 1938). Studies of pycnial production have not been conducted on other species of western white pines.

Aecial production

When aecia are produced they push through the bark over the area previously occupied by the pycnia. On *Pinus monticola* mainly in the coastal region of British Columbia, Lachmund (1933c) found that for cankers that produce pycnia for the first time in a given year an average of about 60 per cent produce aecia the following spring, and at least 90 per cent of the remainder produce aecia the next spring following. Calculated by him in another way, "the cankers resulting from a given infection year produce aecia for the first time after infection in about the following proportions: 36 per cent in the third spring after the year of infection, 43 per cent in the fourth spring, 18 per cent in the fifth spring, and the remaining 3 per cent mainly in the sixth and to some extent in the seventh spring." Some cankers, because of invasion by other fungi, attacks by rodents, suppression of lower branches, or other causes, never do produce aecia.

Within the range of the rust on *Pinus monticola* aeciospore production varies widely with seasonal conditions and locality, maximum sporulation often occurring in May and the main period being from mid-April to mid-June (Lachmund 1933c; Mielke and Kimmey 1935). At higher elevations these periods may be about a month later. Within the commercial range of *P. monticola* centered in northern Idaho the main period of aecial sporulation generally occurs between mid-May and mid-June, being quite comparable in this regard with that for the interior region of British Columbia. Early springs may advance and late springs retard somewhat the advent of aecial production. However, general observations have shown that the time of aeciospore production is less subject to influence by variations in seasonal conditions than is the growth activity in ribes (Lachmund 1934b: III). Aecial appearance has been recorded as early as late February (Mielke and Kimmey 1935), and a sporadic and very light resumption of aeciospore production, induced possibly by warm weather and regarded as of no importance, may occur some years in October and November (Lachmund 1933c).

In addition to affecting somewhat the advent of aecial sporulation, temperature may in various ways influence the duration of the period. Based on records of observations covering a period of over ten years it may be stated that generally seasonal·sporulation occurs first on the smaller branches with thin bark, somewhat later on large branches with thicker bark, and later still on stems. While bark thickness may possibly be a factor in this regard, protection from sun and wind apparently is of considerable importance. As a general rule, when sporulation on branch cankers is practically completed, it is somewhere near its peak on stem cankers, which usually are somewhat more shaded. Also, it is earlier on seedlings and on young trees shortly past the seedling stage growing in the open than on older trees growing in stands, and earlier on south than on north slopes. In years during which the spring weather is unusually warm and dry the main period of aecial sporulation in a locality may be of but two to three weeks duration, whereas in the event of cool spring weather accompanied by frequent rains this period may be extended over two or more months.

Bark thickness may also affect the quantity of aecial production. *Cronartiumribicola* vegetates largely in the inner bark tissues (Colley

1917, 1918), and bark that has large amounts of such tissue seems to favor the growth of the fungus. It has been observed that aecia often do not develop in the thin bark on small twigs of *Pinus monticola,* but if the mycelium in such twigs remains alive and grows into the thicker bark of a branch or stem to which the twig is attached aecia usually appear in due time. This behavior of the fungus is not restricted to *P. monticola* but occurs in other white pine species as well. In addition to differences between small twigs and larger branches, differences in aecial production also occur between some of the species of white pines. According to Spaulding (1925: 596) there is good evidence that the fungus develops much more luxuriantly in the bark of *P. monticola* than in the bark of *P. strobus.* He evidently attributes this to the decided difference in the thickness of the smooth bark of the two species, that of *P. monticola* being thicker. Hirt (I939b), working with *P. strobus* in a newly established plantation in the East, found that the percentage of the infected trees .whichproduced aeciospores was quite low. A correspondingly similar development of the rust was observed in young trees of this same species used for test purposes in the West, whereas on *P. monticola, P. lambertiana, P. albicaulis,* and *P. flexilis* of similar age in the same test plot aecia were produced on a much higher percentage of the infected trees. These four species all have thicker bark than *P. strobus.* The smooth bark of *P. albicaulis* and *P.lambertiana* is somewhat thicker than that of *P. monticola,* and observations to date indicate that the fungus vegetates somewhat more prolifically in the bark of the two former species than in that of the latter one. Also, a somewhat greater swelling of the infected bark of *P. albicaulis* and *P. lambertiana* is apparent and in a few instances theaecia have been noted as occurring somewhat more abundantly per unit of infected bark area.

A white pine species having thick-barked twigs and branches may, however, be inherently resistant to *Cronartium ribicola.* For example, the bark on young growth of *Pinus balfouriana* is relatively thick, yet evidence to date indicates that this species may be classed as resistant. On six young trees planted in British Columbia relatively sparse to no aecial production was observed on the few cankers that formed over a period of about eight years. It would seem, therefore, that bark thickness cannot always be relied upon as a criterion of the quantity of aecial production, Present information indicates, however, that in general there is a correlation between the two. Accordingly, bark thickness, as represented on the various native pine hosts, may be a factor that will affect to some degree the rate of spread and intensification of the rust in many parts of the West not yet invaded by this parasite.

On branch cankers of *Pinus monticola* aecia are produced from the same bark area sometimes only one season, usually two, often three, and occasionally four successive seasons; their production generally extending over a greater number of years on large branches with thick bark than on small ones with thin bark. On larger stems this period is usually from three to five seasons in succession, occasionally longer. In the event of production for three or more seasons the aecia developing from the roughened and fissured bark over the older portion of the canker. are deeper seated and usually appear somewhat later in the season than those on the smoother bark near the outer margins of the aecial-bearing area. Such development prolongs to some extent the seasonal period of aeciospore dispersal. Present indications are that a similar successive aecial production occurs on *P. lambcrtiana* and *P. albicaulis,* and there seems little reason to believe this schedule will differ greatly for the other white pine species of the West when invasion of their stands eventually occurs.

Annual production of the aecia normally continues until that portion of the twig or branch beyond the canker is killed as a result of the girdling action of the fungus. Coincident with the annual increase in size of the canker, a greater volume of aeciospores is produced each succeeding season until death of the affected part occurs. In some cases, however, aecial production is interfered with and brought to a cessation by the activities of other fungi or of insects or rodents. Twigs and branches killed as a result of the presence of the rust in the bark tissues are commonly referred to as "flags" because of the conspicuous red-brown color of the dead foliage of the affected parts. Colley (1918: 650) has described the manner in which girdling by the rust takes place. According to him, when the aecia form and burst through the outer bark the cracks thus formed allow the inner bark cells to dry out and die. This results in the breaking of resin canals and the consequent exudation of resin in large quantities. The girdling of the affected part is therefore regarded as attributable to these two causes working together-namely, the cracking and drying of the bark, and the impregnation by resin of the whole cortex and phloem in the cracked area resulting in stoppage of the conducting elements in the phloem.

Since girdling takes place in and adjacent to the aecial-bearing portion of the canker, the smooth infected bark near its lower limits is not killed and there remains therein live mycelium capable of growth toward the bole unless the entire branch dies. The latter usually happens when cankers occur on suppressed and weakened branches in the lower portion of the crown. In the event the canker is on a lateral branch, growth of the mycelium in a proximal direction may continue after flagging until invasion of the main branch eventually takes place. Aecial production, however, does not occur during this period of growth of the mycelium but may be resumed again after the fungus develops for two or three seasons in the main branch. When girdling and flagging of the latter occurs the mycelium may continue its growth toward the bole. After invasion of the bole resumption of aecial sporulation again occurs in time and may continue until girdling of the bole is completed and death of that portion of the crown above the canker results. Accordingly then, as the result of a single twig or branch infection aecial sporulation may occur at indeterminate intervals over many years. No difference in this procedure of the rust has been found when cankered branches are girdled by rodents feeding on the infected bark or when they sever diseased twigs, and mycelium of the fungus remains in the stubs (Lachmund and Hansbrough 1934; Mielke 1935). The mycelium in the ends of such stubs and in internodes following flagging acts in an unknown way to keep the bark alive and thus provides for growth of the fungus from one internode to the next (Lachmund and Hansbrough 1932).

Flagging of *Pinus monticola* usually occurs in the sixth year following the year of infection, but the time interval may vary depending upon the size of the tree and character of the infected branches. In young and dense natural stands, where slender twigs and branches predominate, the majority of the flags have been observed appearing as early as the fourth year, whereas in heavier-branched.older and more open stands the majority of them may not develop until the seventh year following the year of infection. Abundant flag formation in anyone year involving cankers of the same age may greatly reduce the volume of aeciospores produced the following spring. It is conceivable then, particularly in the earlier years of infection of a stand, that flagging may not only be a factor contributing to the wavelike character of spread of the rust, but may also affect its rate of intensification over an area.

Flagging and canker growth in *Pinus monticola* have been discussed in considerable detail by Lachmund (1934a). Studies of this nature have not yet been made on any of the other white pines of the West, but limited observations on *P. albicaulis* and *P.lambertiana* indicate that the time required for flagging may be similar to that for *P. monticola.*

CANKER ELONGATION

Enlargement of the cankered area takes place through growth of the fungus mycelium and its advance in the bark tissues. The mycelium has been found to extend a short distance beyond the outer limit of surface discoloration in the diseased bark (Ehrlich and Opie J940). Studies on the rate of canker elongation have involved periodic measurements of their longitudinal enlargement as indicated by the limit of bark discoloration.

Lachmund (J934a) concluded, for *Pinus montieola* in British Columbia, that size of the infected stem (i.e., twig, branch, or trunk) and regional site conditions were the predominant influences in the rate of longitudinal enlargement of cankers. To illustrate the influence of site and climate, he compared the average canker-elongation rates for places near sea level with the much slower rates found in places at higher elevations with shorter growing seasons. Measurements on this same species of pine in northern Idaho, reported by Buchanan (J938b), also showed elongation rate to be considerably faster in the larger than in the smaller branches, but it was found that the average annual rate in Idaho is comparable to that occurring on the least favorable areas in British Columbia. His work was performed in typical stands of reproduction in six different localities well within the commercial white pine belt, and in giving consideration to practical application of the results the elongation measurements from all the localities were combined and averaged. The writer feels such procedure in this case was permissible because it is known through personal acquaintance with the studies by both Lachmund and Buchanan that the variations in site were not nearly so extreme between any of the Idaho localities as they were between some of them in British Columbia. Where the measurements were made in Idaho, the growing season is about equal in length to that occurring at the higher elevational study areas in British Columbia.

Bedwell and Childs (J94J) have obtained some information on the rate of longitudinal enlargement of cankers on *Pinus albieaulis*. They have found that cankers in typical stands of whitebark pine advance only about half as rapidly as do similar cankers in typical stands of western white pine, and that the rate is probably a little less rapid on whitebark than on associated western white pines. Canker elongation rate on other species of the western white pines has not yet been studied.

Although not discussed by Buchanan (J938b), there apparently is a close relationship between climate and some of the results he obtained. The climate of the Idaho white pine region, so far as temperature is concerned, is characterized by relatively cold winters and warm summers. During the warmer part of the year, however, the fluctuation between day and night temperatures is usually quite extreme with frosts not uncommon at intervals during most of the growing season. It is believed by the writer that the low night temperatures retard to some degree the development of the rust in the thin bark of the branches, for in general growth of fungi practically stops below 34° F. This, then, may account in part for the relatively slow annual elongation rate of cankers in Idaho, for similar cold nights are not the rule at the places in British Columbia where Lachmund conducted his studies. Probably of greater importance, however, is length of the seasonal period in Idaho over which temperatures are high enough for appreciable elongation of cankers.

Contrary to the case for most fungi, no artificial culture medium has yet been devised on which *Cronartium ribicola* will grow, consequently determinations of its minimum, optimum, and maximum temperatures for growth by customary methods are at present impossible. Apparently because of this situation relatively little information is at present available on the relationship of temperature to the development of the rust. There exist, however, some comparative data that are believed to be significant.

Rhoads (1920), working in the East, found the elongation rate of cankers during the latter part of the summer to be twice as fast as that during the spring and early part of the summer, and concluded "it is likely that the rate of growth of the blister rust on white pines is influenced by temperature." Kimmey (1940), who conducted studies at Rhododendron, Oregon, also believes temperature to be one of the factors governing time of rapid advance, but he did not, however, find an accelerated late summer elongation rate such as reported by Rhoads; instead it was fairly uniform during the months of May to September, inclusive. In the discussion of certain of his data Kimmey called attention to the marked increase in the rate of canker elongation occurring during an unusually early spring with above normal temperatures over that recorded for the same period during springs in which the temperatures were more nearly normal. According to Buchanan (1938b) his data indicated that the period 1933-34 was decidedly more favorable to canker elongation than was 1934-35. Although he did not mention it, the winter during the former period is known to have been one of the mildest.

of record. Lachmund (1934a) reported that canker progress during the winter, or dormant season, is much slower than during the growing season, and calculated that an average of about 85 per cent of the year's elongation took place from spring to fall. He did not, however, carryon measurements in winter to determine whether longitudinal enlargement, stopped during the colder months. Kimmey (1940), on the other hand, continued his investigations throughout the year and found that each of the cankers stopped perceptible advance for at least a month during the winter and most of them for two or three months or longer. His average curves show slight elongation occurring during the winter because of the great differences found in time of elongation between individual cankers. From the results of the above-mentioned studies it would seem reasonable to conclude that temperature has a fairly strong influence on the rate of longitudinal enlargement of cankers. Also, it would appear that the minimum temperature for perceptible elongation is rather low.

It would seem doubtful if winter dormancy of the host influenced canker elongation to an appreciable extent, for Chapman (1934b) found that the mycelium of the fungus continued to develop in the needles of young pines kept out-of-doors throughout the exceptionally mild winter of 1933-34. Also, canker elongation may continue into late fall and early winter (Kimmey 1940), which is long after perceptible growth of pines is evident. In this connection, however, recognition must be given to the fact that evergreen conifers are not dormant during the winter months in the same sense as are deciduous trees.

One effect of the influence of site and climate on canker elongation rate may be in the quantity of aecia produced in anyone season. On sites where the growing seasons are long, there is a greater annual increase in the infected area over which aecia may be produced as compared with that occurring on less favorable sites. The writer has never observed a relationship between rate of elongation and spacing of the aecia per unit of bark area. Lachmund (1932) reported that aecial production was much lighter in Idaho than in other sections of the rust's range with the possible exception of the Olympic Peninsula in Washington. It was his opinion that the slower development of the rust on pines was caused by a generally colder climate and shorter growing season in Idaho. It is conceivable then, that length of the growing season by influencing the quantity of aecia produced may, at least in some cases, have an effect on intensity of ribes infection occurring over an area and possibly also on the distance to which the aeciospores may be wind-borne. This, of course, would be difficult of evaluation but may be of epiphytological significance.

DETERMINATION OF THE YEAR OF INFECTION ON PINES

Pennington (1925), who spent the seasons of 1922 and 1923 in western North America on investigations of *Cronartium ribieola*, found that, by classifying large numbers of cankers according to the year's growth of the part upon which they had their inception and to their stage of development, the year of infection on *Pinus montieola* could be determined. Later, in an elaboration of this method, Lachmund (I933a) showed that the cankers resulting from any year's sporidial infection were distributed in a characteristic pattern on the different year's growth-bearing needles at the time of infection. The important feature of this pattern is the relatively few cankers on the growth of the season of infection as compared with the numbers on growth one and two years older at that time. This apparently results in part from the resistance of the current season's needles to infection (Buchanan 1940; Lachmund I933b; Pierson and Buchanan I938b).

The method of determining the year of infection is based on various factors that must be taken into consideration in the application of the method. These include in part needle retention, mode of infection, the species of ribes responsible for the infection, incubation period, rate of growth of cankers, and the time required for the development and production of the pycnia and aecia. Since the seasonal climate of a locality may influence the rate of development of the rust, this is also a factor of importance. Needle retention, if shorter or longer than the average, may have some influence on the normal character of the pattern, and this may manifest itself particularly in the numerical distribution of the cankers on growth older by a year or more than that of the season of infection.

Since the present known distribution of the rust on pines in the West is largely confined to *Pinus montieola*, the method has been used almost exclusively on that species. Whether it can be applied equally to all of the other white pines of the West seems questionable at the present time. It is believed that this will depend largely upon the reaction to infection of the current season's needles of a species. Snell (1936) has shown the importance of this factor in determining with certainty the year of infection on *P. strobus* in the East. Considerable evidence has been accumulated indicating that the method is applicable to *P. lambertiana,* but additional data are needed before this may be established. with certainty. According to Bedwell and Childs (1941) the current season's needles of *P. albicaulis* appear fully as susceptible as any of the older needles.

It has been amply demonstrated, both in the West (Joy 1932; Lachmund 1926a; Mielke 1938; Pennington 1925; Putnam 1931) and in the East (Spaulding 19II; 1922a), that almost invariably the actual limits of *Cronartium ribicola* have been considerably in advance of the known limits, for it has been found almost without exception that the rust had been present on pines in new localities or regions several years or more prior to its discovery. The method of determining the age of infection on *Pinus monticola* has therefore been most valuable in the investigations of the fungus. Without it, or some other equally reliable method, neither could the early history of this epiphytotic in the West have been determined with a reasonable degree of accuracy nor could its yearly progress of spread after the discovery in 1921 have been so readily followed.

RATE OF INTENSIFICATION AND DAMAGE

Since the rate of intensification and damage is proportional to the abundance and telium-producing capacity of the ribes within and adjacent to a pine stand, it is to be expected that the rate of progress of the rust will be greater in certain local areas than will be the case generally. What may happen locally under very favorable conditions for the development of the rust has been reported by Lachmund (1934C). He conducted plot studies in British Columbia in one of the heaviest infection centers known in western North America. This infection center was invaded by the rust in 1913. On a one-third acre plot established in 1922 when the area was discovered, it was found that over 41 per cent of the *Pinus monticola* were already dead and the remainder infected. By the fall of 1925, or 13 years after invasion, over 96 per cent had succumbed, and by 1929 only one tree, a resistant individual, remained alive. The killed trees ranged up to 35 feet in height and averaged over 20 feet. While this is an exceptional case there are a number of other local areas, mainly in the coastal region of British Columbia, on which the rate of intensification and damage has closely approached it.

In such cases of rapid killing, death of the trees results almost entirely from the killing of individual branches by the numerous twig and branch infections, while trunk infection may play but a minor rôle. Twig and branch cankers have been observed occurring so abundantly on both individuals and groups of *Pinus monticola* on a number of areas in the West that they have been estimated to total from many hundreds to several thousands or more per tree. In comparison, under conditions of ordinary infection, serious damage and killing occur mainly from the girdling of the trunk following growth of the fungus down individual branches. This is the general mode of damage in *Pinus monticola* and requires a longer period of time than when death results from the multiple infection and killing of individual twigs and branches.

The progress of the rust, in an experimental planting of approximately 500 3-year-old nursery seedlings of *Pinus monticola* that had been made at Daisy Lake, British Columbia, in 1923, by the Dominion Department of Agriculture (Davidson 1924a), was followed annually for a number of years. In October 1924, 476 of these trees were alive and 211 were already infected. By May 1929, all but nine had been killed by the rust. Of those remaining, five showed no evidence of the fungus, but in September 1931, when last examined, they were all found to be infected.

Most of the observations and studies mentioned in the two preceding paragraphs were made in British Columbia. Rates of intensification similar to those occurring on many of the severest infection centers in that Province, however, have been noted in other parts of the West and particularly in northern Idaho. Putnam (1931) has reported on studies conducted there in 1930. One (Long Meadow Creek area) was made in a 20- to 40-year pole stand averaging 754 western white pine per acre. The rust, which started from a few cankers in 1923, intensified so rapidly that by 1928 from 75 to 100 per cent of the trees on 2.7 acres had become infected, and an average of 18 per cent of the pines over an area of approximately 48 acres were infected. On another area (Elk-Deep Creeks), where infection also became established in 1923, 26 per cent of the pines on 56 acres were found infected in 1930. Joy (1931) made additional surveys of this same nature in Idaho in 1931 on areas where infection also originated on the pines in 1923. On the Fishhook area all (1,868) of the pines on 8.85 acres were examined and 40.4 per cent found to be infected with an average of 4.4 cankers per tree. On the Ruby Creek area a 2 percent survey was made of 101 acres and 355 pines were examined of which 44.8 per cent were infected with an average of 15.5 cankers per infected tree. In addition to the 2 per cent survey on this area the infection conditions on 3 square chains of dense reproduction within the area at the original center were studied. Of 362 pines examined, 339 or 93.6 per cent were infected with an average of 19 cankers per tree.

The situation over more extensive areas in Idaho may be 'contrasted with that at local infection centers. Following its discovery in the State in 1927, the rust intensified at such a rapid rate on unprotected areas that within 11 years it was already evident that many stands of young white pine probably would be a total loss before the ribes could be eradicated (Bur. Ent. and PI. Quar. 1938: 32). Extensive surveys have provided additional information on the alarming rate of spread of the rust on unprotected areas (Swanson 1939a). In 1936 about 4 per cent of the young white pines in the St. Joe section of northern Idaho were found to be infected, but in 1937 the survey showed 13 per cent of them bearing cankers.

Even under conditions of comparatively light pine infection, resulting either from ribes of relatively low susceptibility and telium-producing capacity on the area or from more highly susceptible species growing at some distance from the pines, the damage to young trees of *Pinus monticola* may progress at such a rate as to prevent a stand of them from producing a merchantable crop or reaching maturity (Buchanan 1938a; Buchanan and Kimmey 1938; Childs and Kimmey 1938; Mielke 1937). On certain unprotected areas in the West the seedlings, saplings, and poles have already been largely eliminated from the stands and the remaining trees are doomed to destruction. Successive crops of seedlings are killed soon after they appear. Under such conditions nothing will be left to perpetuate the stands when the oldest trees are finally killed.

A method for calculating the time element and manner of killing or injury of *Pinus monticola* has been worked out by Lachmund (1934a). It is based mainly on the knowledge of canker growth rate and development, and has been used in various damage studies of this species (Buchanan 1938a; Buchanan and Kimmey 1938; Childs and Kimmey 1938; Mielke 1937). As a result of Lachmund's investigations, studies by others ,(Buchanan 1938a; Childs and Kimmey 1938; Davis and Moss 1940), and field observations, it has been found that the location of a canker in the crown determines ensuing rate, degree, and character of damage. A much higher percentage of branch cankers that originate within a foot or less of stems succeed in reaching the latter than do those originating several feet therefrom. On this account the chances that cankers will reach and girdle the stems are greater in small trees than in large ones. Cankers generally are most abundant in the lower half of crowns. There is, however, a high mortality rate in cankers so situated. This is brought about through the death of entire branches resulting mainly from the action of the canker and from suppression. Consequently, great numbers of cankers die out before they can reach the stem. Dying out of cankers is greatest in larger trees where the branches are longer and the lower and inner portions of the crowns under suppression.

On the average, relatively few cankers are required to damage a tree, particularly in the smaller size classes. Childs and Kimmey (1938) found that the percentage of cankers capable of damage ranged from nearly 100 in the smallest trees to less than 30 in trees from 45 to 50 feet tall. Similar relationships have been reported by Buchanan (1938a) and Lachmund (1934a). In uneven-aged stands of reproduction up to 40 feet in height, although the percentage of cankers capable of causing damage decreases with increasing tree size, the percentages of total trees damaged are nearly always greater in the larger size classes (Childs and Kimmey 1938). Similar, but not so pronounced, differences in this regard have been found in trees ranging up to 160 feet in height (Buchanan 1938a). These relationships may be explained on the basis that large trees offer a greater target of foliage on which drifting spores may land than small ones and their chances for infection are accordingly greater (Buchanan 1938a; Childs and Kimmey 1938; Lachmund 1934a).

From the foregoing it should be evident that, while large trees are more likely to become infected, the rate of damage in *Pinus monticola* is faster in small than in large trees. The results of studies substantiate this (Buchanan 1938a; Childs and Kimmey 1938; Lachmund 1934a; 1934C). It should also be evident that, in trees of equal size, the severity of the infection and the distribution of cankers in the crown will, to a large extent, determine the length of time between infection and death of the tree in each case. Consequently, the time required for the rust to kill trees in given height classes cannot be stated with a great deal of definiteness. Small seedlings may be killed in a few years. Trees up to 30 feet in height may be killed in ten years or less, and 50-foot trees in 15 years, from the time infection becomes established on an area (Lachmund 1934C). Significant damage in merchantable trees 120 to 160 feet in height may not occur until 30 or more years after infection (Buchanan 1938a), but trees up to 200 feet in height and four feet in diameter may ultimately be killed by the rust (Martin 1935).

The rate of intensification and damage in *Pinus lambertiana* is still largely a matter of speculation. There is some evidence, however, that under favorable conditions it may be fairly similar to that in *P. montieola* (Mielke 1938). More information is needed before conclusions may be drawn and this awaits the further invasion of the stands. There is also some evidence that this rate may be very rapid, at least in some localities,. in *P. albieaulis* (Bedwell and Childs 1941). The writer has seen a few naturally infected trees of this species on which cankers occurred on practically every twig and branch, whereas on similar-sized and near-by trees of *P. montieola*, considered to be equally well exposed to the infected ribes, there were few cankers. Both *P. lambertiana* and *P. albieaulis* are more susceptible than *P. montieola* to blister rust. It would seem obvious that the degree of susceptibility of a species would be an important factor in connection with rate of intensification and damage.

SOME FACTORS AFFECTING THE INFECTION OF PINES

Time of pine infection

Providing weather conditions are favorable pine infection may take place at any time during the season that viable teliospores are present on ribes. The length of the seasonal period of telial production may vary from year to year depending upon the character of the seasonal weather and the locality. In the West new telia have been found as early as mid-May, but the peak of their production usually occurs sometime in August or September, occasionally in October (Mielke and Kimmey 1935), and viable telia may be present somewhat later. Accordingly, then., the majority of infections on pines may be expected to take place in the fall and observations indicate that this is usually the case. Also, this is the time of year when moisture conditions usually are more favorable than earlier in the season.

Germination of the tdiospores and sporidia

The sporidia, which are the only spores of the five different types produced in the life cycle of the rust capable of infecting pines, arise from promycelia produced by the germinated teliospores. If sporidia are to be produced and infection is to take place a moist period of sufficient duration is needed not only for the germination of the teliospores but also for the production and germination of the sporidia. Since two types of spores are involved it would seem that the length of this period might be somewhat longer than if there were only one. The moisture required for the germination of teliospores and the production and germination of the sporidia may be in the form of rain, fog, or dew, with rain the most important source of moisture supply.

The germination of the teliospores and sporidia probably constitutes the most critical phase in the life cycle of the rust since the sporidia are very short-lived as compared with the other spore forms. Various investigators have contributed information on it. The following summary of the literature is chronologically arranged so far as possible. It should be noted that different methods were used by the investigators and different results obtained.

Spaulding (1922a: 64) reported the results of weekly germination tests of teliospores in hanging drops of distilled water made by Gravatt and Taylor in 1917. The spores were collected in glass vials. Germination was found to persist in one lot (kept on a window sill in the shade) for 35 days, while it lasted 56 days in another lot that was stored in a refrigerator. Because saprophytic fungi attacked the lot kept on the window sill it was concluded the test probably did not show the longevity of healthy teliospores stored under those conditions. Also according to Spaulding, York in 1918 found that teliospores were still capable of germination in tap water after being kept on plucked leaves 65 days out-of-doors in the shade, while a similar test of teliospores kept in the dark in the laboratory gave germination for 90 days.

Colley (1918: 638) determined that all the spores in a telial column may germinate *in situ.* He also found that upon germination the sporidia may produce either true hyphae or secondary sporidia. Clinton and McCormick (1919) and Hirt (1935; 1942) reported the same findings.

York and Snell (1922) found from observations that had been made in nature and on cultures of telia in damp chambers and in water that sporidia became fully developed from 5 to 6 hours after dry teliospores were brought under conditions favorable for their germination and the formation of sporidia. Temperatures under which this interval prevailed are not stated. In one experiment they placed sporidia on needles of *Pinus strobus* that were transferred to an iceless refrigerator where the temperature was 60° F. and the relative humidity 99 per cent. After one hour a few sporidia had begun to germinate.

Spaulding (1922b) found that teliospores may remain viable under natural outdoor conditions until late fall and early winter and still germinate vigorously, and that teliospores on leaves dropped on the surface of snow, when the temperature was a few degrees above freezing, germinated there naturally and produced sporidia. He also found that teliospores located upon dead leaves or dead spots on living leaves collected in the dry weather of September and October gave no germination, while vigorous living leaves from the same bushes bore teliospores that were strongly viable; and that teliospores on leaves suddenly killed by frosts have maximum germinating powers.

Snell and Rathbun-Gravatt (1925) induced the germination of teliospores and production of sporidia in six hours using the petri-dish moist chamber method described by York and Snell (1922).

York, Snell, and Rathbun-Gravatt (1927) also induced teliospore germination and sporidial production in six hours when pieces of telium-bearing leaves were placed in moist chambers and when the detached telial columns were floated on the surface of water. According to them, teliospores will germinate and produce sporidia by either of these two methods at temperatures of 55° to 80° F. They germinated sporidia in iceless refrigerators where the average relative humidity was 99 per cent and the average temperature 60° F. and also on moist slides placed in a cellar where the temperature ranged from 60° to 70° F.

Spaulding and Rathbun-Gravatt (1925b) obtained decidedly better germination results by floating the telia on water than by using the previously mentioned moist chamber method. The teliospores were germinated outdoors and shielded from sun and rain. No information is given on temperature or relative humidity in these tests. For telial material stored 5, 15, 20, 25, and 29 days the first teliospores germinated in 2, 4, 4, 4, and 5 hours, respectively, after the start of the test, and maximum germination of the columns occurred in 12, 14, 18, 23, and 23 hours, respectively. In a preliminary test of material kept indoors it was found that columns stored for 5, 15, and 25 days started germination in 2 hours, but that a higher percentage of germination occurred in the case of the material stored only 5 days as compared with that stored for the longer periods. They also found that unless teliospores start to germinate, they survive wetting and drying for an indefinite number of times; that the period required for germination of teliospores increases with their age, whether kept dry indoors or exposed to the weather outdoors; and that under outdoor conditions their longevity varied from 19 days for one collection of *Ribes rotundifolium* Michx. to 87 days for *R. nigrum*, which still germinated well at the end of the experiments.

According to Spaulding and Rathbun-Gravatt (1925a), the time required for germination of teliospores varies considerably with conditions. They were found to germinate readily and copiously at 75° F. in 6 hours if tested when fresh and if they had not been formed in droughty weather. Drought injures them if it occurs at the time of, or immediately after, their formation. These authors stated that at temperatures of 50° to 70° F., fresh teliospores germinated and formed sporidia in maximum numbers in about 12 hours.

In additional studies by Spaulding and Rathbun-Gravatt (1926) the telial columns were again floated on water to induce germination. For telia stored 5, 15, 20, 25, and 29 days the first sporidia formed in 3, 6, 6, 13, and 8 hours, respectively, after the start of the test, and maximum sporidial production was reached at 12, 14, 13, 23, and 24 hours, respectively. These results are similar to those obtained by these same investigators in a previous study (1925b). In some preliminary tests, however, teliospores stored indoors for 5, 15, and 25 days started germinating in 2, 5, and 11 hours, respectively, after the start of the test. Considering again the telial material stored for 5, 15, 20, 25, and 29 days, it was not until 11, 15, 17, 20, and 20 hours, respectively, from the start of the test that the first germinating sporidia were observed. Accordingly, there was an elapse of 8, 9, 11, 7, and 12 hours, respectively, between the time from the formation of the first sporidia until they started germinating. These investigators also found that temperature influenced the time necessary for sporidial production; that sporidia apparently need free water for germination, but that the thinnest film is sufficient; that under certain conditions sporidia may remain viable for 26 hours; that small percentages of the sporidia survived short exposures in full sunlight when collected and placed on glass; and that sporidia from all the tested species produced secondary sporidia.

Hirt (1935) found that closed petri-dishes containing water agar made suitable damp chambers for the germination of teliospores and sporidia. In tests of telial columns ranging in age from 6 to 216 hours, the age of the teliospores affected sporidium production largely through the number of sporidia that might be produced. Direct contact with water was not essential for germination of the teliospores and relative humidities between 96 and 100 per cent permitted sporidium production. The optimum temperature range for the production of sporidia was 54° to 64° F., and the minimum and maximum temperatures were 32° to 34° F., and 70° F., respectively. The time required for sporidium production was shorter within the optimum ranges than at lower and higher temperatures. In tests conducted under fluctuating room temperatures, the time required for germination of the teliospores and production of mature sporidia was between 11 and 12 hours. In the case of teliospores that had previously germinated and produced basidia not yet fully mature, sporidia were produced in a minimum of 3½ hours. Comparable results were obtained by this same investigator (Hirt 1942) in a later study. He also found therein that in controlled tests in which the moisture and temperature were held constant, the latter being at 65° F., sporidium production, once it started, was continuous for 24 hours and the average spore cast was approximately the same after the sixth hour although toward the close of the test the spore cast appeared to be increasing. The sporidia themselves (Hirt 1935) germinated at relative humidities as low as 97 per cent, but for the best germination they required 100 per cent relative humidity or direct contact with water. Sporidia on water agar germinated at temperatures between 32° to 34° F., and 70° F. At 50° to 64° F., secondary sporidia were produced in abundance but to a lesser degree at lower temperatures. Between 46° and 64° F., the minimum time required for sporidium germination varied between 4 to 10 hours. Exposure of the sporidia to direct sunlight affects them adversely. Tests showed that sporidia, which were adhering to telial columns and the under surface of *Ribes nigrum* leaves, were affected adversely when exposed to direct sunshine on a hot, clear day by fastening leaves (still attached to the bushes) in such a position that direct sunlight fell upon their under surface. Some of the sporidia were still viable after 3 hours of such exposure and a few at the end of 7 hours. On the other hand, a high percentage remained viable, on leaves left in their natural position on the bushes, throughout 8 hours of exposure during the same day.

The writer found that teliospores in the columns on green leaves attached to bushes of *Ribes roezlii* Reg. buried under newly fallen snow occurring in late October 1939, had germinated abundantly, whereas no evidence of their germination was seen on other bushes of this species not so buried. The air temperature during most of the exposure time ranged from 32° to as low as 21° F.

In consideration of the above-mentioned findings it would seem that the factors involved in the production of sporidia and their germination are not all well understood. Moisture seems to be the prime requisite for the germination of the teliospores and sporidia, while temperature in itself does not seem so important in limiting their germination except above 70° F., although it may affect more or less the time required. In the West, if moisture conditions are favorable, it is believed that temperature conditions also will nearly always be favorable.

Time required for pine infection

There is relatively little definite knowledge regarding the time required for pine infection and particularly with regard to infection under natural conditions. The status of the knowledge on this subject is summarized in the following paragraphs.

So far as the writer has been able to determine York and Snell (1922) were the first to present information on the time required for pine infection. Iceless refrigerators were used for inoculation chambers in their tests. Positive results were obtained within a 12½-hour period of exposure of the pines to viable sporidia. The average temperature and relative humidity in the refrigerators during the experiment were respectively 64° F. and 94 per cent. Based on these results, together with the time they found necessary for the germination of teliospores and formation of sporidia, they concluded that it might require at least 18½ hours of constant duration of favorable moisture and temperature conditions for infection to occur.

Snell and Rathbun-Gravatt (1925) obtained positive results when pines in moist chambers were exposed to viable sporidia for periods of 24 and 36 hours. Shorter exposures were not made and no information was given on temperature and relative humidity.

Spaulding and Rathbun-Gravatt (1925a) in 1925 stated that, "the factors which are necessary for the infection of white pines by *Cronartium ribicola* are many and some of them are not known." Based on the information then known-that there must be a period of sufficient moisture to germinate the teliospores, and that this must be followed by a period of high relative humidity during which the infection can take place-they illustrated some of these conditions graphically. According to them, conditions presumably favorable for pine infection must prevail for a period greater than 18 hours to result in rather heavy infection of pines.

York, Snell, and Rathbun-Gravatt (1927), in a test in which the teliospores were not pregerminated, found that infection of potted *Pinus strobus* seedlings occurred within a period of six hours that the pines were exposed to the inoculum in an iceless refrigerator after which they were placed outside in a shady swamp. These pines were sprayed with water before and after exposure. In the light of present knowledge it would seem probable that infection actually occurred after the wet pines were placed in the swamp and that in the refrigerator only production of sporidia and their deposition on the needles took place. Accordingly, the time required for pine infection in this test may have been considerably longer than six hours. Starting with ungerminated teliospores, pine infection has never been obtained in six hours under controlled conditions and there is no evidence that under natural conditions in the West infection will occur in so short a period of time.

Pennington (1928) found that in tests conducted with *Pinus strobus,* infection resulted during 24-hour periods of more or less rain and high relative humidity whereas relatively little or no infection occurred when such moist periods prevailed for only a part of a day.

Based on his own observations and findings and the findings of others Spaulding (1929) is of the opinion tha.t infection of pines may take place in a period of 18 to 36 hours, depending upon conditions.

Hirt (1936; 1939a; 1939b) at various times exposed potted *Pinus strobus* to infected ribes for periods of 12 to 24 hours. Infection resulted naturally out-of-doors during both of these exposure periods when climatic conditions were favorable, but in one of his experiments (1939a) a higher percentage of trees became infected during 12-hour exposure periods than during 24-hour periods. Moisture conditions and sporidial production during these exposure periods were not discussed.

In a later study with *Pinus strobus* in the East Hirt (1942) found in controlled tests, in which optimum moisture and temperature conditions were used, that the minimum time required for needle infection resulting from inoculation with mature sporidia was 8 hours, but that more trees developed cankers when they were kept in the damp chambers for 16 hours or longer. By adding to these figures 3½ hours, the minimum time regarded by him as necessary for sporidium production, he reported that the minimum time for pine infection to occur under optimum conditions was found to be 11½ hours, but that the amount of infection was greater after 19½ hours. From the text, however, it is evident that the viable sporidia produced within 3½ hours were from partly matured basidia formed from previously germinated teliospores, while 11 to 12 hours were required for sporidium production from mature, ungerminated teliospores. Accordingly, it would seem that starting with ungerminated teliospores the minimum time required for pine infection would be about 19 hours, and that considerable infection would occur after about 27 hours. In tests under natural meteorological conditions favorable for infection a 12-hour exposure period of the pines to mature sporidia was sufficient to permit some infection, but a greater number of cankers resulted from longer exposure periods.

Experiments on the time required for pine infection have not been made in the West but, based on field observations over a number of years, it has been found that abundant infection generally occurs only when favorable moisture conditions prevail for a continuous period of about 24 to 36 hours, while relatively little infection may be expected during moist periods of shorter duration. The character of the moist period is evidently of considerable importance if abundant infection is to take place. This is discussed in the following section.

Rain in relation to pine infection

In a previously mentioned paper, Spaulding and Rathbun-Gravatt (1925a) gave consideration to conditions antecedent to the infection of white pines by *Cronartium ribicola* in the northeastern United States. Therein, conditions presumably favorable for heavy pine infection and some resulting in little or no infection are expressed graphically and discussed. This was based on the information available in the literature at that time plus the experience of these two researchers. A statement was made by them to the effect that very incomplete knowledge existed about all the factors concerned in the infection of pines by the sporidia of the rust. This situation still prevails to a large extent because relatively little additional information has been added on the subject. On account of this the discussion in the following paragraph, dealing with moisture in relation to pine infection, has for the most part been taken verbatim from the paper by Spaulding and Rathbun-Gravatt, for their work is regarded as the most comprehensive treatise on the subject yet published. In general, only such changes or additions have been made as were necessary to bring the information up-to-date particularly with regard to western conditions.

The teliospores of *Cronartium ribicola* need moisture for their germination. Under natural conditions this necessary moisture may be in the form of rain, dew, or fog. Of these three sources, rains are the most important in the West, and evidently also in the East (Hirt 1942). The teliospores have frequently been found germinating and producing sporidia in nature immediately after a rain, especially if the rain is followed by cloudy weather. The mature sporidia, which are set free by being forcibly projected from the tips of the sterigmata (Hirt 1935), are undoubtedly largely wind-disseminated. The slightest air current will carry them. There probably is not an instant when there is not some slight air movement sufficient to carry these extremely light bodies to an indefinite distance. As is well known, precipitated water in the form of rain or snow carries down minute particles such as dust, bacteria, and fungus spores, which float in the air, the amount of such material being at a minimum just after a rain or snowstorm. Therefore, the effective dissemination of the sporidia during a continuous rain is likely to be much reduced or completely prevented, depending on the intensity of the rain.[6] If a rain continues so long that most of the teliospores germinate and form sporidia, the latter, after being set free, will largely have been carried down by falling raindrops or heavy mist. It is not likely that sporidia, once washed to the ground, are ever again picked up in a viable condition by the wind. It appears, then, that natural infection of pines must take place principally during damp cloudy weather following a rain or during foggy weather of such combined length that the teliospores germinate freely and form sporidia. The lowered humidity accompanying clearing weather stops germination of teliospores and the formation of sporidia. The results of field and laboratory studies on *Pinus strobus* in the East, recently reported by Hirt (1942), show the importance of the character of moist periods in relation to pine infection.

Under natural conditions, if the teliospores are to germinate freely and produce an abundant crop of sporidia, and the sporidia are to subsequently germinate and infect pines, the moist period must be of sufficient duration to permit this sequence of events. According to the available information it is necessary that the moist period prevail 18 to 36 hours depending upon the conditions (Spaulding 1929: 15; Hirt 1942), although in tests infection probably has resulted in somewhat less time than 18 hours (York, Snell, and Rathbun-Gravatt 1927). The weather conditions considered by Spaulding and Gravatt (1925a) as presumably favorable for rather heavy infection of pines begin with rain, which should end quite abruptly after 7 hours and should be followed by about 23 hours of cloudy weather and night conditions. As has been mentioned in the preceding paragraph, if the rain continues too long the sporidia that are eventually formed are carried down by the falling drops and thus rendered innocuous to the pines. Obviously, then, the character of

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[6] The results of studies conducted in Russia (Shitikova-Roussakova 1926), showed that the occurrence of precipitation plays an important part in the distribution of fungus spores in the atmosphere by either decreasing their number or reducing it to zero.

the moist period is highly important. This is verified by experience in the West. Instances are known in which relatively little pine infection resulted in seasons when all available teliospores germinated during a single prolonged and heavy downpour of rain. Very gentle rains or mists evidently are relatively much more favorable to pine infection than are heavy rains. Spaulding (1925: 15) is of the opinion that foggy weather provides optimum conditions for sporidia and for the infection of pines. It should be evident that, in general, precipitation records alone are of relatively little value in the determination of seasons that have been favorable to pine infection because they afford little indication of the character and duration of highly humid periods.

It is not definitely known if sporidia that have already reached the needles of pine are washed off by rain but there is some evidence that this may happen. It has been the observation of the writer and others with whom he has worked in the West that a somewhat higher percentage of cankers originate on the top half than on the bottom half of branches. In support of these observations tallies of young cankers on *Pinus monticola* were recently made by members of the Portland Branch of the Division of Forest Pathology. The data are given in Table 1. They show that an average of approximately 60 per cent of the cankers originated on the top half of the branches. At none of the locations where tallies were made were a greater percentage of them found originating on the bottom than the top half. It has been observed that during rains the needles in a bundle tend to draw together over their entire length, undoubtedly because of the tension of the water held between them. This has a stiffening effect on the needles in the bundles. It seems reasonable that sporidia coming in contact with upward-projecting needles on a twig would have a better chance to be held by the cohesive force of the

TABLE I. PLACE OF ORIGIN OF BLISTER RUST CANKERS ON *Pinus monticola.*

Locality data obtained	*Place of canker origin on branch*			
	Top		*Bottom*	
	Number	*Percentage*	*Number*	*Percentage*
Oregon Trail, Oregon	176	60	117	40
Government Camp, Oregon	338	60	223	40
Yocum Falls, Oregon	235	53	212	47
Rhododendron, Oregon	212	69	96	31
Tea Meadows, Idaho	242	54	205	46
Total cankers	1,203	59	853	41

water caught between the needles than those lodging on needles projecting downward from which they should be more readily washed off. Whether the incidence of cankers as here reported may be attributed to rain is not known, but it seems possible that rain may be one of the factors, if not the factor, involved.

Fog in relation to pine infection

As was brought out in the preceding section, the optimum conditions for pine infection evidently occur during foggy or misty weather. In the West fogs are most common during the season of pine infection in the immediate vicinity of the coastal area, which is for the most part outside the ranges of white pines. In the coastal region of British Columbia *Pinus montieola* is found growing practically at sea level and there much infection is believed to have occurred during foggy weather. During the rainy season in spring and fall fogs and mists are not uncommon in mountainous regions inland from the coast and may frequently envelop the higher peaks at any season, even in periods generally clear at lower elevations. The high elevation fogs usually do not extend very far down into the zones occupied by white pines and, since relatively little blister rust so far occurs in the alpine zone in the West, fog and mist at these altitudes have played no appreciable rôle in the general increase of rust infection. However, it may be confidently anticipated that in the future the disease will become more prevalent in high-altitude stands and fogs may well become of more importance in its intensification. Hirt (1942) has found that pine infection may occur during foggy weather in the East.

Dew in relation to pine infection

Heavy dews generally occur throughout the summer along most of the stream courses in the Idaho white pine region. They have been observed to be more common and heavier there than elsewhere within the present known range of the rust in the West. This situation is possibly explained by the marked diurnal range in temperature in Idaho where a rapid cooling is very noticeable as soon as the sun goes down. On normal summer days the dew point is often reached in some of the deep north-and-south-Iying canyons as soon as the west side of the canyons becomes shaded. In such locations dew has been known to form as early as 2 P.M., keeping ribes and pine foliage damp unt'il as late as 10 A.M. the following morning. Over the Idaho region as a whole, however, the period over which foliage remains moist from dew is considerably shorter.

The results of an experiment by York et al. (1927: 500), to ascertain whether pine infection may occur in nature at the time of heavy dews indicate that such infections are possible. They suspended ungerminated telial columns over *Pinus strobus* seedlings in an iceless refrigerator for 6 hours after which time the seedlings were set out-of-doors in a shady swamp. Positive results were obtained. The results of previously mentioned studies on the time required for sporidial production and germination would further substantiate the possibilities that pine infection might occur in some instances as a result of dews. (See section, "Germination of the Teliospores and Sporidia.") Considering time and temperature requirements, however, it is evident that in general the moist periods resulting from dews are of insufficient duration for pine infection to occur. Consequently, in the West dews have been of relatively little importance in this connection. On the other hand, however, dews frequently last long enough to cause the germination of teliospores and thus appear to have been of considerable importance in materially reducing, through dissipation of the sporidia, the potential amount of pine infection that might have occurred in some areas. Hirt (1942), working in the East, has also found that dews are of importance in exhausting the teliospores.

Results of studies by Spaulding and Rathbun-Gravatt (1925b) seem to indicate that teliospores of *Cronartium ribicola*, which do not start to germinate perceptibly, are not noticeably injured by subsequent drying, but when a teliospore once germinates perceptibly drying seems to kill it. Hirt (1935; 1942) found that young basidia present upon teliospores at the beginning of a hot, dry day are able to persist until evening and, if proper humidity and temperature conditions then occur, these basidia can renew their development and may produce sporidia within 3½ hours. He also found that sporidia germinate between temperatures of 32° to 34° F., and 70° F., inclusive, but the optimum temperature for their germination was between 54° F. and 57° F., while at lower temperatures a considerably longer period of time is required for this process. Since the summer nights in Idaho are generally quite cold with a point near freezing often reached and occasional frosts it would seem evident that few of the sporidia that are produced during dew periods have an opportunity to germinate and cause pine infection.

Observations on infected plants of the western black currant (*Ribes petiolare* Dougl.) growing along certain stream courses in Idaho showed that, as a result of the moisture supplied by almost nightly, heavy dews, relatively few telia remained ungerminated for any appreciable length of time. There was no evidence, however, that the sporidia produced under such conditions caused pine infection of consequence. Accordingly, it was apparent that dews were responsible for the dissipation of large quantities of teliospores and sporidia before favorable pine infection conditions in the form of rainy periods occurred. On the other hand, however, there was no apparent germination of telia borne on the sticky currant *(Ribes viscosissimum* Pursh) and *R. lacustre* growing on somewhat higher ground and but a few feet from the streams where dews remained on both of these species and associated pines for a much shorter period of time than on *R. petiolare* growing in the moist creek bottoms. Under such conditions susceptibility and telium-producing capacity can not always be relied upon as an index to the amount of rust a ribes species might transmit to pines. Consequently, such species as *R. viscosissimum* and *R. lacustre,* which are common in the uplands and lower in susceptibility and telium production, may, in some areas, equal or even surpass the importance of *R. petiolare,* which produces telia in abundance.

Receptivity and susceptibility

According to Spaulding and Rathbun-Gravatt (1925a) nothing is known regarding conditions within the pine leaves which favor or inhibit infection. It apparently is well established that the current season's needles of *Pinus monticola* are considerably more resistant than needles one year older (Buchanan 1940; Lachmund 1933a, 1933b; Pierson and Buchanan 1938b), although the nature of this resistance is not known. Lachmund (1933a) found that for infection occurring in a given year on the average about 10 per cent of the cankers form on the growth of the season of infection and over 50 per cent of them on growth one year older. If the current season's needles were about equal in susceptibility to those a year older the blister-rust epidemic in the West would obviously have been more severe than is the case at the present time for many more infections might have become established on pines than have actually occurred. This contention is strengthened by the fact that on young trees of *Pinus monticola* the ratio of the current season's needles to those one year older is about 1.5: 1.0 (Buchanan 1940).

Past history of spread of the rust in both the East and the West has amply demonstrated that heavy pine infections occur only once in several years, the intervening years being periods of relatively light and scattering infections. This has not been entirely and satisfactorily explained on the basis of prevailing weather conditions. Spaulding and

Rathbun-Gravatt (1925a) are of the opinion that there is some unknown factor that has a decisive influence in the infection of pines. According to York et al. (1927: 501), who summed up the results of their experiments together with those of other investigators, the information available seems to warrant the suggestion that the internal condition of the pines may be quite as important as external physical factors in explaining the infrequence of pine infections. Based on his own experience, the writer concurs in these opinions. It is a well known fact that the maturity of tissues has a marked effect upon the development of rusts and that the chemistry of a plant changes markedly as it ages. Recently, Limasset (1939) has drawn a distinction between the susceptibility and the receptivity of a given plant to a parasite. He reported that the amount of infection that develops depends not only on susceptibility, i.e., the physiological aptitude to harbor the parasite, but on receptivity, which is conditioned both by susceptibility and microclimatic factors. It is apparent that there yet remains much to be known about the factors influencing the infection of pines.

Vigor of the host

Raines (1922) found that with cereal rusts and certain other infectious diseases, the vegetative vigor of the host and the virulence of the disease may be in direct relation. The writer has often observed a parallel situation in connection with blister rust in the West. Badly suppressed trees show little or no rust after years of exposure to heavily infected ribes while in the same stands the thriftiest trees, except for rare individuals presumably naturally resistant, become severely attacked. Clinton and McCormick (1919) found that the rust flourishes in trees especially vigorous in growth. Spaulding (1929: 34), working in both eastern North America and Europe, observed the same relationship between vigor of the tree and its susceptibility. Posey and Ford (1924) and Filler (1933) found that the infection percentages in pine stands varied according to crown classes, being highest among dominant trees. Snell (1928) has shown that normal trees are more likely to be attacked by the rust than the suppressed, shaded, and blighted trees.

Resistant individuals within a species

There have been observed during the course of these investigations a few trees of *Pinus monticola* that exhibited considerable resistance to attack by *Cronartium ribicola.* One outstanding example of this nature is a single tree about 20 feet in height near Garibaldi, British Columbia. It is growing on an area where the rust became established on surrounding pines in 1913. By 1930 all other pines in the vicinity had succumbed to infection by blister rust. In 1933, when last seen by the writer, this tree was still alive and showed little evidence of attack by the rust. Apparently, resistant or immune individuals are more common in *P. strobus* in the East, for 163 such trees were recently found on four areas in Wisconsin (Riker and Kouba 1940), and Snell (1931) has reported the occurrence of 147 such trees of this species on a 2-acre study plot in New York.

Size of tree in relation to infection

There is no evidence that size or age of tree affects its susceptibility to *Cronartium ribicola*. Spaulding (1929) noted no indications that old trees of *Pinus strobus* are more resistant than middle-aged or young ones. Blister rust in damaging amounts has been found in *P. monticola* of varying sizes from seedlings up to mature individuals 200 feet in height (Buchanan 1938a; Lachmund 1934c; Martin 1935). It is known, as previously mentioned, that the rust develops more rapidly, i.e., with a shorter incubation period, in seedlings than old trees, but whether this may be taken as an index to greater susceptibility in the former than in the latter has never been established.

Studies (Buchanan 1938a; Childs and Kimmey 1938; Lachmund 1934a) and observations have shown that large trees of *Pinus monticola* become more heavily infected than small ones. There is, however, no evidence that this results from a difference in susceptibility between the two. It apparently may be explained by the fact that large trees, because of their much greater amounts of foliage, are much more likely to become infected than are smaller trees under the same conditions. Filler (1933) has found a similar relationship in *P. strobus* in the East.

In some instances small *Pinus monticola* trees have become more heavily infected, i.e., with a larger number of cankers in proportion to crown size, than large and mature ones in the same stand. Moreover, in all except very small trees, cankers are characteristically much more abundant in the lower part than in the upper part of the crown. It is evident that in such cases the more lightly infected trees or crown parts are at a greater distance from the sporidial source, the ribes on the ground, than those bearing more numerous infections. The influence of distance from the ground is accentuated by the fact that air currents, particularly at times when conditions favorable for pine infection prevail, tend to drift parallel to the ground surface and thus to carry the spores from infected ribes along close to the ground. In addition, moisture necessary for infection usually is retained longer on foliage at low levels than at higher, less protected ones. It would seem, therefore, that factors other than age appear to have considerable influence in the relative amounts of infection generally found in reproduction as compared with that in large and mature trees.

Relative virulence and abundance of sporidia from different ribes species

There is some evidence suggesting the possibility of a difference in virulence of the sporidia borne on different species of ribes (Lindgren and Chapman 1933; York et al. 1927). Also, there is some indication that sporidia from certain species are more tolerant to drying than those from other species (Spaulding and Rathbun-Gravatt 1926). Studies of this nature for important western ribes have not been made. On the other hand, no evidence has yet been obtained to the effect that the sporidia borne on any of the wild species native to the West are incapable of infecting pines, weather conditions being favorable. Ribes species vary considerably in their relative susceptibility and telium-producing capacity (Kimmey 1938; Mielke et al. 1937) and also in the number of sporidia produced per unit of leaf area (Taylor 1922). *Ribes lacustre* is relatively very low in telium-producing capacity as compared with numerous other western species studied (Kimmey 1938). Yet, other studies (Buchanan and Kimmey 1938; Mielke 1937) show that from sporidia borne on this species abundant infection of *Pinus monticola* may occur. Western experience has shown that the intensity of infection in a pine stand is proportional to the number and telium-producing capacity of the ribes within and around it.

Heavy ribes injection and premature leaf cast

Ribes species differ in the degree to which they are susceptible to the rust, consequently some of them are more congenial hosts upon which the rust may develop than are others. Heavy infection, however, may induce killing and premature casting of the leaves to varying degrees. Disposition to the casting of infected leaves seems to depend somewhat upon the species involved, for some of them may readily drop lightly infected green or partially green leaves. It has been observed, particularly in some years, that for various of the highly susceptible species the casting of a high percentage of the infected and telial-bearing leaves occurred during the summer when climatic conditions were relatively less favorable for pine infection than is generally the case later in the season. As a consequence, a high percentage of these fallen leaves were not only in a less favorable position for casting and dissemination of the sporidia, but it is also probable that many of the teliospores lost their viability under such conditions.

Of the western species known to be susceptible to the rust, the gooseberries seem to be more disposed to precocious leaf cast induced by infection than are the currants. Infected plants of the straggly gooseberry *(Ribes diuaricatum* Dougl.) and the whitestem gooseberry *(R. inerme* Rydb.) have often been observed in midsummer with only a small percentage of their original complement of leaves remaining. In tests outside of its native range *R. roezlii* was found to drop even the lightly infected green leaves so readily that very few telia had an opportunity to develop (Mielke and Hansbrough 1933). Limited observations within its native range in California, however, indicate that premature casting of such leaves may occur to a lesser degree than was found to be the case in the tests.

Influence of foliage screens on pine infection

The nature and density of vegetation between ribes and pines appear to have an effect on the intensity of infection on the pines and the distance from ribes at which they may become infected. Heavy screens of deciduous broadleaved species over infected ribes may greatly reduce or prevent damage outside that screen. Spaulding (1922a; 1929) has presented information, obtained mainly in the East, on the effect of plant screens on dissemination of the sporidia, and it is believed that the effect of such screens is dependent in part upon their density and on the abundance of sporidia in the vicinity.

In the West broadleaved trees are generally much less common in association with white pines than is the case in the East. Consequently it is doubtful if broadleaf screens are of as much importance in limiting the dissemination of the sporidia in the West as they may be in the East. Evidence of the effect of such plant screens in this regard is not entirely lacking in the West, however, and their importance may increase after the rust becomes more widespread in the sugar pine region of southern Oregon and California where broadleaved brush species often develop abundantly on cut-over lands and burned areas. Ribes are not uncommon in association with this brush which generally overtops them. It is believed that the brush will be a factor of considerable importance as a screen for the sporidia that may be produced on such ribes.

Plant screens in the West are not limited to the broadleaf species, however, for a few cases have been observed where dense stands of white firs, hemlock, and other shade-tolerant conifers have markedly restricted the dissemination of the sporidia as judged by the short distance from ribes that pines have become infected and the rapid tapering off in intensity of cankers. To what extent pine foliage may be effective as a screen is not known, but it would seem that dense and practically pure stands of white pines might limit to some degree the distance of dissemination of sporidia. In such cases the pines immediately adjacent to concentrations of ribes would become heavily infected while a relatively rapid tapering off in the intensity of the infection would occur with increase in distance from the ribes. Instances of rapid diminution in intensity of infection in dense stands of *Pinus monticola* have been observed, but it is not known to what extent screening was a factor in the decrease.

Effective Distance of Dissemination of the Sporidia

Ribes are so common in the white pine forests of the West that opportunities for obtaining trustworthy evidence on the distance of dissemination of sporidia are limited and must usually be provided by the artificial isolation of infection centers through the removal of all other ribes for wide distances around. The effective range of dissemination is governed in part by mathematical laws of dispersion and in part by the conditions and influences of the environment. Of these, the meteorological influences are among the most important and are also very variable. Experience has shown that, as a result, the distance that rust may spread from ribes to pines may differ widely on different areas and on the same area may vary widely from year to year.

As has been previously mentioned, results of studies with sporidia show that high humidity is required for these spores to live any length of time. All evidence indicates that they are largely, if not entirely, airborne and disseminated. The intensity of local prevailing winds during periods of sporidial production might therefore be expected to govern in part the distance that these spores are transported from ribes to pines.

Heavy rains occurring at the time the sporidia are being produced evidently wash them from the air and thus may greatly restrict the distance they might travel. The exposure of ribes and the species involved are of importance. A greater distance of spread may be expected from large concentrations of highly susceptible ribes than from those low in susceptibility because of the greater volume of sporidia produced on the former. The height, density, and composition of vegetation between the ribes and the pines are apparently important factors because of their screening effect on the sporidia. The growth habits of the ribes and their heights with respect to surrounding vegetation also influence dissemination of the sporidia. The topographical features of the area must be taken into consideration. Observations in the West have shown that the intensity and distance of spread may be greater down a slope than up it. There no doubt are other factors of importance involved in the distance of dissemination of the sporidia.

Some of the knowledge on the subject has been obtained through general experience. The results of observations made during the past 20 years in the West show that the distance of spread of the rust from ribes to pines seldom exceeds 600 to 900 feet. A few instances are known, particularly in the humid coastal section of British Columbia, where spread to pines in damaging amounts has occurred over nearly a mile and possibly farther. In the aggregate, however, such cases are exceedingly rare and have involved exceptionally favorable moisture conditions and large concentrations of highly susceptible ribes.

Buchanan and Kimmey (1938) reported on the results of studies on distance of spread and intensity of infection on *Pinus montieo/a* from *Ribes /aeustre* and *R. viseosissimum*-two species relatively low in susceptibility and telium-producing capacity. In 12 tests on a total of 7 plots it was found that both species were capable of spreading appreciable rust to pines for a distance of at least 150 feet, but in one test spread occurred from *R. viseosissimum* over a distance of about 250 feet. For both species the intensity of infection was heaviest near the ribes and fell off to relatively low values at a distance of 50 to 60 feet from them. In these tests a few small and centrally located ribes were used, all others having been removed for a considerable distance around.

Near Arrow Park, British Columbia, a number of western white pines in a young, natural stand of this species were found infected. The diseased trees were centered around a small, escaped *Ribes nigrum* bush. No other ribes were found close enough to have been responsible for the infection.

An examination of the pines in the vicinity of this bush revealed that most of the cankers were on trees within 25 feet of it and none on those beyond 75 feet.

On a plot established. near Chee Kye for the purpose of determining the maximum distance blister rust will spread from native ribes to *Pinus monticola* under field conditions, it was found that under the conditions existing there no protection of the planted pines against the rust was obtained by the removal of ribes for a distance of 1,250 feet (Putnam 1932). Furthermore, there was no doubt that pine infection on the plot resulted from ribes more than 1,250 feet away. Extremely favorable climatic conditions, topography, and large numbers of highly susceptible ribes apparently were largely accountable for the distance of spread in this case which is exceptional for the West.

A few cases have come to attention in the West where the highly susceptible *Pinus albicaulis* has become infected at distances upwards to a mile or more from ribes (Bedwell and Childs 1941). The trees in question were growing on high peaks on which mists, usually accompanied by strong winds, are common in the fall of the year and often persist for several days.

Much information on the distance of spread of the rust from ribes to pines has been obtained in connection with the control of this fungus. Experience thus gained over a long period of time has demonstrated that while the infecting range of the sporidia may vary under different forest conditions a zone 900 feet in width free of wild currant and gooseberry bushes usually gives adequate protection to the pines (Darrow and Detwiler 1934; Detwiler 1933; Martin 1939; Bur. Ent. and PI. Quar. 1938). With *Ribes nigrum,* however, a wider protective zone is generally needed since spread from this species may occur over distances up to a mile (Detwiler 1933). This evidently happens not only because it is the more susceptible of all species, but also because it produces an abundance of telia, bears relatively large amounts of foliage, and holds infected leaves well.

Considerable attention has been given to the distance of spread from ribes to pines in the East (Posey and Ford 1924; Spaulding 1922a; 1929). The results of these experiences and investigations indicate that the situation there does not differ markedly from that prevailing in the West. According to Spaulding (1929), 600 feet is usually a sufficient distance over which to remove ribesaround a pine stand to prevent serious damage to *Pinus strobus* from all ribes except the European black currant.

Conditions in Europe, however, differ from those in North America (Boyce 1926; Spaulding 1929)' *Ribes nigrum* is a common garden plant in many parts of Europe. Apparently because of the extreme susceptibility and resultant great abundance of sporidia produced on this host, heavy infection of planted *Pinus strobus* has occurred at distances of two-thirds of a mile or more on a scale not approached within the altitudinal limits of commercial timber in North America.

THE RUST ON RIBES

RIBES IN THE WEST AND THEIR SUSCEPTIBILITY

THERE are approximately 60 native species of wild ribes in the western part of the United States and western Canada (Coville and Britton 1908). The majority but not all of them occur within the ranges of the western white pines. Some are quite limited and local in their distribution, others widespread. Oregon and California with about 30 each are richer in the number of species than any of the other western States. The writer has seen 15 species in British Columbia and that number is believed to be very near the total for the Province. One of the most common species within the range limits of the western white pine is *Ribes lacustre.* In the Inland Empire region (northern Idaho, northeastern Washington and western Montana) of the total number of over 393 million bushes of 8 species of wild ribes destroyed in the blister rust control operations from 1923 to 1939, inclusive, over 43 per cent have been this species and 49 per cent *R. viscosissimum* (Swanson I939b). The latter species, however, is not so common elsewhere within the known distribution of the rust in the West.

Wild ribes are common plants in the white pine forests of the West. In the main white pine regions of the Inland Empire there is an average of approximately 195 ribes bushes per acre. This figure is based on the total number of bushes eradicated and the total number of acres worked in the control operations during the period 1923 to 1939, inclusive (Swanson I939b). Computed in the same way and covering a similar period of time, but involving a somewhat smaller basis, it is found that ribes average approximately 160 bushes per acre in the main sugar pine region of California and about 85 per acre in the sugar pine region of southern Oregon (Benedict 1939)' In comparison, an average of only about 25 ribes per acre has been encountered in the protection of *Pinus strobus* in the eastern part of the United States where control operations have covered a larger area than in the West (Bur. Ent. and PI. Quar. 1938). Furthermore, the eastern bushes generally are smaller in size (Boyce 1938: 241). Considering the situation from the standpoint of numerical abundance of ribes, and of total leaf area, it is readily obvious that the West is a more favorable region for spread and intensification of blister rust than is the East.

Approximately three-fourths of the western ribes species are known to be susceptible to the rust. This has been determined either under natural conditions, in test gardens, or in greenhouses (Hahn 1928; Kimmey 1935, 1938; Mielke and Hansbrough 1933; Mielke et aI. 1937; Spaulding 1922a). No species yet tested or naturally exposed has been found to be immune. Between species there are not only wide differences in susceptibility but also in telium-producing capacity. The most intensive studies on susceptibility have been devoted to those ribes numerically important as associates of western white and sugar pines (Kimmey 1935, 1938; Mielke et aI. 1937; Mielke and Hansbrough 1933). For many of the species less prominent as associates of white pines or occurring outside the ranges thereof little more may be said at the present time than that they are susceptible. This is mainly because the bases of tests have been very small and no consideration has been given to telial production. The only information available on the susceptibility of some of the western ribes is from the results of infection experiments made in the East and reported by Spaulding in 1922 (1922a). Kimmey (1938) has summarized the available data on about 30 species obtained from western studies on susceptibility and telium-producing capacity and has arranged them as to their relative importance in these regards. Based on the evidence to date, it is believed possible that any native ribes, given time, may carry enough blister rust to damage seriously closely adjacent pines. Since, however, it is rare to find but a single species occurring over a pine area of any great extent, the potential damaging power of anyone ribes may not be outstandingly important in the spread and intensification of the rust over a region.

Within the white pine belt in the coastal section of British Columbia, the most common native ribes are the stink currant *(Ribes bracteosum* DougI.), *R. divaricatum,* the winter currant *(R. sanguineum* Pursh), and *R. lacustre.* The first three are highly susceptible to blister rust, but the latter one in comparison is very low (Kimmey 1938). These four ribes also occur commonly in western Oregon and Washington. Many of the coastal species do not grow within the interior white pine belt of British Columbia, where *R. viscosissimum,* which is moderate to low in susceptibility, and *R. lacustre* are by far the most common species. These two ribes and the highly susceptible *R. petiolare* and *R. inerme* (Mielke et al. 1937) are the most common species in the Inland Empire, while in the adjacent Rocky Mountain region of Colorado and Wyoming *R. inerme,* the wax currant *(R. cereum* Dougl.), and the gooseberry currant *(R. montigenum* McCl.) are of frequent occurrence (Joy 1938). The only information available on the susceptibility of the latter species is that slight infection developed in the case of a single test of one plant in a greenhouse (Spaulding 1922a: 19). Tests of native *R.cereum* in British Columbia have shown it to be lower in susceptibility than any other species of ribes tested in the West (Kimmey 1938), but it is felt that additional studies must be made of this widely distributed species before its relative position in the susceptibility scale is established with reasonable certainty.

The principal ribes associates of sugar pine within its main range in the Sierra Nevada of California are the Sierra currant *(R. nevadense* Kell.) and *R. roezlii.* Of the two, the latter is by far the more important numerically. In tests conducted outside their natural ranges both of these species proved to be highly susceptible, but it was found that very few telia formed on *R. roezlii* (Mielke and Hansbrough 1933). Recent observations within their natural range, however, not only substantiate the previous tests showing a high degree of susceptibility but also indicate that telia may be produced in abundance on *R. roezlii.* Besides these two species, *R. cereum* is also fairly common within some parts of the range of sugar pine.

The European black currant *(Ribes nigrum),* or the cultivated black currant as it is commonly called, is the most susceptible and profuse in telium production of any ribes species known. Because the species is such a serious menace to the growing of white pines, a number of States forbid its possession and growth by statute, and Federal quarantine regulations restrict interstate movement of the plant or parts thereof (Martin 1939). Destruction of the species in some of the western States was started in 1922 (Office of Blister Rust Control 1923), and by 1927 it had been eradicated from Montana, Idaho, Washington, and Oregon, and from approximately two-thirds of California (Wyckoff 1927). In British Columbia, however, where white pines constitute a relatively very small percentage of the merchantable timber stands by volume

(Whitford and Craig 1918), there are no restrictions governing the possession of *R. nigrum* and the species is still an important one in the progress of the rust in the interior of the Province. Experience has shown that under western conditions the cultivated red and white currants are, on the whole, quite resistant to blister rust and very low in telium-producing capacity. They are not grown in abundance within the white pine forest regions. Hahn (1930) has shown a large number of varieties of these currants to be quite susceptible under greenhouse conditions but gives no information on telium production, a highly important factor. On the other hand, Snell (1942) has found that, as compared with several other species of ribes found in the East, the red currants produce relatively very few teliospores and sporidia and that these spores are of lowered viability.

There have been found not only great differences between species in susceptibility and telium-producing capacity but also in teliospore production per unit of leaf area bearing telia. The latter results from differences in size of the telial columns on the infected area. Because of these factors there are marked differences in the potential pine-infecting capacity of ribes species (Mielke et al. 1937; Taylor 1922). Some species that rank high as producers of telia are *Ribes nigrum, R.petiolare, R. inerme, R. divaricatum, R. sanguineum, R. bracteosum,* and *R. nevadense* (Kimmey 1938).

The ecologic or growth forms of ribes are another important factor. In most cases the individuals of a species growing in partial shade or in shade of other plants are more susceptible and generally produce more telia than individuals growing in the open (Kimmey 1938; Mielke et al. 1937; Mielke and Hansbrough 1933).

A number of western species of ribesshow varietal differences. Very little is known, however, regarding the occurrence of biotypes. Some evidence has been accumulated indicating that varieties of certain species react differently to the rust than the species themselves, and that biotypes, occurring particularly in some species of very wide distribution, vary in degree of susceptibility. *Ribes cereum* and *R. roezlii* appear to be species in this latter category.

Age and size of the plant are also factors to be considered. It has been found almost without exception that young and thrifty ribes are more susceptible than very old, slow growing, and large bushes of the same species.

Susceptibility to aeciospores is not always a criterion of the ultimate amount of rust that may develop on a species during the season. Recorded information (Mielke et al. 1937) and observations show that during the early 'part of the season the disparities between species resulting from aeciospore inoculation offer little or no indication of their relative susceptibility as it finally appears. With some species the great bulk of the infection develops from late June to early September through uredial intensification. With other species, and particularly *Ribes lacustre*, this pyramiding of infection during summer is usually relatively unimportant, although in the case of such species they may show a greater susceptibility to aeciospores than those producing an abundance of rust later in the season.

Investigators generally agree that resistance of a host plant to attack by a parasitic fungus is physiological rather than anatomical in nature. Investigations recently reported by Anderson (1939) and by Offord (1940) provide the first evidence indicating that the resistance of *Ribes* spp. to *Cronartium ribicola* is of a physiological nature. Results of their studies show that the number of stomata per unit of leaf area, thickness of protective tissue, and other anatomic characters are not factors in resistance or susceptibility of a species, but the work of Offord suggests the possibility that tannins may be of importance in this regard.

DEVELOPMENT OF THE RUST ON RIBES

Parts of tbe plant attacked and mode of infection

The usual place of development of the uredia and telia of *Cronartium ribicola* on ribes is on the lower side of the leaf. Their formation elsewhere on the plant is exceptional. They have been found, however, on the upper surfaces of leaves, on leaf petioles, green fruits, floral bracts, peduncles, rachises, cotyledons, bud scales, and young stems and bark (Kimmey 1938; Spaulding 1922a). It seems well established that the germ-tubes from aeciospores and urediospores enter the leaves by way of the stomata (Anderson 1939; Clinton 1918; Colley 1918; Spaulding 1922a). Stomata have been found to be far more common on the lower than on the upper surface of leaves or than on other green parts of the plant (Spaulding 1922a: 50). The place of occurrence of the stomata in abundance compares favorably with the relative occurrence of the uredia and telia on the various parts and suggests the possibility that infection of all of them may take place in the same manner, i.e., by way of the stomata.

Occasionally telia may be fairly common on parts other than the leaves. Telial columns normal in size were found in abundance on rachises of *Ribes petialare,* particularly during one season, on a large number of heavily infected bushes. Telial formation on leaf petioles as a result of direct infection is probably more common on the relatively resistant *R. lacustre* than on any other species in the West, and a few instances have been observed where the great majority of the telia found on large groups of these bushes were on the petioles.

Incubation period on ribes

From 1924 to 1929, inclusive, the writer assisted on large scale ribes susceptibility studies in which thousands of bushes *in situ* were infected with the rust as a result of dusting them prior to rainstorms with aeciospores of *Cranartium ribicola* (Mielke at al. 1937; Kimmey 1938). Since the time at which infection took place was known these studies afforded an excellent opportunity to secure information on the incubation period of the rust on ribes under natural conditions. For the purpose of this paper the incubation period is regarded as the time between infection and the first evidence of the rust to the unaided eye. This evidence is characterized by etiolated spots or flecks that are indicative of infection by C. *ribicola.* In all cases, however, verification of the infection in this stage was made by subsequent examinations to determine positively that uredia developed on these spots. Immature uredia usually formed two or three days later and urediospore production generally occurred 6 to 8 days after the appearance of the flecks, the time required being influenced by prevailing weather conditions. These studies were conducted for the most part in and immediately adjacent to the Okanagan Valley of British Columbia. Most of the inoculations were made in May, which in that region has an average monthly mean temperature of slightly over 50° F.[7]

Under the conditions of these studies the minimum incubation period was found to be 13 and the maximum 30 days. In the majority of the cases it ranged from 16 to 20 days. These figures are somewhat higher than those given by Lachmund (1934b: 103). According to him the usual period out-of-doors in the West is approximately 2 weeks, with a

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[7] From British Columbia Department of Agriculture Weather Records.

variation from as little as 10 days to as much as 3 weeks. The basis on which this was determined, however, is not given. Also, he apparently regards the incubation period as the time from inoculation until fully matured sporulating uredia have developed. This would tend to shorten still more the period reported by him as compared with that found by the writer.

In studies conducted within the range of the rust in northern California, and in which aeciospores were also used as the inoculum, the period in three tests in May 1938 was 11, 13, and 13 days, respectively, whereas in six different tests in May 1939 it was 14, 17, 20, 22, 22, and 24 days, respectively. Weather records show temperatures were somewhat higher during the periods of incubation in 1938 than was the case in 1939. Eight other tests made in the summer and fall of 1939, and in which urediospores were used as the inoculum, showed periods of 11, 14, 14, 15, 16, 17, 17, and 20 days, respectively. The longest of these incubation periods occurred in late August and September during periods of weather in which temperatures averaged lower than was the case at other times during the tests.

As a result of these studies it seems evident that temperature has a strong influence on the length of the incubation period on ribes. Based on his experience in the West Lachmund (1934b) is of this same opinion. This is also confirmed by Spaulding as a result of studies in the East (1922a). According to him the length of the incubation period is affected not only by external conditions of temperature and moisture but also by the age and condition of the leaves infected. The influence of age and condition of the leaves has not been studied in the West.

Under outdoor conditions the period of incubation between infection by aeciospores and urediospores and the production of mature uredia appears to be somewhat longer in the West than in the East. In the latter region Spaulding (1922a) reported it varied from 11 to 18 days, but usually it was 13 to 15 days in mature leaves and somewhat longer in leaves that were very young when inoculated. In the greenhouse he found the period to be somewhat shorter. Out of 493 inoculation tests the range was 7 to 17 days with slightly over 50 per cent of the cases fruiting in 10 to 12 days. Hahn (1928), who also conducted experiments in a greenhouse in the East, found that mature uredia usually appeared in 8 to 14 days with the average length of time 11 days. In the West, Pierson and Buchanan (1938a) found that 11 to 12 days elapsed between inoculation and the appearance of the fleck stage on *Ribes petiolare* kept in a greenhouse. Temperature conditions generally should be more uniform and somewhat higher in a greenhouse than out-of-doors and this possibly accounts for the shorter periods encountered indoors as compared with those under natural conditions. Also, temperature conditions may account for the shorter time in the East as compared with the West.

The uredial stage

Following infection of ribes in the spring of the year by aeciospores there occurs, as previously mentioned, a period of incubation generally of between two and three weeks duration before the uredial stage appears. This period, however, is markedly shorter in practically all cases than the interval of time between the appearance of the first aecia on pines and the occurrence of the first uredia on ribes. As a result of studies conducted over a number of years in British Columbia and northwestern Washington, it has been found by the writer and others that the uredial stage does not make its appearance until approximately 3 to 9 weeks, usually about 7 to 9 weeks, after the first aecia are produced (Mielke and Kimmey 1935).

This lag, however, generally does not represent a longer than normal incubation period. Instead, it apparently is related to the time of occurrence in comparative abundance of both aeciospores and ribes leaves and also to weather conditions favorable for infection. At the time of production of the first aeciospores in the spring few, if any, leaves may be present on ribes. Although tests have shown that the youngest leaves, at least of some species, are more susceptible than older ones (Lachmund 1934b; Pierson and Buchanan 19J8a), their small size and the limited number of them that may be exposed early in the spring together with the relatively few aeciospores being disseminated at that time reduce considerably the chances for ribes infection. While aecial production has started in the West as early as late February in a few instances and somewhat more commonly in March, generally abundant sporulation does not occur until some time in April or May and occasionally not until in June depending mainly upon the location and the elevation, and upon the character of the seasonal weather (Mielke and Kimmey 1935). These factors also have an influence on the time the first uredia are developed. In the coastal region of British Columbia the first uredia have been observed in a few years as early as late April, generally they appear in May, and occasionally not until June, while in the interior region of that Province they usually have not been found until some time in June (Mielke and Kimmey 1935). Relatively few observations in this connection have been made in the Inland Empire white pine region centered in northern Idaho, but it is believed that the time at which the first uredia appear on ribes there does not differ greatly from that obtaining in the interior of British Columbia since climatic differences between the two regions are not marked. Also, comparatively few records have been secured in Washington and Oregon but, based on observations and a knowledge of climatic conditions within the white pine belt of those States, it seems likely that the first uredia will generally be found appearing there in Mayas is the case in the coastal region of British Columbia to the north. The rust has not been present long enough in California to obtain records of value in this regard.

In addition to the factors of locality, elevation, and character of the seasonal weather, the time at which the leaf buds break on different species of ribes may also have some influence on the time the first uredia appear in the spring. One of the earliest species to leaf out is *Ribes lacustre* and uredia have generally been found on it at a somewhat earlier date than on its common associates. This may suggest the possibility that the incubation period is shorter on *R. lacustre* than on other species. Infection experiments conducted over a number of years and involving in the aggregate thousands of bushes showed no evidence, however, that there is a difference in the length of this period on the different species.

For abundant uredial intensification, a good distribution of favorable moist periods in synchronization with the production of urediospores is more important than the total amount of precipitation during the season (Mielke et al. 1937). In the West as many as six or seven generations of uredia have been observed to develop during the season in a few very favorable years and localities. Generally, however, four or five generations form, and occasionally only two or three. In the Okanagan Valley of British Columbia in 1927 a few cases were noted in which but a single generation had developed on highly susceptible wild species up to the middle of August. The bushes involved were naturally infected by aeciospores some time in the spring. Such cases, however, are extremely rare and occur only when moisture conditions unfavorable for intensification extend over a long period of time. Spaulding (1922a: 55) reported the production of seven distinct generations of uredia developing in one locality in the East in 1918, but in 1919 the generations in another locality were not so distinct and after August 1, because of rain every day or so, became overlapped and confused with each other. In a few instances in the West many more than seven generations must have developed, but their number was impossible of determination because of almost continual intensification and overlapping of generations induced by heavy dews occurring almost every night. Uredia may continue to form as long as there are green leaves on the ribes bushes in a given locality. Fresh uredia have been observed as late as the first part of November. It often happens, however, that some of the last uredia to form in the fall never produce urediospores, this spore stage being skipped and telia being produced instead.

The species of ribes involved is another factor affecting the number of generations of uredia and the length of the period over which urediospores may be produced during the season. Spaulding (1922a:56) reported this period to vary with species, being shorter on *Ribes lacustre* than on any other of a number of ribes studied. This same situation occurs in the West where it has repeatedly been observed that the period is also shorter on *R. lacustre* than on other species. In a few instances, following infection from inoculation with aeciospores in the spring, no intensification whatever occurred on large groups of bushes of this species, whereas on infected *R. uiscosissimum* growing on the same area four or five generations of uredia developed. Most of the intensification on *R. lacustre* generally occurs during the first part of the season, whereas a similar development of the rust has not been observed on any other of a large number of species studied in the West.

Spaulding and Rathbun-Gravatt (1925b: 914) often found that leaves apparently bearing only telia also have fresh urediospores borne around the bases of the telia. They regarded these spores as a probable source of new uredial sori that often appear on new leaves late in the season. The writer has frequently seen evidence indicating that these spores may also infect old leaves late in the season, thus initiating a new generation of uredia as long as two months after the telial stage became the only spore stage apparent.

It is obvious that in general the more numerous the generations of uredia the greater the amount of telia that may be produced and consequently the greater the potential possibilities for pine infection. This will particularly be the case in connection with the establishment of the rust in new localities as a result of long-distance dissemination of the aeciospores, and for abundant intensification in stands where the disease is already present.

The telial stage

The season of production of the telia lasts from the formation of the first ones in the spring until the shedding of the leaves of their ribes hosts. The date when the first telia form varies from year to year with the earliness of the season, the condition of the host leaves, and the species of ribes. Generally they may be found earlier on *Ribes lacustre* than on associated species. Possibly this may be explained by the fact that the leaves of that species usually mature considerably earlier than is the case with its common ribes associates. The earliest that telia have been noted in the West is mid-May, usually they appear in June, and occasionally not until some time in July. The peak of their production sometimes is reached in July, generally in August or September, and occasionally in October, apparently depending more upon the character of the season than the locality (Mielke and Kimmey 1935). In the coastal region of British Columbia a few fresh telia were still present in mid-November of one season. The latest date at which they may form depends upon the weather conditions of the latter part of the season and the ribes species since some ribes normally mature and cast their leaves earlier than others.

Western records show that from about 2 to 6 weeks, generally 3 to 4 weeks, may elapse after the formation of the first uredia in the spring before the first telia appear. Allowing 2 to 3 weeks for incubation of the fungus in ribes leaves, the first telia may generally be expected to appear 5 to 7 weeks after infection occurs. In the East, they may be formed at almost any time from 12 days up to 2 or 3 months after infection (Spaulding 1922a: 40).

Spaulding and Rathbun-Gravatt (1925a) are of the opinion that, while weather conditions somewhat retard or accelerate the formation of the first telia, they seem to have a potent influence upon the formation of telia in abundance. With this the writer concurs. It has been observed that telia are generally not found in abundance during the warm and dry part of the summer, but with the advent of cooler fall weather their production is stimulated. Possibly, photoperiodic conditions may also have some effect in this regard by inducing changes in the ribes leaves. Moshkov (1938) found that, under natural conditions in Leningrad, Russia, the teliospores of *Cronartium ribicola* developed only in the autumn when the day length is less than 16 hours. While length of day may he a controlling factor under certain conditions or for certain species it does not appear to be the only one, for telia commonly form in June in British Columbia where the day length during that month is greater than 16 hours. Spaulding (I922a: 40) has reported for the East: "There are times when the fungus produces only uredia in the greenhouse as well as in the field. The behavior of the fungus is not entirely controlled by weather conditions, but is greatly influenced by the condition of the host leaves. At other times the fungus will produce nothing but telia. At such times telia are produced in a very short time. Telia have been obtained in 9 to 10 days after infection." He also reported that in many cases telia have been obtained directly from infections resulting from aeciospore as well as urediospore inoculations upon mature leaves. Such behavior of the rust has rarely been observed in the West.

In the West generally 4 or 5, occasionally 6, and rarely as many as 7 distinct waves of telia may form in a season. As is the case with uredia, they are generally produced in relatively greater abundance with each succeeding generation. The production of new telia may be limited by drought or by heavy infection still mainly in the uredial stage both of which are likely to cause early shedding of diseased leaves, particularly of some species. *Ribes roezlii* casts a high percentage of its infected leaves while the rust is still in the uredial stage and before telia have had time to develop. The leaf tissues are more readily killed on some species than others as a result of rust attack and on these necrotic or dead areas relatively few if any teliamay develop.

According to Colley (1918: 637), telial columns arise. either from old uredia or as entirely new and separate entities. Under outdoor conditions in the West the first telia have always been found to arise from old uredia, and their formation as entirely new and separate entities has been observed to occur only late in the season. The latter is probably more common on *Ribes lacustre* than on any of the other species. The length and diameter of the mature telial columns vary with the host species upon which they are borne (Mielke et al. 1937; Spaulding I922a; Spaulding and Rathbun-Gravatt I925b) and the time of year they form, late season telia often being relatively quite short.

Snell (1929) has regarded the telial stage as a combination of an emergency stage, which insures the continuance of the rust cycle by developing just prior to the death of the host tissue, and a multiplication stage, whereby the fungus apparently puts forth its entire available energy in producing a multi-seriate column of teliospores, each of which multiplies itself again in the formation of four sporidia. Spaulding and

Rathbun-Gravatt (1925b) found that the teliospores may survive outdoor conditions from the time of the formation of the first ones in the season until after winter has set in. Thus, the telia may tide over the rust during dry periods of weather in summer and then germinate vigorously later in the season when climatic conditions are favorable for pine infection to take place.

SOME FACTORS INFLUENCING INFECTION OF RIBES

Injection resultingjrom· aeciospores

According to Snell (1929), who has discussed the functions of the spore stages of *Cronartium ribicola,* the aecial stage not only initiates the rust's cycle on ribes but, more important, is primarily the stage responsible for long-distance dissemination. The latter phase will be discussed later. There are a number of factors involved in the infection of ribes by aeciospores, and probably one of the most important is length of life of these spores.

The results of studies made up to 1922 by various investigators on the longevity of the aeciospores have been summarized by Spaulding (1922a). These show that the aeciospores may retain their viability for 5 or 6 months under favorable conditions and for several weeks even when conditions are unfavorable. There was, however, considerable variation in the results that are possibly attributable to differences in conditions and technique. In a later study Doran (1922) obtained no germination under any conditions when the aeciospores were more than 8 weeks old. In a number of tests conducted over a period of several years, the writer has found them to germinate well after storage of sporulating cankers in paper bags indoors for periods of 4 to 6 weeks. Probably the majority of the aeciospores lose their viability under natural conditions within about a month. This assumption seems a logical one based on the experiences of others (Doran 1919, 1922; Spaulding 1922a). According to Doran (1922), although there is at first a sharp falling off in viability, that of the remaining spores is retained for a comparatively long time and only gradually lost. He found that connection with or detachment from the parent had no effect on the length of life of the aeciospores, viability decreasing the same in both cases. Doran also found that temperatures of 40° F., 57° F., and 73° F., in which freshly collected aeciospores were kept indoors, had no effect on their longevity, that the spores stored in moist air retained their viability longer than those stored in drier air, and that they germinated with diminishing vigor as the season advanced.

Fresh aeciospores taken from pines early in the season germinate more vigorously than those collected later in the season (Doran 1919, 1922; Spaulding 1922a). The viability of the fresh spores is generally high, as many as 95 to 100 per cent germinating under favorable conditions (Doran 1922; Spaulding 1922a). Older aeciospores are erratic in germination (Spaulding 1922a). Klebahn (1904) found that scarcely any of the aeciospores of *Cronartium ribicola* germinated in water after storage in a dry condition for 48 days, but that they readily germinated and infected all the inoculated leaves of *Ribes aureum* Pursh, while on a ribes-decoction agar germination was slow at first but later germ-tubes were produced in considerable quantity. The results of his studies indicate the possibility that these spores germinate more readily when in contact with ribes leaves than when they are germinated upon the surface of water. According to Colley (1918:634), too much water is often as inimical to germination as too little. Aeciospores from cankers stored indoors in paper bags for varying periods of time up to about 7 weeks have often been tested for viability by the writer by dusting them on the surface of the tap water in a glass tumbler, which was then covered with a piece of paper. The tests were always started early of an evening and conducted under room temperatures. In every case by morning, or within 8 to 12 hours, the interwoven germ-tubes had formed a mycelial mat that usually could be lifted from the surface of the water on the point of a pencil.

Under natural conditions the necessary moisture for the germination of the aeciospores is generally supplied during rainy periods. Infection of ribes may occur during foggy weather if the period of such weather is of sufficient duration, but fogs are of minor importance as a source of moisture supply for infection in the West. Spaulding (1911:30) placed aeciospores upon the leaves of ribes growing outdoors and exposed to dew nearly every night, but no infection developed. Possibly the negative results in this case may be attributed to insufficient duration of the nightly moist periods for germination of the spores and infection to occur. Gravatt (Spaulding 1922a:43) obtained infection on ribes kept moist under bell jars for 7 hours. This is probably about the minimum length of time for germination of the aeciospores and infection to take place. Outdoor inoculations of thousands of ribes bushes of different species by dusting the leaves with aeciospores have shown that these are capable of causing abundant infection during rainy periods of 8 to 12 hours or more duration.

Although moisture is necessary if ribes are to become infected by aeciospores, an overabundance of it may markedly limit the amount of infection that these spores may cause. Heavy rains are believed to beat down the aeciospores from the air (Spaulding 1922a:33). The apparent efficacy of such rains in inhibiting dispersal of sporidia and the infection of pines has been treated in a preceding section, "Rain in Relation to Pine Infection." Pennington (1925: 604) has observed that heavy precipitation in the period of aeciospore production reduced greatly the dispersal of the spores by washing them out of the aecia. He also noted that in moist weather many of the aeciospores germinate within the aecia, their germ-tubes then preventing or retarding the dispersal of the remaining spores. These same conditions have been observed by the writer. In the coastal region of British Columbia in 1926 the main period of aeciospore production occurred between mid-April and late May. During that time exceptionally rainy and moist weather prevailed, there being very few warm and dry days. Initial infection of ribes that year was extraordinarily light even around centers of heaviest pine infection areas. Similar reductions in the amount of rust on ribes initiated by aeciospores have been found to occur in certain other years, particularly 1941 and 1942 in Idaho, which were characterized by abnormally moist weather during the period of production of these spores. The heaviest natural infection of ribes by aeciospores has been observed in those years in which rains occurred with only moderate frequency during the period of aeciospore dispersal. The writer has obtained excellent infection results when aeciospores were dusted onto the lower surface of ribes leaves just prior to heavy and prolonged rainstorms, thus indicating that these spores were not easily dislodged or washed from the leaves by such rains.

Doran (1919) found the minimum, optimum, and maximum temperatures for the germination of the aeciospores to be 41° F., 54° F., and 66° F., respectively. In 1919 he reported that these spores require 8 to 10 hours to germinate in most cases (1919), but in a later study (1922) he found that at the optimum temperature (54° F.) 12 hours were required for germination, while at temperatures approaching the minimum and maximum a longer period of time was required. Hirt (1937) did not attempt to determine the minimum or optimum temperatures at which the aeciospores will germinate, but did find that they will germinate at temperatures as high as 82° F. He obtained the highest percentage of germination, however, at about 54° F., which was the lowest temperature used in his tests. The latter corresponds closely with the optimum determined by Doran. Hirt concluded that the results of his experiment indicate ribes infection may occur at temperatures as high as 82° F. but is more apt to occur at the lowest temperatures used in his experiment. He obtained abundant germination with germ-tubes of good length within 12 hours in all cases. This would indicate that germination started in somewhat less than 12 hours.

The effect of exposure of the aeciospores to the rays of the sun does not seem to have received much attention, the writer having found in the literature but one reference to this factor. Pennington (Spaulding 1922a: 39), in 1919, found that the viability of aeciospores after they had been exposed to direct sunlight showed a decrease of 50 to 75 per cent in viability after three hours' exposure. After an exposure of 8 hours some of them (I in 1,500 or 2,000) were still viable. Details of the method of exposure were not given.

In addition to longevity of the aeciospores and the time, temperature, and moisture conditions involved in their. germination, there are a host of factors of importance in the infection of ribes. Experience has shown that western species vary greatly in degree of susceptibility to aeciospores, the range in this regard extending from highly resistant to extremely susceptible (Kimmey 1938). In most cases the part-shade and shade forms of a species are more susceptible than the open or sun. form (Kimmey 1938; Mielke et al. 1937). Also, there apparently are, at least for some species, inherent differences in susceptibility between bushes of the same species (Mielke et al. 1937). The nature of the resistance to infection by aeciospores is not definitely known, but, as previously mentioned, there is evidence indicating it may be physiological rather than physical.

Also of importance in the infection of ribes is the age of the leaves. Lachmund (1934b), who studied four western species under field conditions, found that in the case of three of them *(Ribes petiolare, R. inerme,* and *R. lacustre)* the leaves between the ages of 2 and 16 days were considerably more susceptible to aeciospores than were older leaves, but in the case of the fourth species tested *(R. viscosissimum)* there was no uniform correlation between age and susceptibility. For all four species the leaves were susceptible from the time they emerged from the buds. No rust developed on 30-day-old leaves of *R. lacustre* growing in the open and 38-day-old leaves on the shade-form bushes, whereas 40-day-old leaves on both forms of the other three species were still susceptible. The results of studies by Pierson and Buchanan (1938a) conducted on *R. petiolare* in a greenhouse showed that the leaves of this species of all ages from those 2 to 6 days old to those 71 to 74 days old were susceptible to aeciospores. Older leaves were not included in their experiment. They also found that the leaves were in their most susceptible state during the first few days after emergence and that they remained highly susceptible until about the time of size-maturity, after which their susceptibility declined. This is in close agreement with the findings of Lachmund on this species. Other species of western ribes have not been studied to determine the most susceptible ages of their leaves, but since there was little difference in susceptibility between leaves of *R. viscosissimum* ranging in age from 4 to 44 days it seems logical to expect that at least some other species may react similarly. Lachmund mentioned that his findings were at variance with those of eastern investigators who found that ribes leaves are immune or resistant in the beginning and that they reach their most susceptible stage when they have attained full size but have not yet hardened off.

The significance of the age of ribes leaves in relation to their susceptibility to aeciospores lies in the fact that the time of aeciospore production is less subject to influence by variations in seasonal conditions than is the commencement of growth activity in ribes (Lachmund 1934b). Consequently, at least for some species, the maximum stage of susceptibility may be passed before aeciospores are produced in abundance. This may therefore be of importance, particularly in some seasons, in the degree of initial infection on certain species.

Infection resulting from urediospores

It is generally acknowledged that the function of the urediospores is to intensify the rust on ribes. In order that intensification may occur, moisture is needed for the germination of these spores. Under natural conditions the necessary moisture is generally supplied during rainy periods. In comparison with rain, fog and dew as sources of moisture supply are of relatively little consequence, but of the two dew is probably of more importance than fog. Summer fogs are most common in the immediate vicinity of the western coastal area, which is largely outside the ranges of white pines. Uredial intensification as a result of dews is in practically all cases much less than that caused by rains, and is limited almost entirely to those ribes growing in swampy areas and along moist stream bottoms. The heaviest dews observed by the writer in the West were along certain moist stream courses in the western white pine belt in northern Idaho. Apparently the periods of wet foliage caused by dews are generally not of sufficient duration for germination and infection to occur.

Since the infection of ribes by urediospores generally occurs during rainy periods, which may in some seasons and localities be quite infrequent in the West, the longevity of these spores is of importance in connection with intensification of the rust on ribes. All available information indicates that the urediospores of *Cronartium ribicola* may remain viable for a long time (Spaulding 1922a; Spaulding and Rathbun-Gravatt 1925b). Results of various studies summarized by Spaulding (1922a) show a longevity ranging from 7 to 270 days under varying conditions. It is his opinion that these results indicate a sensitiveness of the urediaspores to external factors and that in addition it is quite possible the physiological conditions of the host plant also has a profound effect on these spores. Possibly the majority of urediospores lose their viability within about a month.

Colley (1918:638) reported that the urediospores exhibit the same irregularity in germination in artificial cultures as do the aeciospores. He found that even when they are dusted over the surface of young, fresh, moistened leaves and placed in a damp chamber they mayor may not germinate in large numbers. The experiences of Spaulding (1922a) have been similar. According to him, "the urediospores of *Cronartium ribicola* have been generally found to be erratic in germinating. At one time excellent germination occurs; at another, none at all." All evidence indicates that the newly matured spores are more viable than the older ones (Spaulding 1922a). Pre-cooling appears to stimulate germination (Spaulding 1922a). Exposure to bright sunlight has a deleterious effect on the urediospores (Duff 1918; Spaulding 1922a), the ultraviolet rays apparently being the destructive agent (Duff 1918). Doran (1919) found that the urediospores germinate in about 5½ hours in drops of distilled water on glass slides, and that the minimum, optimum, and maximum temperatures for germination are 47° F., 57° F., and 77° F., respectively. In a later publication (Doran 1922) he gives 5½ hours as the time required for germination under optimum conditions in aerated distilled water, but no time is given for germination under other conditions. He seems to be the only one to have studied these phases of the subject.

In general ribes species that show resistance to aeciosporesare also low in susceptibility to infection by urediospores. One outstanding example of an exception in this regard is *Ribes lacustre.* Young leaves of this species formed in the spring have usually been found to show a higher degree of susceptibility to aeciospores than is the case with the highly susceptible *R. petiolare.* With *R. lacustre,* however, it generally happens that relatively little intensification of the rust results from the urediospores that form following aeciospore infection as compared with *R. petiolare* and many other species that maintain a high degree of susceptibility to urediospores throughout the season. The writer has seen a few cases where no uredial intensification at all occurred on large groups of *R. lacustre* from the urediospores developing as a result of aeciospore inoculations, whereas on the other species inoculated at the same time and growing intermingled with it or nearby under the same environmental conditions several generations of uredia developed during the season.

The comparative infecting ability of aeciospores and urediospores has not been determined. Lachmund (1934b: 109) is of the opinion, however, that not only are the urediospores more effective in infecting ribes than are the aeciospores, but also that the leaves remain susceptible to them for much longer periods. The results of greenhouse tests of one species *(Ribes petiolare)* showed that the leaves retain a high degree of susceptibility to urediospores for a somewhat longer period of time than they do to aeciospores (Pierson and Buchanan 1938a). Based on the experiences of the writer, it is believed that in general this same relationship not only is maintained outdoors but also may be more pronounced there. Also, the results of extensive inoculations and observations by the writer in the West indicate that urediospores have.a greater infecting power than aeciospores. This corroborates Lachmund's contention (1934b: 109). A factor apparently contributing to the greater effectiveness of urediospores as compared with aeciospores in infecting ribes is the difference in time required for germination of the two types of spores. As previously mentioned, aeciospores under favorable moisture conditions were found to require 8 to 12 hours for germination whereas but 5½ hours sufficed for germination of the urediospores. This shorter time for the latter would therefore favor them over the aeciospores in infecting ribes since infection by the urediospores could take place during moist periods obviously too short in duration for aeciospore infection.

The amount of rust that may ultimately develop on a species during the course of a season as a result of uredial intensification may be regulated to some extent by the character of the ribes leaves as influenced by the conditions under which they have developed. It has been found that, in general, infection develops in greater abundance on bushes growing in the shade or part shade than on those growing in the open. A factor that is believed to be important in this connection is the rate at which ribes leaves mature, maturation being more rapid on bushes growing in the open than in the shade. According to Arthur (1929: 241), it is a well-recognized fact that the maturity of host tissues has a marked effect upon development of plant rusts. Also, since it is well known that the chemistry of a plant changes markedly as it ages, this may possibly be an additional factor of importance. Studies have shown that the character of the seasonal climate, particularly midsummer heat waves and droughts, not only affects the amount of rust that may develop but also has a profound effect upon ribes themselves, especially those growing in the open (Mielke et al. 1937).

SOME EFFECTS OF AECIOSPORE SOURCE ON RIBES INFECTION

It has been commonly observed in the West that ribes growing in close proximity to pines bearing sporulating cankers almost invariably become infected not only earlier, but more severely, than those at a distance. Between the two situations the time difference in the appearance of the first rust on ribes may be as great as two months in some years and localities. Minkevicius (1939), working in Lithuania, has reported this same relationship occurring in his experiments conducted over a period of four years with *Ribes nigrum.*

The first aeciospores generally appear in the spring several weeks or more before the main period of their production. Other things being equal, the chances are greater that some of these relatively few spores first disseminated will come in contact with and infect leaves of ribes growing nearby than would be the case with bushes at some distance away. Also, the maximum distance of dissemination is not likely to be as great during the early period of aeciospore dispersal as would occur during the peak of their production somewhat later in the season.

In the epidemiology of the rust the species of ribes involved may be of importance because they do not all leaf out at the same time in the spring. Consequently, the rust may often be found from two to three weeks earlier on certain species than on others. Also, ribes differ considerably in their susceptibility to the rust. The fungus may therefore be found earlier on the more highly susceptible species since they are more apt to become infected by the first spores reaching them than is the case with species low in susceptibility to aeciospores.

There is not only a rapid tapering off in the degree of infection of a ribes species as the distance from the aeciospore source increases, but also a rapid decrease in the numbers of bushes that become infected. As might be expected, this is more pronounced with highly susceptible species than with those low in susceptibility. It is not unusual to find but few infected bushes beyond 200 or 300 yards from heavily diseased pines, whereas on immediately adjacent bushes the rust attack is not only much more severe but also includes most if not all of them. An example of the rate of tapering off in degree of infection with increase in distance from the aeciospore source is given in Table 2.

TABLE 2. DECREASE IN AMOUNT OF BLISTER RUST INFECTION ON *Ribes lacustre* AND *R. divaricatum* WITH INCREASE IN DISTANCE FROM THE AECIOSPORE SOURCE

Species and growth form	*Distance from pines*	*Percentage of total lower leaf surface infected*				
		1926	*1927*	*1928*	*1929*	*1930*
R. lacustre, shade	Within 25 feet	12.6	4·3	4.8	5·9	6.6
	50-75 “	7·3	1.7	2.8	1.8	0·5
	100-125 "	3·5	0·9	1.7	1.1	0·3
R. divaricatum, shade	Within 25 feet	34.8	22·7	21.9	36.1	34·7
	50-75 “	27.0	14·4	15·4	27.0	6.6
	100-125 "	17.8	9·3	10.6	17.1	4.0

The data shown in Table 2 were obtained in studies conducted near Garibaldi, British Columbia. The two ribes involved were growing under large northern black cottonwood trees *(Populus trieboearpa* var. *baslala* Henry) bordering a stand of severely diseased *Pinus montieola* reproduction. The percentage given in each case is the accumulated total of infection developing during the season. All bushes became initially infected with aeciospores every year. The basis in number of plants in each group ranged from 31 to 70 with an average of about 50. The same bushes were used each year except for some of the groups in which a few bushes died from natural causes before the study was completed. Results of the study show that in every year and with both ribes species the degree of infection tapered off quite rapidly even though the maximum distance from the aecial source was only 125 feet. It should not be surprising, then, that on areas many miles from the aeciospore source the rust may be found almost without exception) even during years favorable for the rust's spread and development, only on an occasional bush.

EFFECT ON RIBES OF ANNUALLY REPEATED HEAVY INFECTION

Studies made a number of years ago in the East revealed that repeated annual defoliation by *Cronartium ribicola* may cause the death of infected ribes bushes (Pennington et al. 1921; Pennington 1922). In some instances certain species were found to have been entirely destroyed in the immediate vicinity of heavily infected pine trees.

No such killing of these host plants has been observed in the West) even on areas of heaviest pine infection and involving ribes species highly susceptible to the rust. Occasional dead bushes have been found) but suppression by competing vegetation and infestation by scale insects have often been contributing factors in their death. Lachmund (1934C» who conducted studies over a number of years on one area in British Columbia) found that the ribes growth was killed back to some extent during the period in which the infected trees immediately associated with it remained alive and. produced aeciospores) but it began to increase again after the trees had died from the rust attack.

Judging from one report (Pennington 1922» defoliation by the rust may occur relatively early in the season in the East. Under western conditions) however) heavy losses of leaves as a result of attacks by this fungus usually do not occur until late summer. At that time the effect on the plant apparently is less disastrous than if it occurred earlier in the season and during its most active growth period. In the West) therefore) the effect of the fungus on ribes cannot be regarded as a rust palliative of any consequence.

TIME OF TELIAL DEVELOPMENT ON SOME WESTERN RIBES

The time during the season that telia start to form and their main period of production is not the same for all species of ribes. This may have a strong influence on the amount of pine infection occurring on some areas in a given season. *Ribes lacustre* is one of the commonest of western ribes. Despite the fact it is quite low in susceptibility and telium-producing capacity as compared with other species) young stands of western white pine may become severely damaged because of the presence of this currant. The numerical abundance and pine-infecting capacity of

R. lacustre have therefore caused it to be of considerable importance in the intensification of the rust in the West. Additional information on its importance as a host of the rust has been obtained as a result of studies of the time that telia start to form and of their main period of production on it as compared with some other ribes species.

The bases for the present results and conclusions are the field data obtained during the course of large-scale investigations on the susceptibility and telium-producing capacity of the four principal ribes *(R. petiolare, R. inerme, R. viscosissimum,* and *R. lacustre)* found within the commercial range of *Pinus monticola* (Mielke et al. 1937), plus much additional data on the development of the rust on these and other ribes and the results of experience not included in that report. These basic data include periodic observations and records made seasonally over a number of years on a total of several thousands of ribes bushes growing in numerous localities in the West. An analysis of the data has yielded the following information on telial development.

The telia, on which the sporidia or pine-infecting spores form, generally begin developing earlier in the season (from about two weeks to almost two months) on *Ribes lacustre* than on the other ribes species studied and especially does this appear to be the case when compared with *R. viscosissimum.* Also, the peak of telial production usually is reached earlier on *R. lacustre.* As a rule most of the telia formed on this host are produced in June and July, but in some cases practically all of them may develop in June, and often relatively few and sometimes none may form in August and September. In most seasons the rust is more or less dormant during the summer in the leaves of *Ribes lacustre* while in the fall renewed growth may occur around the margins of old and dead-appearing infection spots with the result that there is a resumption of telial production on a comparatively limited scale. Quite frequently by fall, however, the rust may be difficult to find on *R. lacustre* except for some individuals considerably higher in susceptibility and telium-producing capacity than the average for the species. This condition has been known to lead to erroneous conclusions regarding the seasonal development of the rust on this host particularly with regard to the amount and character of the rust produced. In general, blister rust is easiest to find on most infected bushes of *R. lacustre* relatively early in the season.

On *Ribes petiolare, R. inenre,* and *R. viscosissimum,* the species. that were more frequently used than others in the comparative tests with *R. lacustre,* only minimal amounts of telia are ordinarily found in June and July, with the bulk forming in August or in August and September. A small percentage of the total produced in a season may develop in October or even somewhat later. Telial production quite similar to this has also been recorded for a number of other species, including *R. nigrum, R. sanguineum, R. divaricatum,* and *R. bracteosum.*

The earlier telial formation on *Ribes lacustre* as compared with the other species cannot be attributed to any difference in time that the plants became infected or to environment. Most of the data were obtained from ribes dusted with aeciospores in the spring of the year. Large groups of bushes of two or more species growing under comparable environmental conditions were used in the studies that were conducted at a number of localities, some of which were widely separated. The comparative groups of two or more species on an area were dusted the same day. Consequently the rust had an even start on the different species in each comparative test. That environment was not a factor influencing the early telial formation on *R. lacustre* is indicated by the fact that the results obtained on the different areas were consistent. Furthermore, no differences of consequence were found in the data obtained from naturally infected bushes and from those that were dusted with spores.

Teliospores may retain their viability for two or three months, but generally the highest germination percentages are obtained when they are relatively young. Providing weather conditions are favorable, pine infection can occur at any time that mature and viable teliospores are present. Based on the results of this study, it is possible therefore for pine infection to take place earlier in the season when *Ribes lacustre* is present than is apt to be the case with the other species of ribes common in the region, and particularly *R. viscosissimum.* When these two species grow in association the potential period of pine infection is increased. Therefore, the probabilities of infection taking place are increased because the chances of the occurrence of favorable moisture conditions should be greater over comparatively long periods than over shorter ones. Also, with the longer period combinations of situations that might not otherwise occur are possible. With moisture conditions favorable only comparatively early in the season *R. lacustre* could be responsible for the majority or all of the pine infection resulting during the year on a given area. If the favorable conditions occurred in late summer or fall *R. viscosissimum* would likely be largely responsible. Consequently, it is possible that the heaviest return of the rust to pines from these hosts would take place in a year in which moisture conditions favorable for infection occurred relatively early in the season and during the peak of teliospore production on *R. lacustrc* and again later in the season when these spores were most abundant on *R. viscosissimum.*

The time of telial production on *R. lacustrc* is also a factor that must be considered in connection with the determination of the year of infection on pines. Cankers having their origin early in a given season, for example those resulting from *R.lacustrc,* may make their appearance sooner than those having their origin later in the same season and resulting from *R. viscosissimum* or some other species. Consequently, the species of ribes involved in the infection of pines must be taken into account when attempts are made to determine the year of pine infection in a given locality.

Spaulding (1929), in discussing the season of production of the uredia on a number of ribes species under observation in the East, reported that under average conditions urediospore production lasted about 120 days, and that it continued the longest time (185 days) on *Ribcs nigrum* and the shortest time (65 days) on *R. lacustrc.* Quite comparable relationships exist in the West where experience has shown that the period of production of these spores is considerably shorter on *R. lacustrc* than on any of the other species studied. Instances have been observed where urediospore production ceased after the first crop following aeciospore infection. Almost invariably there is a rapid tapering off in the intensification of the rust on *R. lacustrc,* whereas on the other species the reverse is true with the most pronounced uredial intensification occurring in late summer or early fall. Usually the first rust of the season may be found on *R. lacustrc.*

An explanation of the behavior of the rust on *Ribcs lacustrc* appears to lie in the development of its leaves. Some of the other species leaf out just as early in the spring but none of them mature their leaves so rapidly. As a rule, the leaves of *R. lacustrc* are quite mature and hardened by early summer. When that condition is reached development of the rust on them is slowed up considerably and they are quite resistant to infection by urediospores. Also, much of the older infection either dies out or becomes relatively inactive. The rapid maturity of the leaves, therefore, is believed to be the principal factor responsible for the character of telial development noted on *R. lacustrc.* It is known that for rusts in general the maturity of the plant's tissues has a marked effect upon the development of the fungus (Arthur 1929).

SCOUTING FOR THE RUST

SINCE the rust is most likely to be found on species of ribes that are most susceptible to attack, search for it has usually been concentrated upon such species. During the earlier years of scouting *Ribes nigrum* was used as an indicator host because it was previously known to be highly susceptible at maximum distances from infected pines. Also, being a cultivated plant, it generally was much more accessible to the scouts than were the wild species, the relative susceptibility of which at that time was not well known.

Because field observations in the East had shown that *Ribes nigrum* was almost invariably the first species to show infection in newly invaded regions and that it was the most active species in establishing and spreading the rust, a program for its eradication from western States was started in 1922 (Office of Blister Rust Control 1923). By the fall of 1927 this work had been finished in Montana, Idaho, Washington, and Oregon, and nearly finished in California. Thus, *R. nigrum* was eliminated from a large area of the West not only as an indicator plant for tracing annual spread of the rust or detecting its presence in new regions, but also as a potential factor in the further spread and intensification of the fungus. Consequently, in subsequent years scouting for the disease on ribes in western United States has been confined to wild species. In British Columbia, however, *R. nigrum* has not been eradicated and was used in connection with surveys on annual spread of the rust conducted there from 1922 to 1930, inclusive.

Since it was relatively easy to locate *Ribes nigrum*, because it is a cultivated plant, practically 100 per cent of the bushes of this species could be inspected. The much more common wild ribes, on the other hand, occur in the West over large areas mainly in the timbered and mountainous regions. Because of their abundance, distribution, and the relative inaccessibility of the districts in which most of them grow, it has been impossible, with the limited personnel available for the work, to examine all or even a hundredth part of the wild ribes in a given region in anyone year. For practical purposes this has not been necessary. Consequently, the scouting of these species has involved a sampling procedure in which numerous bushes might be examined at each of a number of selected locations. In this manner it has generally been possible to trace, with a reasonable degree of accuracy, the limits of seasonal spread to ribes in a given direction. Also, it has thus been possible to obtain information on the intensity of annual spread over a given region, or to determine whether or not seasonal climatic conditions have been favorable for such spread.

EARLY HISTORY OF BLISTER RUST IN THE WEST

FOLLOWING the discovery of blister rust at Vancouver in the early fall of 1921 a considerable portion of the time devoted to the general investigations of this fungus during 1922 and 1923 was spent in determining its range in British Columbia (Davidson 1922, 1924) and adjacent United States (Office of Blister Rust Control 1923, 1924; Posey 1922). Based on the results of this work, by the end Qfthe 1923 field season the actual limits of distribution in the West seemed to be established, the rust evidently being confined to British Columbia and Washington. This appeared to be substantiated by the scouting results for 1924, in which year practically no change was noted in the previously known range of the disease (Davidson 1924; Wyckoff 1924). Its known limits of distribution up to 1923, inclusive, have been reported by Pennington (1925). Subsequent investigations, however, have disclosed that the rust was considerably more widespread by the fall of 1923 than was known to be the case at that time.

During the field investigations in 1922 and 1923 every effort was made to detect any possibilities of artificial introduction at all places where the rust was found, but evidence was negative except for the original introduction on pines in 1910 near Vancouver. Also, there was no evidence that the rust was introduced on ribes. In the coastal region of British Columbia the infection centers were found to be located mainly in associations of native white pines and ribes away from any cultivated plants.

Since blister rust was introduced on the Pacific Coast in 1910 and its presence was not detected until 1921, an II-year period elapsed during which no record was obtained of the annual progress of this pathogen. In attempting to reconstruct a history of the rust's spread during that interim it was therefore necessary to determine as nearly as possible by field studies the year of infection at outlying points as well as the amount and direction of spread. Accordingly, special efforts were made to determine the year of infection at all places where diseased pines were found. Pennington (1925), who devoted time to this phase of the investigations in 1922 and 1923, found that, by classifying large numbers of cankers according to the year's growth on which they had their inception and to their stage of development, the year of infection on pines could be determined. By this method, which was elaborated upon later by Lachmund (1933a), it was possible to obtain a history of the spread to ribes and pines, particularly to the latter, for the period in question.

It was thus found by Pennington that during the intervening II-year period the most widespread dissemination and heaviest infection occurred probably in 1913, 1917, and 1921, while lighter waves of infection seemed to have occurred in 1918, 1919, and 1920. Pines bearing cankers determined as of 1913 origin were found at several places northward from Vancouver, the farthest point being Thurston Bay about 120 miles distant. Pines bearing cankers having their inception in 1917 or 1918 were found more widespread and occurred at a greater number of places than those with 1913-origin cankers. Evidently in 1917 or 1918, probably in the former year, infection became established on pines in the interior of British Columbia at an extreme distance of approximately 265 miles from Vancouver and 225 miles from the nearest known 1913 center. In 1918 or 1919 there was a little infection in the vicinity of the oldest cankers in the coastal region. In 1920 there was considerable infection in the immediate vicinity of ribes near 1917 pine infections, while in 1921 there was a much heavier infection than in 1920.

Scouting results in 1922 showed the range of the rust to include almost the entire coastal white pine region of British Columbia and three points in the interior pine region of this Province, viz., Canoe, Revelstoke, and Beaton. In the western United States the rust was found only in western Washington west of the Cascades. On pines in that State it was noted at only two points, on a total of but three trees, near the International Boundary. On ribes (mainly *Ribes nigrum),* however, the disease was practically continuous from this line to the southern end of Puget Sound and also occurred at several points in Grays Harbor and Pacific Counties, the southernmost of these being at Ilwaco at the mouth of the Columbia River. These points were many miles outside the range limits of white pines.

In 1923 blister rust was considerably more widespread in British Columbia than during the previous year. It was noted on pines at a number of additional places within the coastal white pine area and was more or less common in occurrence on ribes practically throughout this area and in some instances for many miles outside of it. Infected bushes were found at a few places upwards to about 110 miles north of the range limits of white pines on the coast. The rust was general on *Ribes nigrum* practically all over that portion of the interior dry belt (a wide area devoid of white pines) from the main line of the Canadian Pacific Railway southward about 120 miles to the International Boundary. Within this area the fungus appeared on ribes at a number of places where it was not found in 1922. Within the range of white pine in the interior of the Province no extension in the range of the rust on that host over that noted in 1922 was found, although there was a marked increase in its range on ribes to the southward. In Washington no additional pine infection centers were discovered. West of the Cascades in that State blister rust was not neatly so widely distributed on ribes as in 1922, being observed on them only at a relatively few places in the Puget Sound region. East of the Cascades outside of the range limits of pines, however, infected *Ribes nigrum* bushes were found at several places immediately adjacent to the infected dry belt area in British Columbia.

These findings, i.e., the spread of the rust to ribes as observed in 1922 and 1923 and the results obtained from analysis of canker tabulations made at outlying pine infection centers, were regarded as providing circumstantial evidence which, although not conclusive, was so strong it was concluded that blister rust could spread directly from pines to ribes by means of wind-borne aeciospores to a distance of 110 miles and probably much farther (Boyce 1924; Davidson 1924; Pennington 1925). Pennington also found from a study of weather records that the summer seasons in which the most intensive and greatest distances of spread occurred, i.e., 1913, 1917, and 1921, were characterized by abundant precipitation and winds.

Ever since the method for determining the year of infection on pines was developed it has been to a greater or lesser extent in continual annual use, making possible the obtaining of additional information on the early history of the rust arid also the following of its annual progress since then with a greater degree of accuracy than might otherwise have been possible. Other than the paper by Pennington (1925), covering the known spread of the rust as determined from field investigations conducted in 1922 and 1923, there has been but one publication in which consideration has been given to the subject. In it Lachmund (1926a) summarized the early history of the fungus as reported by Pennington and briefly mentioned the spread to ribes in 1924 and 1925. The attempt has therefore been made here to bring the known information on the spread of blister rust in the West up-to-date.

SPREAD OF THE RUST BY YEARS

SPREAD FROM 1910 TO 1913, INCLUSIVE

AS previously mentioned herein the early history of spread of *Cronartium ribicola* in the West, i.e., between the time of its introduction at Point Grey near Vancouver, British Columbia in 1910 and its discovery in that Province in 1921, has been determined as nearly as it has been possible to do so, from field studies started in 1922.

All evidence accumulated to date indicates that spread from Point Grey to outlying points did not occur until 1913. Why spread should not have occurred in 1910, 1911, and 1912 can only be conjectured.

Unfavorable weather is one possible influence that might have prevented spread, but a study of weather records for Vancouver gave no evidence of this. During the years 1910, 1911, and 1912 no frosts occurred from May to September, inclusive; consequently, low temperatures could not have been a factor. Also, since none of those years were abnormally dry (Table 3) the lack of spread cannot be attributable to a deficiency in precipitation.

TABLE 3. PRECIPITATION AT VANCOUVER, BRITISH COLUMBIA

Year	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*
1910	3.60	2.15	1.98	.24	1.38	2.47
1911	1.96	5.39	2.09	.92	1.23	4.41
1912	3.92	2.35	2.28	1.54	5.86	2.84
1913	2.53	4.33	3.81	2.02	.85	3.89
1914	3.28	.74	3.58	.42	.75	6.86
1915	3.04	3.42	1.07	.91	.36	.80
1916	4.07	1.41	1.34	5.25	.58	1.28
1917	8.20	1.69	5.40	.48	.93	3.30
1918	1.70	1.15	1.00	2.29	4.59	.30
1919	4.47	3.60	1.02	.15	1.15	1.16
1920	2.51	1.94	3.06	.67	2.91	10.37
1921	3.62	2.52	3.64	.32	2.84	5.03
1922	2.63	2.46	.17	.02	2.01	5.76
1923	2.14	2.84	2.07	.52	.73	2.97
1924	3.84	.31	.91	.71	1.88	5.81
1925	2.44	2.20	.38	.74	2.36	.44
1926	2.58	4.17	.78	.36	2.10	3.26
1927	1.88	5.12	1.16	.94	3.74	3.07
1928	4.29	2.22	1.93	.47	.20	1.35
1929	4.81	1.25	3.24	1.41	1.50	1.77
1930	4.72	2.86	2.18	.08	.07	2.65
Normal[1]	3.31	2.86	2.32	1.13	1.69	3.73

[1] Normal as of 1930. British Columbia Department of Agriculture Weather Records.

A more plausible explanation for the apparent lack of spread of the rust in 1910, 1911, and 1912 is that the *Pinus strobus* seedlings involved in the introduction did not bear cankers that had yet reached the aeciospore-production stage in 1910, and that few if any such spores were produced on these trees in 1911 and 1912. This probability is supported by other evidence.

Hirt (1936) found that in seedlings of *Pinus strobus* 3 years old at the time they became infected the percentage of trees which produced aeciospores was quite low, being exceedingly so in the first year that production of these spores occurred. In explanation he pointed out that the diameters of the needle-bearing stems and branches on such young white pines are very small. These small parts are girdled by the fungus soon after it extends into the bark, and the portions beyond the cankers die. Although the fungus continues to invade new living tissues it only occasionally has the opportunity of producing aeciospores because the early death of the newly invaded tissues does not allow sufficient time for these spores to develop. As the trees become older the diameters of the stems and branches increase and the fungus is then able to persist longer and develop the aecial stage.

The writer has observed the same thing happening in large numbers of young test trees of *Pinus strobus* planted in British Columbia and Oregon, but only in occasional trees of a number of other white pine species of similar size growing on the same test plots. It was also observed that the bark on young trees of *P. strobus* is much thinner than the bark on similar-aged trees of most of the other white pines This also is believed to be an important factor in the relatively scanty aeciospore production of that species as compared with others and, particularly so, when it is in the seedling stage. According to Spaulding (1925), *Cronartium ribicola* vegetates in the bark of *P. monticola* much more prolifically than it does in the bark of *P. strobus.* He attributes this to the difference in thickness of smooth bark of the two species, and believes that the greater abundance of phloem in the bark of *P. monticola* directly favors the growth of the fungus. Because of the apparently normal reaction of young *P. strobus* to the fungus it would seem possible therefore that few, if any, aeciospores were produced on the imported trees prior to 1913.

The plantation on which the infected *Pinus strobus* were growing was in an exposed situation upon one of the highest points of Point Grey, where the escaping aeciospores could have been caught and carried easily by the winds. Judging from the evidence obtained from studies on pines at infection centers, however, spread in 1913 apparently was mainly in a northerly direction. Infected pines bearing cankers regarded as having had their inception in that year have been found along the coast to approximately 120 miles northwest of Point Grey and to about 85 miles to the north along the line of the Pacific Great Eastern Railroad practically to the range limits of western white pine in that direction, and 45 miles east to Abbotsford. One pine infection center possibly originating in 1913 has been found in the Cascade Mountains of Washington about 100 miles southeast from Point Grey. Otherwise there has been no evidence uncovered indicating that spread in a southerly direction occurred in that year.

In Figure 2, the places are shown where there have been found pines regarded as having first become infected in 1913. No doubt there must have been a number of other centers established in that same year. The immense size of the territory involved and the ruggedness of much of it precluded the possibility of thorough coverage by the limited number of individuals available for the work.

The wide distribution of pines that became infected in 1913 gives some index of the spread to ribes from Point Grey that year. Experience in the West has demonstrated that the limits of rust infection on ribes in a given season often exceed those of rust establishment on pines for the year, since ribes frequently become infected in places where no pines are present and even where pines occur they do not always become infected. In such cases the rust runs its course on ribes during the season and dies out following the dropping of the infected leaves in the fall. On this account it can be assumed with considerable confidence that rust infection on ribes in 1913 was more widespread than that shown for pines.

SPREAD FROM 1914 TO 1921, INCLUSIVE

According to Pennington (1925), the tabulations made in 1922 and 1923 of cankers in the immediate vicinity of those resulting from the 1913 wave of infection did not indicate infection in 1914 and 1915. They did indicate, however, that there was a little infection in 1916; much in 1917, a little in 1918 and 1919, much in 1920, and a great deal in 1921. The results of investigations subsequent to 1923, involving analysis of canker tabulations made at many additional pine infection centers, are in accord with these findings.

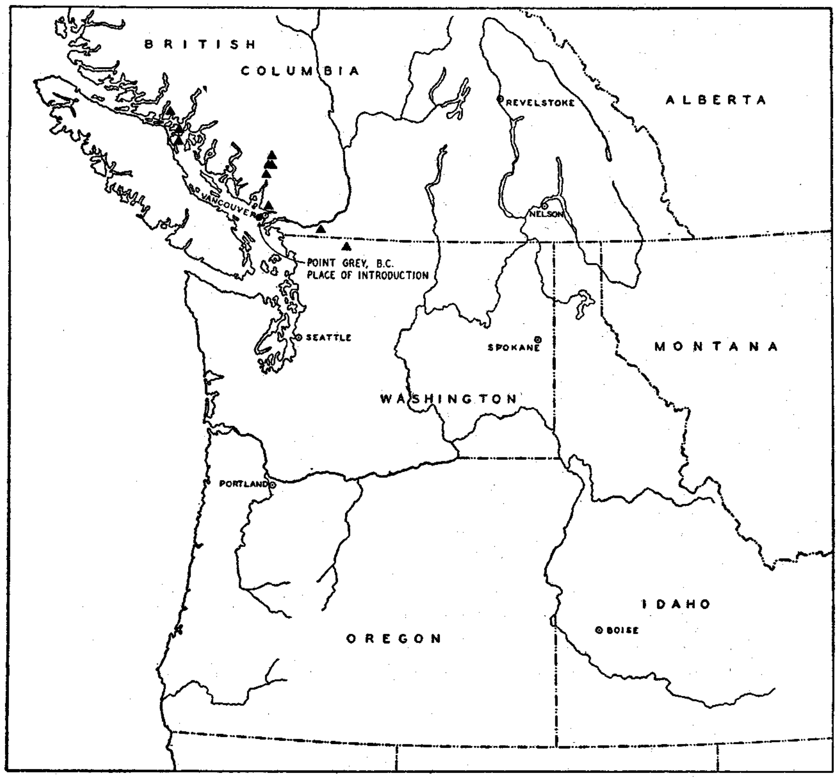

FIGURE 2
Known pine infection centers regarded as having become established in 1913.

At the time Pennington conducted his studies the time required from infection to the production of aecia in *Pinus monticola* had not yet been determined with certainty. Based on his previous studies in the East and experience gained in the West, he believed, however, that the first aecia are usually produced in the third year after infection occurs (Pennington 1925: 596). This has been corroborated by later studies conducted in the West (Lachmund 1933c), the results of which have shown that on *P. monticola*, except for very young trees, the cankers resulting from a given infection year produce aecia for the first time after infection in about the following proportions: 36 per cent in the third spring after the year of infection, 43 per cent in the fourth spring, 18 per cent in the fifth spring, and the remaining 3 per cent in the sixth and to some extent in the seventh spring. Accordingly, about 80 per cent of the cankers from a given infection year may be producing aeciospores in the fourth spring after the year of infection. In this connection it should be remembered that aeciospore production may occur for three or four seasons in succession from the same bark. Consequently, with the increase in size of cankers and the increased numbers of them producing aeciospores the volume of these spores produced is much greater in the fourth spring after the year of infection than in the third spring thereafter. Considering the above, it therefore should be obvious that a knowledge of canker development and the time required for aecial production is not only essential in determining the year of infection on pines, but that such knowledge is also valuable in the analysis of past spread of the rust based on field evidence.

As previously mentioned, from all data obtained during the course of the studies, it is evident that the rust became established on pines in several localities, probably in 1913. No evidence has been found to indicate that it was at any other locality before 1917. The summer seasons of 1914 and 1915 were relatively dry (Table 3) and this may account for the fact that no apparent spread occurred in those years from the introduced *Pinus strobus* at Point Grey as it did in 1913. The lack of any intensification in the vicinity of the outlying 1913 centers in 1914 and 1915 is explainable on the basis that insufficient time had elapsed for the cankers having their inception in 1913 to produce aeciospores. This stage probably was reached on some of them first in 1916 since there was a little evidence that a small amount of pine infection may have occurred in that year in the immediate vicinity of these centers. By the spring of 1917, however, the majority of these cankers should have produced an abundance of aeciospores.

All evidence obtained indicates that such aeciospore production occurred, for in 1917 there apparently was a much wider and more intensive spread of the rust than in any previous year. As a result the fungus became established on *Pinus monticola* in a number of new localities practically throughout the range of this species in the coastal region of British Columbia. It advanced to the northwest along the coast nearly 140 miles, to the north along the line of the Pacific Great Eastern Railway about 90 miles, and to the east approximately 60 miles to Agassiz. It also apparently jumped the dry belt to the eastward and became established within the interior pine belt on western white pine at least at four places, the easternmost of these being at Beaton approximately 265 miles from Point Grey. Spread in that year also occurred southward into Washington with the result that pines became infected in that State at a number of places the known limits of which were about 100 miles to the south and southeast from Point Grey.

In British Columbia, rainfall during the month of May in 1917 was considerably below normal, a condition that would favor dispersal and wide dissemination of the aeciospores. June was. considerably wetter than normal, providing abundant moisture both for the infection of ribes and subsequent intensification of the rust on these hosts. Precipitation during the remaining months of the season was below normal.

In 1918 there was a little infection in the vicinity of the oldest cankers in the coastal region of British Columbia, and a few of the pine infection centers regarded as having become established in 1917 may possibly have had their inception in 1918. In either 1917 or 1918, probably in the former year, the rust spread south to at least one locality in Oregon-Minto Creek in the Cascade Mountains where it became established on pines and was not found until 1930. Air line this is approximately 325 miles from Point Grey.

The places where blister rust has been found in the West on *Pinus monticola* and determined as having become established on that host in 1917 or 1918 are shown in Figure 3. Also shown are pine infection centers of previous origin.

Analysis of canker tabulations and observations on the ground, made in 1922 and 1923 in the coastal region of British Columbia, showed that in 1919 there was a little infection in the vicinity of the oldest cankers, but there was no evidence in those two years or at any time since then of spread from the old centers and establishment of new ones in 1919. In that year the weather during the months of July, August, and September was unusually hot and dry. In 1920, however, considerable infection of pines occurred in the immediate vicinity of ribes near 1917 infections. In 1921 there was much heavier infection than in 1920. Considering normal development of cankers, the intensification of the rust on pines that occurred in 1920 and 1921 might have been anticipated. Of the cankers that had their inception in 1917, normally a portion should have produced aeciospores for the first time in 1920, and in 1921 the majority of them should have produced these spores with a total spore volume much greater in the latter than in the former year. Evidently this is what happened.

FIGURE 3
Known pine infection centers regarded as having become established in 1917 or 1918 shown as triangles, and centers of previous origin as circles.

What did not become apparent during the investigations in 1922 and 1923, however, but was found to be the case in later years, was the widespread establishment of rust on pines in 1920 and 1921, particularly in the latter year, at a number of places miles from the known 1917 infection centers. The failure to find the new 1920 and 1921 pine infection centers at outlying points in 1922 and 1923 may be attributed to the stage of development of the new cankers. None of them having their inception in 1921 was old enough to produce aeciospores in 1923. The cankers having their inception in 1920 were not so numerous as the 1921 cankers and apparently only part of them produced aeciospores in 1923, and not in sufficient quantity to cause general infection of ribes in the new localities and thus lead to their more ready detection in that year.

Judging from all findings climatic conditions in 1920 and 1921 seem to have been more favorable for spread of the rust to the south and east than to the north. Pine infection centers determined to have become established in those two years, and in years previous thereto, are shown in Figure 4. The extent of ribes infection in those years is not known. However, the indications, gained from the studies on pines, were that the rust was quite widespread on ribes in northwestern Washington in 1920 and 1921.

The spring and summer of 1921 were unusually cool in the western portion of British Columbia. Precipitation was somewhat below normal

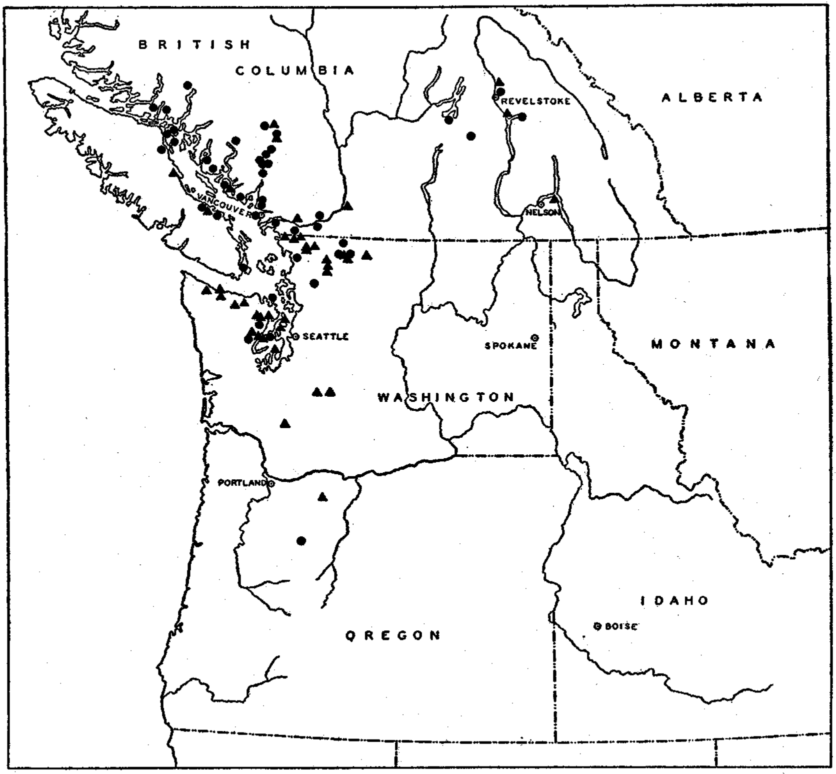

FIGURE 4
Known pine infection centers regarded as having become established in 1920 and 1921 shown as triangles, and centers of previous origin as circles.

in May and above normal in June, providing weather conditions apparently favorable for the dispersal and wide spread of aeciospores to ribes and infection of these hosts. July was very dry, but above normal precipitation occurred in August and September.

To recapitulate, the spread of *Cronartium ribicola* to 1921, inclusive, as found by later studies, was briefly as follows: From the introduction point the first evident wave of rust infection to pines occurred in 1913. Coincident thereafter with normal development of cankers and apparently favorable weather conditions there were two more very prominent waves of rust spread-one in 1917 and the other in 1921. Smaller but definite waves of spread occurred in 1918 and 1920. By the end of the 1921 season the fungus had become established on western white pine at numerous places practically throughout its range in the coastal region of British Columbia and at several places in the eastern part of that Province. It was also present on this species over a wide area in western Washington and at least two places in northwestern Oregon. Measured from Point Grey, the place of introduction, the limits of the rust on pine extended northwest 140 miles, north 90 miles, east 265 miles, and south 325 miles.

SPREAD IN 1922

The year 1922 marked the inauguration of field studies on blister rust following its discovery on the Pacific Coast late in the fall of 1921. The course of the rust's spread during the period 1910 to 1921, inclusive, as outlined in the two preceding sections, has been reconstructed from the results of these studies on diseased pines conducted over a number of subsequent years. Ever since 1922 the progress of the fungus on both pines and ribes has been followed annually in the field.

As a result of the field studies made in 1922 to determine the distribution of the rust, infected *Pinus monticola* trees were found at about 25 different places in the coastal region of British Columbia. Most all of these pine infection centers were north of Point Grey, and their limits included most of the range of western white pine in the coastal area. In the interior white pine belt to the eastward the rust was found on *Pinus monticola* at three rather widely separated points, the eastermost of these being about 265 miles air line from Point Grey. Both in the coastal and interior regions the fungus was observed to be somewhat more widespread on ribes than on pines. The ribes host most commonly found infected was the European black currant, probably because scouting was confined largely to this highly susceptible host. Plantations of this currant, however, were seldom found in close association with white pines. Infected wild ribes were most common in the coastal region of British Columbia, where diseased pines were much more abundant than elsewhere.

In the United States, although scouting was done in seven of the western States, the rust was found only in western Washington. There it was known to be present on pines at only two points (on a total of but three trees) near the Canadian Line. The discovery of one of these was made during the late fall scouting of 1921. Of singular importance was the finding of the rust to be rather common on *Ribes nigrum* in the extreme southwest corner of the State many miles outside the range limits of pines. Nowhere else in the West was it found that year so far from the pine host. Intensity of infected bushes was greatest in the Puget Sound region in the northwest portion of the State.

The distribution of the rust on ribes in 1922, as found that year, is shown in Figure 5. This should be compared with Figure 4 showing the known distribution of the fungus on pines in 1921 as determined from investigations conducted over a number of subsequent years. From a comparison of these two figures it is evident that blister rust was already considerably more widespread on pines in 1921 than was known to be the case by the end of 1922.

Weather conditions, i.e., precipitation and winds, in the spring of 1922 were favorable for spread of the rust from the main area of pine infection in British Columbia southward into western Washington. In British Columbia the summer months were unusually fine, dry, and warm. This probably accounts for the absence, in general, of the rust on ribes at distances more than about 25 miles from diseased pines in that Province. Also, the season was not noticeably favorable for the infection of pines except in the general vicinity of Revelstoke in the interior white pine belt. This has been substantiated by later findings.

SPREAD IN 1923

During 1923 further scouting on a large scale was done to determine extensions, if any, in the previously known range of the rust. This work was conducted over an extensive area in British Columbia and in Washington, Oregon, Idaho, Montana, and California.

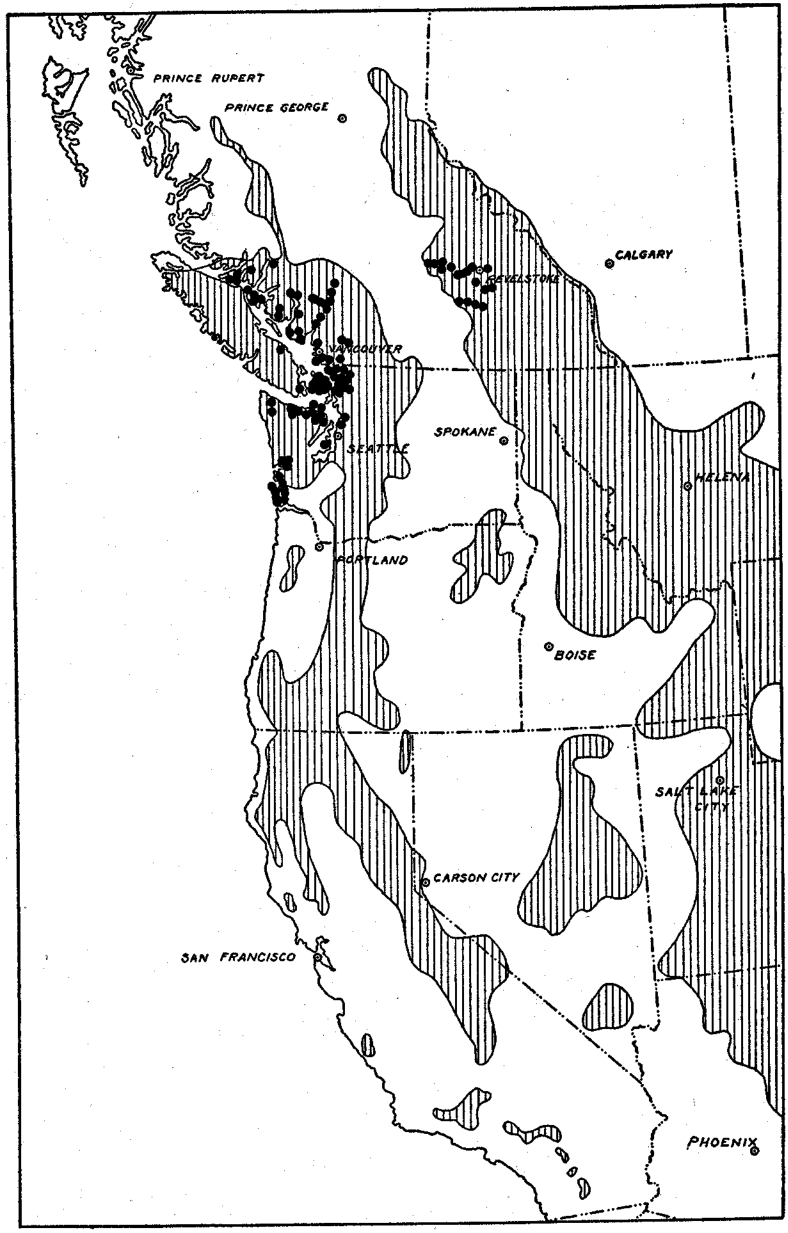

FIGURE 5
Known distribution of *Cronartium ribicola* on ribes in the West in 1922 shown by dots. Shaded area is the composite range limits of white pines in the West.

In British Columbia spread of the rust, particularly to ribes, was found to be considerably more extensive in 1923 than in the previous year. It was more or less general on this host practically throughout the range of *Pinus monticola* in the coastal area. On pines there the fungus was found at many additional places and aeciospores were found to have been produced in abundance. Also, the disease had reached destructive stages at several points, notably at Daisy Lake (later renamed Garibaldi) and Thurston Bay where many trees were already dead and others in a dying condition. The extreme northern limits at which the rust was found on ribes were at two places approximately 90 and 110 miles, respectively, north of the range limits of white pines on the coast.

In the interior dry belt of the Province the rust was general on *Ribes nigrum* practically all over that portion from the main line of the Canadian Pacific Railway southward about 125 miles to the International Boundary. Within this area the fungus appeared on ribes at a number of places where it was not found in 1922. In the interior pine region no additional pine infection centers were discovered, although the rust was general on *R. nigrum* over a fairly large area surrounding the three places where diseased trees were found in 1922. It also occurred on the European black currant from Revelstoke southward throughout the Arrow Lakes region and to Nelson on Kootenay Lake.

In Washington no additional pine infection centers were discovered. West of the Cascade Mountains in that State blister rust was not nearly so widely distributed on ribes as in 1922. It was observed on them only in the Puget Sound region. Within this area infected bushes generally were much less frequent in occurrence than they were over much of the coastal pine region in British Columbia. East of the Cascades, outside the range limits of white pines, infected *Ribes nigrum* were found at several places in the dry belt immediately adjacent to the infected area within this belt in British Columbia.

Negative results were obtained from scouting in the States of Idaho, Montana, Oregon, and California.

The distribution of the rust on ribes as determined in 1923 is shown in Figure 6. The known distribution of the fungus on pines in that year included most of the western white pine area in the coast region of British Columbia, three places in the interior of that Province and two places in extreme northwestern Washington. That blister rust was considerably more widespread on ribes in 1923, however, than the results of scouting then showed is indicated in Figure 7, which gives all present

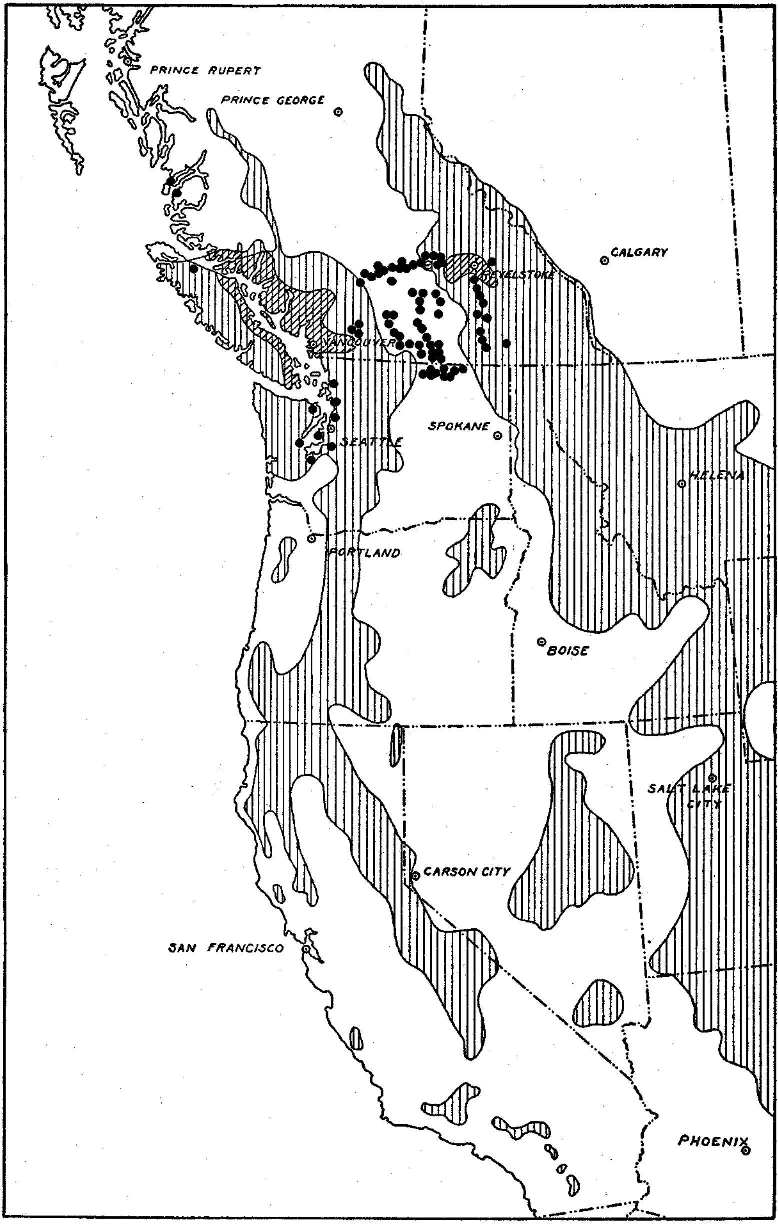

FIGURE 6
Known distribution of *Cronartium ribicola* on ribes in 1923. Crosshatching represents general infection of this host. Dots are infections at outlying points. Shaded area is composite range limits of white pines in the West.

known pine infection centers determined as having become established in that year. It can be seen from this figure and the previous one that spread to ribes in 1923 was most intensive to the eastward. As a result pines became infected in a number of new localities in southeastern British Columbia. Also, in that year, establishment of the rust on western white pine occurred at 16 known places in northern Idaho, mainly in the southern portion of the range, as shown in Figure 1, of that tree in the State. No pine infections determined as having had their inception previous to 1923 have ever been found there. In Washington pine infections occurred at many additional places in the northwestern part of the State and at one place in the extreme eastern part at Newman Lake. At least two new pine centers had their inception that year in northern Oregon.

The character of the weather in 1923 no doubt had much to do with the spread of the rust that year. Abundant aeciospore production occurred in April and May in the coastal region of British Columbia. There, the temperature during the season, i.e., from April to September, inclusive, was generally above the average and precipitation below. The somewhat drier than normal spring favored aeciospore dispersal, but probably accounts, at least in part, for the relatively limited distribution of rust on ribes over that of the previous year in western Washington, where the season was also relatively dry. In the southern interior of British Columbia during the summer, thunderstorms accompanied by rains were common, bringing precipitation considerably above normal. This condition was favorable for infection and intensification of the rust on ribes over a wide area including a large portion of the dry belt, and its establishment on *Pinus monticola* at a number of places within the interior pine belt.

SPREAD FROM 1924 TO 1926, INCLUSIVE

A wide spread of the rust to ribes, such as was noted in 1922 and 1923, did not occur in 1924. Seasonal intensification of the disease on the various ribes species was quite limited as compared with that occurring in 1923, and almost without exception infected plants of these hosts were confined to the immediate vicinity of pines bearing sporulating cankers. This undoubtedly is accounted for by the weather, the season being very dry and characterized by subnormal rainfall, high temperatures, and low relative humidity. The only extension noted in the previously known distribution of the rust on pines was a slight one in the Puget Sound

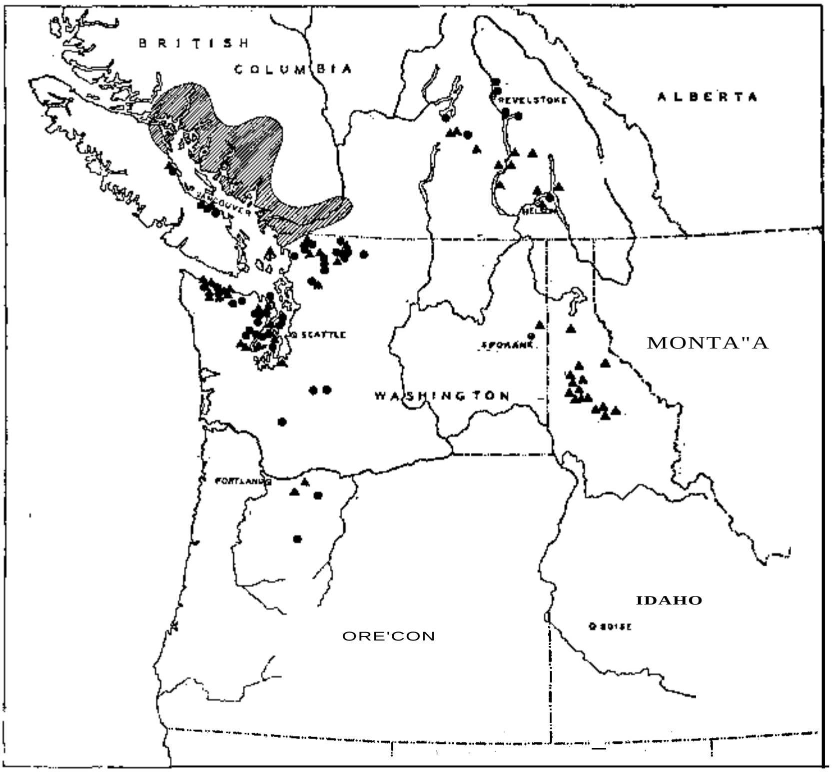

FIGURE 7
Known pine infection centers regarded as having become established in 1923 shown as triangles, and centers of previous origin as circles. Hatching is area of general pine infection.

region of northwestern Washington. By the fall of 1923 it was thought that the range limits of the rust in the West were quite well known. The results of scouting during 1924 were regarded as confirmation of this.

In 1925 early season conditions were very favorable for spread of the rust to ribes. In the chief area of pine infection in the coastal region of British Columbia. the main period of aeciospore dispersal was quite long, starting in late March near sea level and ending in late June at higher elevations inland. There was also a very abundant production of these spores. During the period of their dispersal there were several moist spells. The result was that the rust became distributed on ribes in 1925 over a greater range in parts of the West than it had ever before been found.

In the coastal region of British Columbia blister rust was more or less general, but not abundant, on ribes over most of the range of *Pinus monticola.* It was found again at the numerous places in the interior dry belt where it had occurred on *Ribes nigrum* in 1923, and in the Cariboo District of the dry belt at scattered places extending to about 125 miles farther north than previously recorded. The discovery of infected *P. monticola* in the southern portion of the interior white pine region of the Province near Nelson constituted the only extension noted in 1925 in the range of the rust on pines in the West as it was then known.

In Washington the rust reappeared on ribes at several places in the southwestern part of the State where it had not been found since 1922. The first blister rust to be found in Oregon was noted on ribes at three places in the extreme northwestern part of the State. Subsequent studies, however, showed that it had already been established on western white pine in the Cascade Mountains to the eastward for several years (Figs. 3, 4, and 7), and that infection of this host occurred at a few additional places in the vicinity of the older centers either in 1925 or 1926, probably in the former year. Also, in one or the other of these two years-probably in 1925 since 1926 was a very poor year for southward spread-the rust became established on sugar pine at one place in extreme southwestern Oregon. This was not found until 1936, however, and is the oldest sugar pine infection center known.

The distribution of the rust as found on ribes in 1925 is shown in Figure 8.

Although weather conditions in the spring of 1925 were favorable for spread of the rust to ribes, intensification of the fungus on these hosts was generally light because of the extremely dry summer. Dry weather also continued throughout the fall in the West and very little pine infection resulted.

In 1926, except for the month of May, temperatures during the season were above, and precipitation below, average. June and July were exceptionally dry and spring was one of the earliest on record in the Pacific Northwest. In the coastal region of British Columbia ribes leaf development was in general about a month earlier than previously noted. While a few aeciospores were produced there earlier than ever before, the main period of their production and dispersal occurred between mid-April and late May. They apparently were as abundant as in 1925, if not more so. The daily precipitation records for Vancouver, British Columbia, which

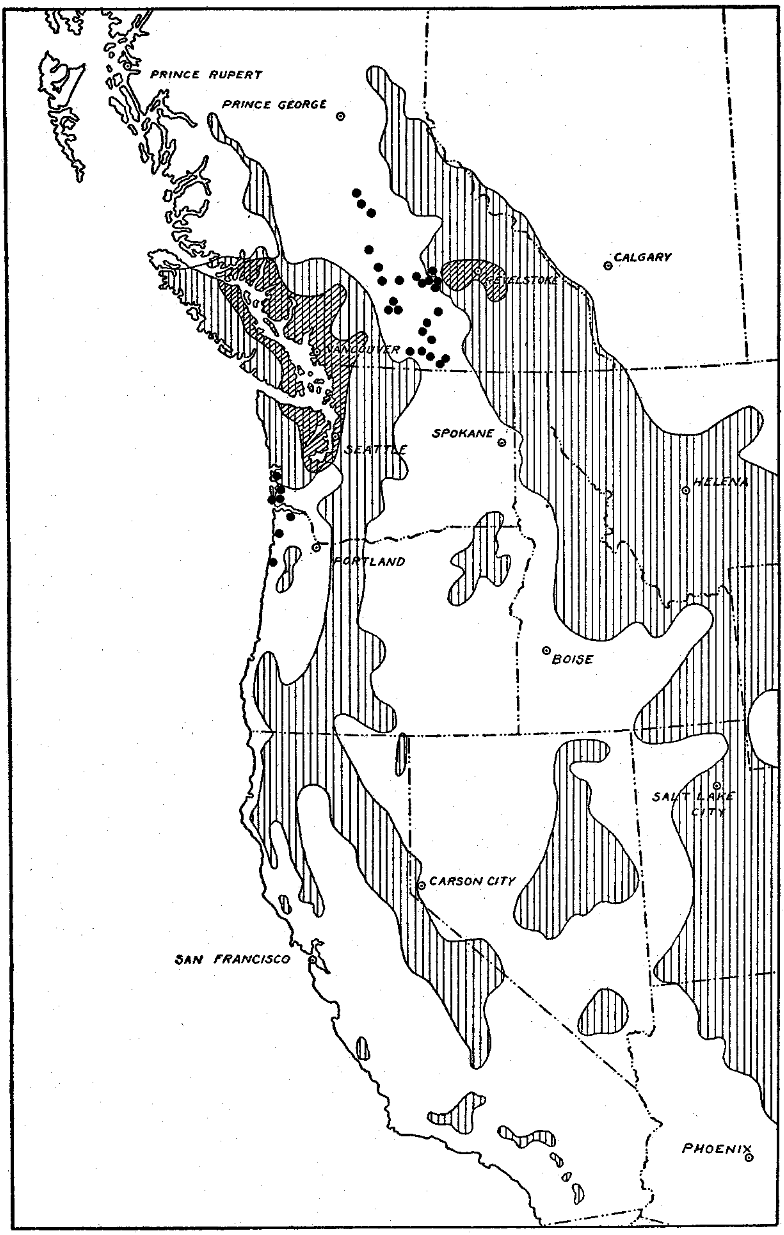

FIGURE 8
Known distribution of *Cronartium ribicola* on ribes in 1925. Crosshatched areas are regions where the rust was general on these hosts. Dots are places where infected bushes were found outside these areas. Shaded area is composite range limits of white pines in the West.

is quite representative of the climate over a large portion of the surrounding coastal region, show that for the 44-day period from April 15 to May 29, inclusive, rain fell on a total of 31 days. This unusually abnormal precipitation was observed to have prevented to a large extent the dispersal of the aeciospores. Large numbers of them were washed from the aecia by falling raindrops and carried to the ground, while in addition many others germinated in the aecia before being dispersed, their tangled and interwoven germ-tubes forming thick mats or secondary peridia covering and hindering dispersal of the spores that progressively formed later. Mold on the aecia was common. Also, many of the aeciospores must have been washed from the air by the rain.

As a result it was found that infection of ribes was very light even in the immediate vicinity of heavily infected pines, and that long-distance spread' of the rust was confined to a northerly direction in British Columbia where a few scattered infected ribes were found from 100 to 200 miles north of the range limits of *Pinus monticola* in the coastal region. The direction of spread that year has been explained by Lachmund (1934b) on the basis of the unusually early advent of spring with ribes leaves forming much earlier than normal and passing through their most susceptible stage of development before maximum aeciospore dispersal. He believed that as a result infection of ribes to the south was thus largely precluded, whereas infection of these hosts was most likely to occur to the north where they leafed out later than did those in the latitude of infected pines. In the opinion of the writer the abundance of precipitation in April and May had much to do with the pattern of spread of the rust to ribes and with the scanty infection of these hosts generally as found in 1926. Lachmund did not give consideration to this as a possible factor in limiting dispersal of the aeciospores. It has already been discussed herein under "Some Factors Influencing Infection of Ribes." Winds may also have been a factor in the direction of spread noted in 1926. Storms in the Pacific Northwest are ordinarily accompanied by southerly winds. Considering the abundance of storms during the main sporulation period in 1926 it would seem possible that winds that year would be more likely to transport aeciospores over greater distances to the northward than in the opposite direction.

Only a slight extension in the previously known range of the rust on pines was found. The discovery of blister rust on *Pinus albicaulis* in the coastal region of British Columbia constituted the first record of the fungus on this species within its natural range (Lachmund 1926b).

SPREAD IN 1927

The evidence obtained by scouting in 1927 indicated that the intensity of spread of blister rust to ribes was greater in that year than ever before. Also, the distance of spread to ribes occurring outside the range limits of pines was greater than previously recorded.

At the pine infection localities in British Columbia a greater volume of aeciospores were produced than ever before. In the coastal region their production on a large scale was sustained more or less continuously from mid-April to mid-June. It started first in the pine infection localities near sea level and ended latest at those in the higher elevations farther inland. In this manner reductions in sporulation in the former were compensated by increases in the latter. At areas of heavy pine infection in the interior most of the aeciospores were liberated in May.

Although precipitation at most stations in the coastal area of British Columbia was below normal in April, above normal in May, and below normal in June, moist periods were rather frequent during the main period of aeciospore production in these months. Apparently as a result there was a heavy initial infection of ribes in the vicinity of infected pines. The month of July was drier than average, but above normal precipitation occurring in August and near normal in September served to intensify the rust on ribes and cause considerable pine infection. At stations throughout the dry belt of the interior the months of April to July, inclusive, were in general drier than normal. In this region also precipitation was above the average in August and September. As a result considerable intensification of the rust on ribes occurred, making it relatively easy to find the disease there on both wild and cultivated ribes. Judging from scouting results weather conditions were likewise favorable for infection of ribes in other parts of the West where the rust was found on these hosts, while subsequent findings showed, as had been anticipated, that much pine infection occurred generally in 1927, evidently as a result of the abundant precipitation in August and September.

In the coastal region of British Columbia the rust was traced to the north over 300 miles beyond the northern limits of western white pine there and about 190 miles farther north than in any preceding season. Its spread in this section also included the Queen Charlotte Islands, on which no white pines are known to occur. The closest are over 200 miles to the southeast on Vancouver Island and about an equal distance to the east on the mainland. The islands were scouted for infected ribes in 1923 and 1925, two very favorable years for spread of the rust, with negative results. Within the range of *Pinus monticola* in the coastal region the fungus probably was more common on ribes than ever before.

In the interior dry belt blister rust was widely distributed on ribes. Its range in this section extended south of the International Boundary for a way and was traced northward to a point nearly 100 miles farther than previously noted. In the interior white pine region to the eastward infected ribes were more or less common from Revelstoke southward nearly to the Idaho line. No scouting was done for any distance to the north and east of this area in which the rust was found.

Scouting in Washington was more intensive than during any previous year. Whereas but 14 pine infection centers had been noted in the State from 1921 to 1926, inclusive, 45 additional ones were found in 1927, bringing .the known total to 59. These findings provided ample evidence that the rust had gained considerable momentum in its spread to pines. All of the known centers were in the western part of the State and west of the summit of the Cascade Mountains. In this region infected ribes were encountered more commonly than ever before. In northeastern Washington the rust was found on ribes at several places, practically all of which were outside the range limits of pines. It had not been recorded previously as occurring so far east in this part of the State.

In Oregon blister rust was found only on ribes. It was noted on these hosts in the northwestern part of the State at a number of places, all of which were not far south of the Columbia River and the majority within the range of *Pinus monticola.*

Northern Idaho had been scouted more or less thoroughly for blister rust each year since 1921. Previous to 1927 the fungus was not known to occur there. In that year it was found on ribes only at one place located in the extreme northern tip of the State. The results of scouting in western Montana and northwestern California were negative. However, two areas were later found in western Montana where blister rust was believed to have become established on pines in 1927.

The places where blister rust was found on ribes in the West are shown in Figure 9. This should be compared with Figure 10 showing the previously known distribution of the rust on pines and centers of known advance infection that became established in 1927 as determined from later studies. It is evident therefrom that blister rust was considerably more widespread on ribes in 1927 than the scouting results showed, particularly in Idaho and Oregon.

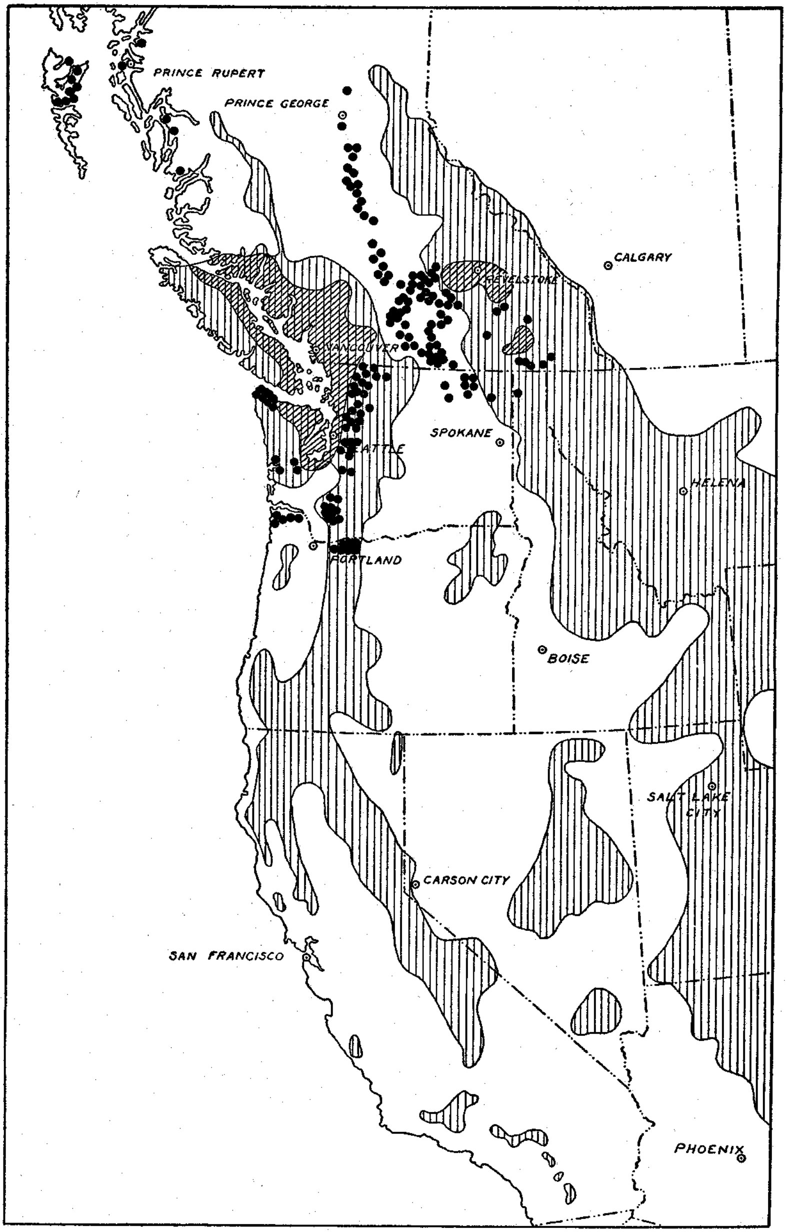

FIGURE 9
Known distribution of *Cronartium ribicola* on ribes in 1927. Hatched areas are regions where the rust was general in occurrence on these hosts. Dots are places where infected bushes were found outside these areas. Shaded portion is composite range limits of white pines.

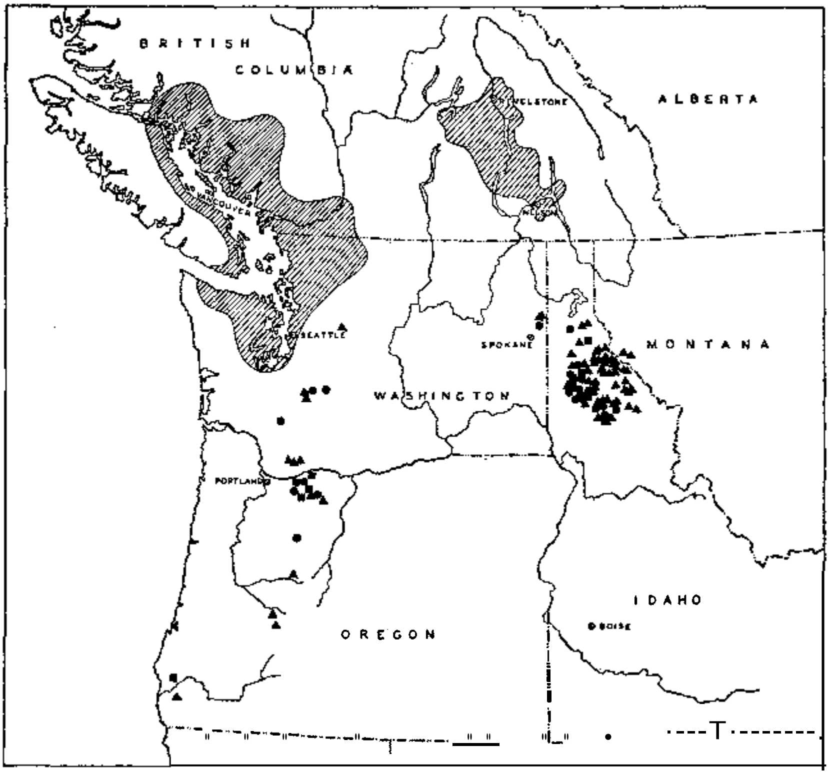

FIGURE 10
The distribution of *Cronartium ribicola* on pines in 1927–28. Hatched areas are regions of general pine infection. Advance centers outside are designated as follows: circles are known pine infection centers that became established in 1923 and previously; squares are known centers regarded as originating in 1925 or 1926; triangles are all known places where pine infection became established in 1927 or 1928. Those regarded as of 1928 origin are relatively few in number, but are included with those of 1927 because the probable year of origin is sometimes difficult to determine. Throughout the West generally very little pine infection occurred in 1928 because of the extreme dryness of the summer and fall seasons.

One feature of the spread of blister rust in 1927, regarded as especially noteworthy, was its much wider distribution on wild ribes than ever before. In the dry belt and Cariboo districts of British Columbia, situated between the white pine belts of the coast and interior, the fungus was in general as readily found on the more highly susceptible wild species as on its most susceptible host, *Ribes nigrum.* With but few exceptions no more than a short search was required to find it on these wild hosts wherever they were examined. The places where it was looked for and not found on them were exceedingly rare. In previous years, although scouting of the wild species in the dry belt was not nearly so intensive, the rust was found there on *R. nigrum* only and in some years its distribution was very limited on it. In Washington and Oregon blister rust was more commonly found on wild ribes than ever before, but in no instance was the distance of spread from infected pines to these hosts nearly so great as that found in British Columbia. In those two States *R. nigrum* no longer existed because of the completion of the eradication programs against it. Consequently, information on the relative intensity and distance of spread to wild species as compared with *R. nigrum* was not obtainable there as it was in British Columbia.

SPREAD IN 1928

All evidence obtained from scouting in 1928 and from subsequent studies of infected pines in various parts of the West indicated that spring weather conditions were more favorable for spread of the rust in a northerly and easterly direction than to the southward.

In the main area of pine infection in the West, situated in the coastal region of British Columbia, aeciospores were produced in great abundance from late April into early June. Precipitation at most stations there was considerably below normal in May and fell mainly during the latter part of the month. These dry conditions were very favorable for aeciospore dissemination. The general storms of late May and above-normal precipitation in June provided adequate moisture for abundant initial infection of ribes in the vicinity of infected pines.

In the interior dry belt and Cariboo district of the Province similar weather characteristics prevailed. There, the results of fall scouting showed that both wild species and the European black currant became initially infected apparently in greater numbers than ever before. However, the remainder of the season, i.e., July to late October, inclusive, was so abnormally dry that very little intensification of the rust occurred on these hosts. In nearly all cases there were only a few infected leaves per bush, a condition that required very careful inspection of the plants to detect the rust. In some instances infection was so light that only a single lightly diseased leaf was found. As a result of the exceptionally dry late summer and fall weather *over* the range of the rust in the West in general very little pine infection occurred that season.

In 1928 blister rust was first found in northeastern Washington on pines on the western fringe of the Inland Empire white pine belt. This center was determined to have become established in 1923 (see Fig. 7). In the western part of the State only a limited amount of scouting was done. The rust was found on ribes only at a few places outside the general area of infection in the Puget Sound region.

On ribes in Idaho the rust was found at *over* 40 points, mainly in the southern half of the range of *Pinus monticola* in that State. In all cases it was noted on wild species and was, with but few exceptions, confined to the highly susceptible *Ribes petiolare* and *R. inerme.* Possibly most of the rust on ribes there that season may be attributed to infected pines present in the region (see Fig. 7) but not then known to exist.

The first blister rust discovered in Montana was found on a single ribes in the western part of the State near the Idaho line. In Oregon the rust was recorded on pines for the first time in 1928 (see Figs. 3, 4, and 7). Lightly infected trees were found rather widely scattered *over* a considerable area in the Cascade Mountains near Rhododendron, southeast of Portland, and at one place (Palmer) northeast of Rhododendron near the Columbia River. Diseased ribes were scattered *over* this general area. To the westward in the coastal region infected ribes were found at 19 different places. Later studies indicated that diseased pines were present in this vicinity at the time. All rust found on ribes in Oregon in 1928 is therefore possibly traceable to infected pines in the State and not to long-distance spread from the north. In nearly all cases it was noted on *Ribes bracteosum,* a highly susceptible species frequenting stream courses and other moist sites.

The distribution of the rust on ribes as determined in 1928 is shown in Figure 11.

SPREAD FROM 1929 TO 1935, INCLUSIVE

The season of 1929 was unusually dry over practically all parts of the West and consequently not a favorable one generally for wide spread of the rust to ribes, its intensification on these hosts, and the infection of pines. The results of scouting in British Columbia indicated that aeciospores had again been widely disseminated *over* the interior dry belt, but that considerably fewer ribes, both wild and cultivated, became

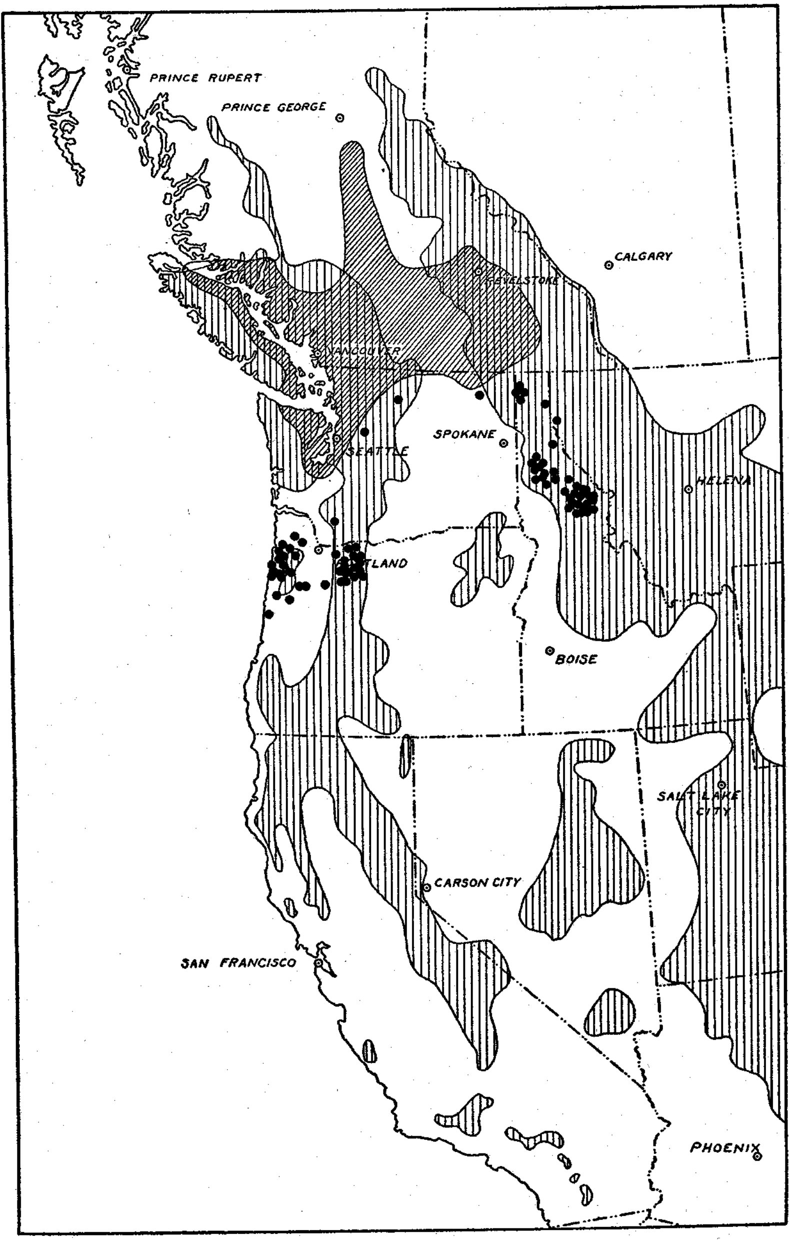

FIGURE 11
Known distribution of *Cronartium ribicola* on ribes in 1928. The area over which the rust was known to be general in occurrence on these hosts is designated by crosshatching. Dots are places where infected bushes were found outside this area. Shaded portion is composite range limits of white pines.

infected than in the previous two years. Although blister rust became established on pines in Idaho in 1923 its presence there on them remained undetected until 1929. This discovery constituted the only important extension in the previously known range of the rust on pines. The only noteworthy extension observed in the previously known range of the fungus on ribes was in Oregon where four infected bushes were found in one locality in the southwestern corner of the State about 40 miles from the California line. While this was about 200 miles farther south than it had been noted before along the coast, it is doubtful if this was a case of long-distance spread for later studies disclosed that sporulating cankers were present on sugar pines in 1929 within 10 miles of the infected ribes.

Spring weather conditions in 1930 were favorable for a very intensive spread of the rust to ribes in some sections of British Columbia but definitely unfavorable in other parts of the West. Over the West in general the summer and fall seasons were very dry and as a result relatively little intensification of the rust on ribes or infection of pines occurred.

With the end of the fall season of 1930, studies on annual spread of the rust in British Columbia were discontinued. Thereafter the investigations on this phase of the blister-rust problem were limited to the Inland Empire and adjacent Rocky Mountain region and the States of Oregon and California. Although the rust became established on pines in California probably as early as 1930, it was not found thereon either of its hosts until 1936.

By the fall of 19JI blister rust on ribes or pines had been found scattered over practically the entire western white pine region of Idaho, and was most abundant in the southern part coincidental with the occurrence of large numbers of *Ribes petiolare.* Aeciospore production was much more abundant than ever before because of the tremendous increase in number of cankers (principally those having their inception in 1927 and 1928) that had developed to the sporulating stage. Despite this condition, ribes in the vicinity of diseased pines did not become initially heavily infected owing to the dry weather that prevailed during most of the period of aeciospore dispersal. As a result of the abnormally dry summer season that followed, uredial intensification was less than normal. Although precipitation was above normal in the fall heavy pine infection did not occur because of the scanty amount of rust on ribes. Infected ribes were fairly common in places along the north coast of Oregon within the area where the rust had been noted in some of the previous years; otherwise, spread to these hosts at considerable distances from diseased pines was not observed to have occurred. Except for the discovery of infected pines in the coastal region of northwestern Oregon for the first time in 1931, no extension of importance was noted that year in the previously known range of the rust on either pines or ribes.

The abundant spring rains in 1932 probably inhibited dispersal and wide spread of the aeciospores, for in those western States where scouting was conducted that year infected ribes were found largely within the areas of diseased pines. Within the main area of pine infection in Idaho diseased ribes were fairly common. Previous to 1932 practically all rust on ribes there, was on those species occurring along stream courses, but in that year more rust was found on *Ribes viscosissimum,* an upland species, than ever before. Precipitation was below normal from June to September, inclusive, but there were three or four well-spaced periods during that time in which light rains fell for two or three days. As a result the rust intensified fairly well on ribes and moderately heavy pine infection occurred in some parts of Idaho. Elsewhere in the western States the summer and fall seasons were quite dry and relatively little pine infection occurred.

No evidence was found of wide spread of the rust toribes in 1933. In general, infection of pines was light either because of the relatively meager amount of rust on ribes or the dry summer and fall weather, depending upon the locality. Blister rust was discovered in northeastern Oregon for the first time, being found there on ribes at three not widely separated places. In the Cascade Mountains of Oregon infected pines were found at a point about 70 miles farther south than was recorded before. Otherwise no extension of importance was found in the previously known range of the rust on pines or ribes.

Spring was abnormally early in 1934. Temperatures were considerably above normal and there was exceptionally little precipitation during the main period of aeciospore dispersal. As a result the initial infection of ribes in association with diseased pines was light and spread of the rust to ribes was limited. The summer and fall seasons were very dry and relatively little intensification of the rust on ribes or infection of pines occurred, the year being considered a poor one in these regards. In the Inland Empire region the rust was found on pines over a considerably wider area than 'it had been noted before. The extension of the previously known range on this host included extreme western Montana where infected pines were found at four not widely separated places near the Idaho line. This constituted the first record of blister rust on pines in Montana. Practically all of the pine infection centers discovered in 1934 had their inception in 1927.

In 1935 moisture conditions in the Inland Empire were favorable for initial infection of ribes by aeciospores in the spring and uredial intensification in early summer, but late summer and fall were so abnormally dry that little or no pine infection occurred that year. No evidence was found of a wide spread of the rust to ribes. Numerous additional pine infection centers were found, but practically all of these were within the previously known range of the rust on pines. In Oregon the spring was late, and the year unusually dry, particularly the period from May to September inclusive. In general ribes in association with diseased pines were lightly infected and very little pine infection occurred. On ribes the rust was found at one point in the Cascade Mountains 35 miles farther south than previously recorded, placing it within 65 miles of the California border.

SPREAD IN 1936

More than twice as many pine infection centers were found in the Inland Empire in 1936 than had been recorded in all previous years, providing evidence of the general occurrence and rapid intensification of the rust on pines in that region since its invasion in 1923. A number of these additional centers were in both northeastern Washington and northwestern Montana, but all of them were within a relatively few miles of the Idaho boundary and not far outside the previously known range of the fungus on pines. A wide spread of the rust to ribes did not occur, but within the areas of diseased pines initial infection of ribes was heavy and a fair amount of uredial intensification occurred during early summer. As a result of the exceptionally dry summer and fall there was relatively little infection of pines that season over the region as a whole.

West of the Cascade Mountains in Oregon the spring of 1936 was abnormally moist, but from June 19 on until very late fall precipitation was markedly deficient. Very similar weather occurred in northwestern California. Spring moisture conditions were fairly good for initial infection of ribes but a marked wide spread to ribes was not observed. This latter condition is believed attributable to the abundance of moist spring weather that largely inhibited dissemination of the aeciospores in quantity for any great distance. Because of the exceptionally dry summer and late fall little if any pine infection occurred that year.

Although the search in California was started in 1917 and continued every year thereafter on a greater or lesser scale, blister rust was not found in the State until 1936. In that year it was observed there at one place on sugar pine only, one place on both sugar pine and ribes, and three places on ribes only. All five of these points were in the extreme northwestern corner of the State and within a few miles of the Oregon line. One of the pine infection centers was determined as probably having become established in 1930 and the other in 1931. The rust was also found on pines in southwestern Oregon for the first time in 1936. There, it was noted at three places on sugar pine and one place on both sugar and western white pine. Analysis of canker tabulations indicated that the oldest of the centers (Panther Mountain) probably became established in 1925, and the nextoldest (Windy Valley) in 1927. In both those years wide dissemination of the rust from pines to ribes occurred in the West. The other two centers were of more recent origin, and these together with the two found in adjacent California are believed to represent spread from the Panther Mountain infection area where aeciospores evidently had been produced ever since 1929. The few scattered infected ribes found in southwestern Oregon and northwestern California indicated that rust was not prevalent on these hosts in that general region in 1936. This year was not only the first in which blister rust was found in California, but also the first in which it was found on sugar pine within the natural range of this tree.

No extension was noted in the previously known southern limits of the rust in the Cascade Mountains of Oregon. However, within those limits lightly infected sugar pines were found at two places, infected whitebark pines were noted over a large area on the south slope of Mt. Hood, and in the McKenzie River region the rust was observed to be more widespread on western white pine than previously recorded. These findings, together with those of previous years, showed that the fungus was intensifying at a fairly rapid rate in the northern part of the Cascades, but that its invasion of the southern part of the range was relatively slow.

SPREAD IN 1937

The year 1937 was found to be by far the most favorable since 1927 for wide spread of the rust to ribes and infection of pines in the western States.

In the Inland Empire region precipitation was below normal in the spring during the main period of aeciospore production. There were, however, several moist periods of sufficient duration and so spaced as to favor moderately heavy initial infection of ribes. During the remainder of the season, i.e., from July to September, inclusive, precipitation was also below normal, but there did occur four well-spaced moist and cloudy periods all of which were of three or more days' duration. These showery periods were very favorable for intensification of the rust on ribes and infection of pines.

A limited amount of scouting, conducted southeastward from the main area of pine infection in Idaho, revealed that blister rust was more extensive on ribes in western Montana than ever before noted there. Three of the outlying points at which infected ribes were found were in the Beaverhead National Forest and one on the Gallatin National Forest. The discovery of these marked the first extension of the known range of the rust in the West to the east of the Continental Divide. The most easterly of these points was within about 25 miles of the northwest corner of Wyoming. Also, it was about 150 miles farther east than blister rust had previously been recorded in the West. No additional pine infection centers were noted in Montana, and the closest known diseased pines to the most easterly of the points where the rust was observed on ribes were on the Selway National Forest in Idaho, approximately 180 miles to the northwest.

In western Oregon spring was somewhat late in 1937. The month of April was cooler than normal and unusually cloudy and wet. May, on the other hand, had above normal temperatures and was relatively dry. This condition favored the production of aeciosporesand their dissemination, while three or four rainy periods during the month provided adequate moisture for rather heavy initial infection of ribes in the vicinity of diseased pines. Weather conditions in the spring were also favorable for long-distance spread of the rust to the southward. Over a period of seven consecutive days, May 29 to June 4 inclusive, northerly winds of medium to high velocity prevailed. Aeciospores were still being produced in abundance at that time in the northern part of Oregon, where the heaviest pine infection areas in the State are situated. Apparently as a result of these winds blister rust became widely distributed on ribes in southwestern Oregon and northern California for the first time.

Diseased ribes were found more or less generally scattered over the infected area in Oregon, and over a portion of it and the adjacent Klamath River region in California about one ribes bush out of every hundred on an average was infected. Scattered infected bushes were found in California to about 125 miles south of the Oregon line both in the coastal mountains and in the Sierra Nevada. These limits coincided closely with the southern limits of a general rainstorm, which occurred over southwestern Oregon and the northern portion of California shortly after the termination of the windy period mentioned above.

Evidently the aeciospores responsible for the rust found on ribes over the area in question did not have local pine infection centers as their source but instead came from somewhere to the north because, (I) in the fall of 1936 all known diseased pines in California that were bearing sporulating cankers were destroyed, (2) no infected pines have since been found in California that bore sporulating cankers in 1937, and (3) the infected ribes in California were found scattered over a front approximately 85 miles in width.

No additional pine infection centers were found in California or in southwestern Oregon in 1937. Also, there was no extension noted in the previously known southern limits of the rust on pines in the Cascade Mountains of Oregon, but it is now known that in 1937 the fungus did become established on these hosts in the southern Cascades at a number of places, some of which were very close to the California line.

The early fall rains occurring in California in 1937 were at the time believed to have provided favorable moisture conditions for infection of pines. This has been substantiated by subsequent reconnaissance, the results of which showed that the rust became established on these hosts in the coastal mountains at a considerable number of places in the Klamath River region near the Oregon line and in one small area about 70 miles south of that line. With but one possible exception no evidence has yet been found of pine infection having occurred in the Sierra Nevada in 1937. This small center, which is situated on the Plumas National Forest and which may have had its inception in that year, is about 160 miles south of the Oregon line.

The known spread of the rust to tibes in 1937 and the known limits of its distribution on pines and ribes to 1936, inclusive, ate shown in Figure 12.

SPREAD IN 1938

In the Inland Empire region 1938 was another good year for the development of blister rust. Below normal precipitation occurred in May

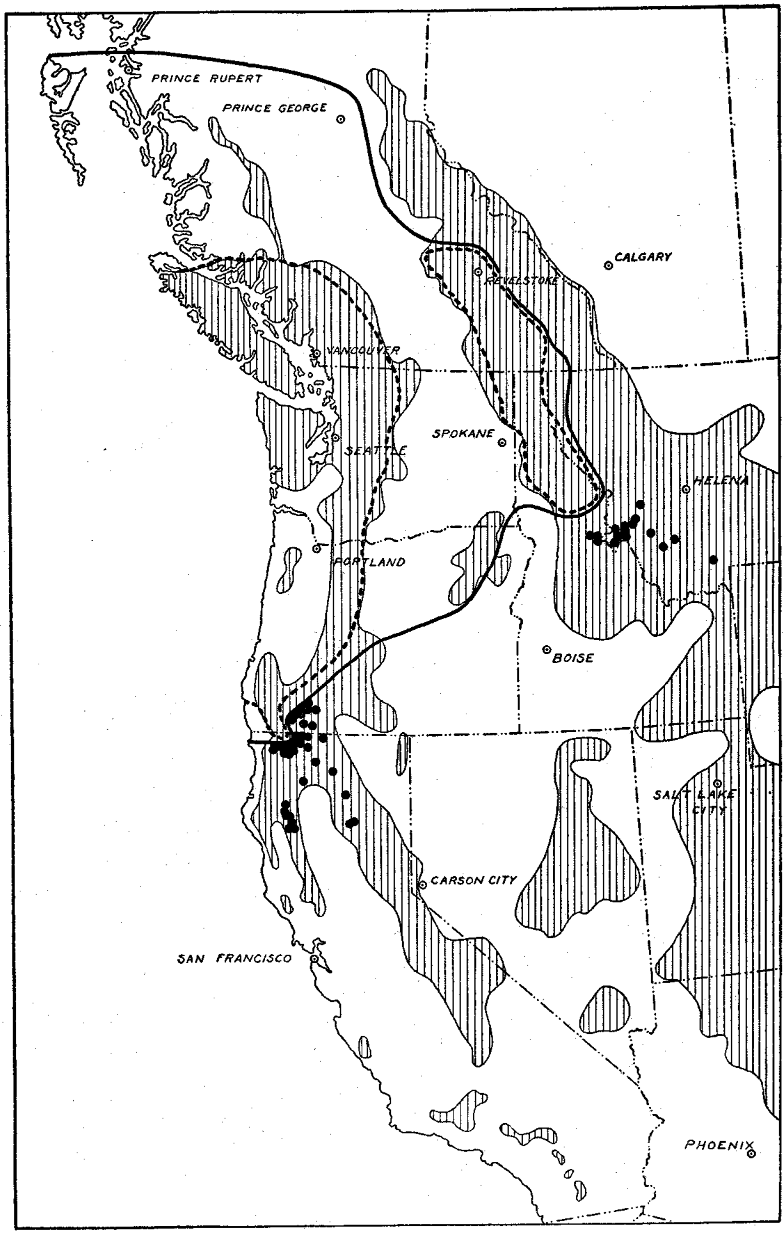

FIGURE 12
Known distribution of *Cronartium ribicola* on pines (broken line) and ribes (solid line) in the West to 1936, inclusive. Known spread to ribes in 1937 shown by circles. Shaded portion is composite range limits of white pines.

and June, *but* during that time rainy periods were rather frequent and so spaced that they provided favorable conditions for both the dissemination of aeciospores and the initial infection of ribes. Although precipitation was also below normal during the remainder of the season, there occurred several periods of weather characterized by intermittent light rains and cloudiness that varied in length from two to eight days. These provided not only adequate moisture for the uredial intensification of the rust on ribes and the development of abundant telia, *but* also conditions favorable for the production of sporidia and infection of pines.

Scouting outside of the known infected area in the Inland Empire revealed the presence of blister rust on ribes at five locations distributed over Glacier National Park in Montana on *both* sides of the Continental Divide. This represented a marked eastern extension of the known limits of the rust in the northern part of that region, *but* was not so far east in the Rocky Mountains as it was found in 1937. In that year it was recorded on ribes within a short distance of Yellowstone National Park, *but* the results of an intensive search on highly susceptible ribes at a number of places within the Parkin 1938 were negative.

In western Oregon the advent of spring was at about the usual time. April was characterized by frequent and above normal precipitation. While May had above average temperatures and less than half normal precipitation, there were three or four moist periods during the month. The wea.ther conditions of that month evidently were quite favorable for dissemination of aeciospores and initial infection of ribes. June was dry and with *but* one showery period, which was of several days' duration. This occurred near the middle of the month and provided ample moisture for intensification of the rust on ribes. From then on, however, the summer was extremely dry and fall rains were unseasonably late. In some regions, in fact, the first fall precipitation was in the form of snow rather than rain. Consequently, the year developed into a very poor one for intensification of the rust on ribes and infection of pines. Relatively little scouting was done in Oregon in 1938 and no extension in the known range of the fungus was noted nor were any additional pine infection centers found therein.

On the other hand, the results of intensive scouting in California showed blister rust to be more prevalent and widespread on ribes in the Sierra Nevada than in 1937, the first year it was noted in that region. The previously known southerly limits there were extended about 35 miles, placing them 160 miles below the Oregon line. In addition to scattered diseased ribes, a concentration of the rust occurred on these hosts in two localities. At one of the localities infected bushes were found scattered over four sections and at the other over 24 sections, but at places within each, 10 per cent or more of the ribes were diseased.

In contrast with the situation in the Sierra Nevada, the rust was observed to be practically absent on ribes in the northwest corner of the State where it had been found very common in occurrence in 1937. Except for some infected bushes in a small area where there were a few diseased pines, the rust was found at but one other place. The almost total absence of the rust in this region in 1938 further substantiated the previous belief that the aeciospores responsible for the infection found so generally there on ribes in 1937 came from a distant source. No additional pine infection centers were found in California in 1938, and the only ones known there were the two recorded in 1936 a few miles from the Oregon line.

A period of northerly winds occurred over the Pacific Coast States from May 16 to 21, inclusive, at which time aeciospores were still being produced in abundance at the main pine infection areas in northwestern Oregon. This prolonged windy period is believed to have carried aeciospores into the Sierra Nevada of California. It was followed by rains of somewhat patchy occurrence throughout the sugar pine region of northern California between May 27 and 29. These rains evidently occurred within sufficient time to induce infection on ribes by aeciospores apparently carried into the State during the period of north winds.

A few showery periods in June and thunderstorms during the last half of July provided moisture for the intensification of the fungus on ribes. From then until the end of September there was no precipitation. Then, very heavy rains occurred for two days or more at a number of places in northern California. However, the intensity and duration of these rains were apparently inimical to the transfer of the rust from ribes to pines for relatively few blister-rust cankers have been found within the two areas where the fungus was common on ribes in 1938. The conditions found at these places are therefore believed to provide an excellent example of heavy and prolonged rains inhibiting infection of pines.

SPREAD FROM 1939 TO 1942, INCLUSIVE

In the Rocky Mountain region blister rust was found again on ribes in 1939 for the second consecutive year in Glacier Park. Also, infected ribes were found at two places not far south of the Park, thus extending a short distance in a southerly direction the previously known range of the fungus in that area. No evidence was found of long-distance spread to ribes in the Rocky Mountain region in 1940 or 1941, but in the latter year three diseased *Pinus monticola* trees bearing young (non-sporulating) cankers having their inception in 1938 or 1939 were found at one place a few miles west of the Continental Divide in Glacier Park. This discovery placed the rust on pines about 70 miles farther east in Montana than it was previously recorded and constituted the first notable extension in an easterly direction of the rust's range on this host since 1927. No scouting was done in the Rocky Mountain region in 1942.

In Oregon no extensions were noted in the previously known range of the rust on either pines or ribes in 1939, but in 1940 two small pine infection centers were found in the southern Cascade Mountains. The southernmost of these was within 35 miles of the California line and placed the known limits of the fungus on pines about 65 miles farther south than it had been recorded there before. This was the first time since 1934 that a southward extension in its range on pines was noted in the Cascades of Oregon and provided additional evidence of its slow progress there in a southerly direction. In 1941 and 1942, however, numerous pine infection centers were found scattered over this general area and the adjacent Siskiyou Mountains as far south as the California line. Two of these centers had their inception in 1933 or 1934 and practically all of the remainder in 1937, which was a very favorable year for rust development. Weather conditions in Oregon were unfavorable in 1939, only fairly favorable in 1940, quite favorable in 1941, and very unfavorable in 1942 for the development of the rust on ribes and infection of pines. In none of these four years did a wide spread of the rust to ribes occur.

A wide distribution of the rust on ribes in California, such as was recorded in 1937 and 1938, did not occur in either 1939, 1940, 1941, or 1942. This evidently is accounted for by the fact that during the main period of aeciospore production in the Pacific Northwest in each of those years there were no periods of north winds favorable for long-distance transport of aeciospores southward into California. If aeciospores had been carried into the State from the north, a widespread infection of ribes should have occurred because the necessary moisture was provided each spring by rains, and particularly so during the unusually moist season of 1941. Yet, in 1939, 1940, and 1942 the rust was found on ribes only in the vicinity of diseased pines bearing sporulating cankers, and this was also the case in 1941 except in one instance. In December of that year infected ribes were found at several places scattered over an area situated in the north coastal region of the State. No white pines were observed growing nearby and the source of the responsible aeciospores, which may possibly have been a not-distant pine infection center yet undiscovered, was not determined. It is probable, however, that the rust spread to ribes within this area in some previous year, possibly in 1937, and has since been overwintering on them, for in the mild coastal climate there this host retains some of its leaves the year around.

Up to 1939 blister rust had been found on pines in California at only two places and in that year only one additional infection center was discovered. All three of these small centers were in the coastal mountains and within a few miles of the Oregon line. In that same general region in 1940 diseased pines were noted at 14 different places extending from a point near the Oregon border south over 40 miles. In 1941 and 1942 a number of additional pine infection centers were found within the 1940 limits and also in one locality about 30 miles to the southward. All of the centers discovered in 1940, 1941, and 1942 had their inception in 1937. In the Sierra Nevada infected pines were found for the first time in 1940. There, a few diseased trees were observed in two localities where infected ribes were common in 1938. The southernmost of these was about 100 miles from the Oregon line. In 1941 additional diseased pines were found in those two localities and the limits of the rust on pines were extended 70 miles farther south to a locality where 13 small infection centers were discovered scattered over an area of several square miles. One of these centers had its inception possibly in 1937, but the others were definitely of 1938 origin. A few more cankers were observed within this area in 1942. Sugar pine is the only white pine species that has yet been found infected in California.

The known limits of blister rust on pines and ribes in the West to 1942, inclusive, are shown in Figure 13.

GENERAL ASPECT OF SPREAD

THE evidence accumulated to date indicates that, on the whole, host and environmental conditions over that portion of western North America now invaded, have been very favorable for epidemic spread and development of blister rust.

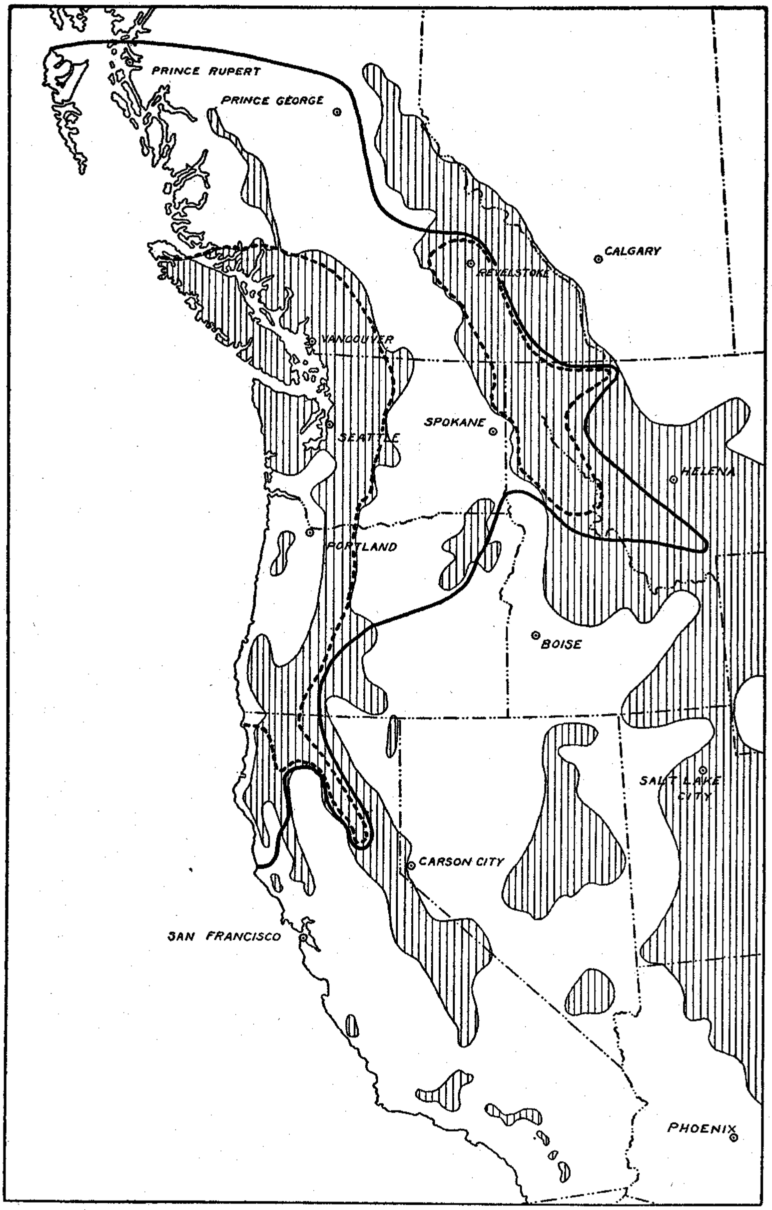

FIGURE 13
Known limits of *Cronartium ribicola* on pines (broken line) and ribes (solid line) in the West to 1942, inclusive. Shaded portion is composite range limits of white pines.

The place of introduction of the rust, situated as it was on an exposed and windy point in the south coastal region of British Columbia, probably could not have been more ideally located as a starting point for the spread of the pathogen over the white pine forests of the West. The moist, mild climate, the prevailing inland course of the winds, the abundance of highly susceptible young western white pine and native ribes over large adjacent areas of cut-over lands and old burns, all combined to facilitate the rapid development and spread of the rust so that within 3 years after its introduction western white pine to a distance of some 120 miles had become infected. Within a few more years these in turn were producing aeciospores in abundance as the source for a new wave of spread of the rust. During this time the presence of the disease went unrecognized and consequently no control measures were undertaken that would have interfered with its natural progress.

During the period of aeciospore dispersal prevailing winds over that portion of western North America under consideration are from the west or southwest, and no doubt these winds have had. much to do with the pattern of spread as it has occurred up to the present time. The coastal region of British Columbia is very mountainous and topography of this kind causes local variation in the direction of surface winds. Such winds are not only favorable for local dissemination of aeciospores in various directions but also for carrying them to higher elevations where they may be transported over long distances in the path of the prevailing winds. In the Pacific Northwest rains are ordinarily preceded and accompanied by southerly winds. Winds therefore were most favorable for spread in a northerly and easterly direction and from the coastal region spread to ribes over varying distances in those directions occurred almost every year.

By 1917 the rust, in its progress inland from the coast, had invaded the interior belt of western white pine in British Columbia by jumping the dry belt east of the Cascade Mountains. But host and environmental conditions there were not so favorable for spread and intensification of the disease as in the coastal region. Seasonal precipitation is somewhat less, white pines are not so common, and highly susceptible ribes are numerically scarce. These factors, particularly the latter, prevented a rapid spread of the fungus over that region.

In Idaho host and environmental conditions for rust development probably are more uniform than anywhere else in the West. Although summer precipitation is somewhat less in amount there than in the interior infection area of British Columbia to the northward; the hosts are much more common. Practically pure stands of western white pine occur over extensive areas in Idaho, and in the reproduction stage the tree is particularly abundant on old burns and logged-off lands. The dense concentrations of the highly susceptible *Ribcs pClio/arc* along stream courses and the common occurrence of less susceptible species in the uplands provided an abundance of the alternate host plants in associations highly favorable for the rust. Initial invasion of the white pine stands in Idaho, which took place in 1923, occurred via ribes along the stream courses, and from the adjacent centers of pine infection the rust became widely distributed in the uplands in about 10 years. Although intensification of the disease on pines in Idaho was rapid for a number of years following the invasion it has now been slowed down materially by the destruction of ribes over extensive areas during the course of control operations.

The eastward progress of the rust on pines from northern Idaho and immediately adjacent Montana into the Rocky Mountain region has been very slow. To date but one center of pine infection, which is of recent origin, has been found there. Why the rust has been so slow to spread eastward is not known. One of the factors of some importance probably is the patchy occurrence of white pines but, based on present knowledge, it seems that there must be some epiphytological aspect to the situation that is not yet sufficiently understood to account for the lack of continued spread in that direction.

Although the intensity of spread has been greater to the eastward the rust has progressed somewhat farther to the southward. Evidently this character of the spread is attributable mainly to host distribution, precipitation, and winds. While ribes are common throughout the forest areas of western Washington and Oregon and northern California, the more or less patchy occurrence of white pines provides less favorable host associations for the rust there generally than is the case to the eastward in Idaho. Moisture necessary for the intensification of the fungus is less, for the amount of spring, summer, and fall precipitation diminishes to the southward. North winds are not common during the spring. Southward spread of the rust to ribes has been at relatively infrequent and irregular intervals and has not always involved ribes in association with pines. It has occurred only in those years in which there have been periods of north winds favorable for the long-distance transport of aeciospores from northern sources followed by moisture conditions necessary for the infection of ribes. Then, a southward extension in the range of the rust on pines has resulted only when summer and fall weather conditions have been favorable for the intensification of the fungus on ribes and the infection of pines in association with diseased ribes.

As early as 1917 or 1918 the rust spread southward into the northern Cascade Mountains of Oregon where it became established on pines at one place, and in 1925 or 1926 infection of pines occurred at one place in the southwestern part of the State. But, because these outlying infection points were isolated by the limited distribution of hosts they were but of relatively minor significance in the intensification and spread of the disease. The general or intensive progress of the rust southward through Washington and Oregon into California has been comparatively slow. It was not until 1937, or about 20 years after the fungus entered Oregon, that an extensive spread to pines in the, southwestern part of the State and adjacent California occurred. In 1938 sugar pine became infected in three widely separated localities in the Sierra Nevada of California, or within the main commercial range of this host for the first time. There, the rust is yet too early in its invasion stage to have had an opportunity to exhibit its capacity for spread and intensification under the existing host and environmental conditions.

Since its introduction in 1910 the rust is now known to have spread to pines at an average annual rate of about 15 miles to the eastward and 23 miles to the southward. However, this rate has not been a steady one. Instead, the progress of the disease has been in jumps or waves, which have occurred at irregular intervals or only in those years in which weather conditions have been favorable for the development of the fungus.

Contrary to its status in the East the European black currant played only a minor rôle in the epidemic spread of blister rust in British Columbia and has been a negligible factor elsewhere west of the Rocky Mountains, where spread has been associated wholly with the native wild species. The rust has now spread over most of the range of western white pine and, at the present time, is largely confined to that species. The only other species on which attack has occurred in their natural stands are whitebark and sugar pines.

DISSEMINATING AGENCIES AND SPORE STAGES INVOLVED

BEFORE *Cronartium ribicola* was found in the West in 1921, long-distance spread by means of wind-borne aeciospores had been suspected in the East (Spaulding 1922a). This was impossible to prove there, however, because the fungus originated at a large number of places more or less simultaneously as the result of importations of large numbers of diseased *Pinus strobus* seedlings that were widely distributed for reforestation purposes. In the West, however, the rust spread from a single point, making it possible there to determine facts that could not be ascertained in the East.

As a result of investigations in the East conducted prior to 1922, it had been found that wind-borne aeciospores might, under favorable conditions, cause infection of ribes upwards to about seven miles distant and possibly farther; that spread of the sporidia from ribes to pines seldom exceeded 200 or 300 yards; that urediospore spread from ribes to ribes might possibly occur to distances of 1,000 yards or more; and that overwintering of the fungus was of very little if any importance in its spread (Spaulding 1922a). This constituted the most reliable information on the spread of *Cronartium ribicola* in existence at the time studies were started in the West in the spring of 1922.

It was previously stated herein that, as a result of the investigations in 1922 and 1923, strong evidence was found that *Cronartium ribicola* had been introduced in the West at but a single place, namely Point Grey near Vancouver, British Columbia in 1910. The studies also showed that spread from the introduction point first occurred in 1913 in which year pines became infected at scattered points upwards to 120 miles distant, and that further spread, even to greater distances, occurred in 1917. Furthermore, in 1922 there was observed a wide distribution of the rust on ribes in western Washington, and in 1923 its presence was noted on these hosts to 100 miles or more beyond the range limits of white pines. Based on the eastern experiences, these great extensions of the rust in single years in the West seemed difficult to explain for such great distances of spread of any fungus by means of wind-borne spores had previously been unheard of. Consequently, during the investigations consideration was given to every possible agency or means by which such spread of the rust might have occurred.

In the investigations in 1922 and 1923, Pennington (1925) found that spread from ribes to ribes by means of urediospores and from ribes to pines by means of sporidia was local in character. There was no evidence of overwintering of the fungus on ribes. Accordingly, its presence on ribes at great distances from pines could not be explained by a gradual spread over a number of years from the center of infection in British

Columbia, with the fungus maintaining itself from year to year on infected ribes. Migrating animals or man could not have carried spores over the wide area in which infected ribes were found, although browsing animals such as cattle and deer sometimes are agents in intensifying the rust locally on ribes by feeding on or otherwise coming in contact with these plants. For some locations, particularly north of the range limits of pines, birds could have been possible, but highly improbable, spore-carrying agents. Pennington concluded that all the evidence seems to indicate that long-distance spread of the rust has been caused by wind-borne aeciospores.

In 1926, Lachmund (1926a) reviewed the early history of the rust in the West and presented additional circumstantial evidence, obtained in 1924 and 1925, in support of the theory of long-distance spread by means of wind-borne aeciospores. As the result of continued investigations, which have been conducted annually since then up to the present time, there has been collected such an overwhelming amount of additional circumstantial evidence to this effect that the contention originally advanced by Pennington is believed to be substantiated without question. In support of it is the fact that during the course of 21 years of study devoted to the subject no evidence whatever of spread of the rust over long distances by any other means has been found.

The results of recent studies have shown that there has been no spread of the rust to ribes in California in years in which periods of north winds to carry aeciospores southward from northern pine infection areas have been lacking, and that southward spread into the, State has occurred only in those years in which there have been periods of north winds favorable for the transport of these spores followed by suitable moist periods for infection of ribes. These findings seem sufficient evidence in themselves that long-distance spread of the rust takes place by means of wind-borne aeciospores.

POSSIBLE LIMITS OF LONG-DISTANCE SPREAD

THERE is a large literature on the dissemination of fungus spores by winds-much too large to be reviewed here.[8] Reports on distances

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[8] Papers containing reviews of the more important literature on aerial dissemination of plant pathogens have recently been published by Craigie (1941) and the American Association for the Advancement of Science (1942).

of spread of spores as great as those mentioned herein for the aeciospores of *Cronartium ribicola,* however, are relatively few. Most of the investigations of this nature have been on the cereal rusts. The studies on the epiphytology of wheat rust in Canada (Craigie 1941; Craigie and Greaney 1927; Craigie and Popp 1928; Popp 1929; Popp and Craigie 1931; Peturson 1931), the United States (Lambert 1929; Stakman 1934), and Mexico (Stakman et al. 1940) have amply demonstrated that viable spores may be carried hundreds of miles by winds. Many other investigators have contributed evidence in support of this. The long-distance spread of piñon rust will be mentioned in a later section.

That micro-organisms are distributed by air currents has long been known (Ehrenberg 1872), and numerous investigators utilizing spore traps have studied the rôle played by surface winds as carriers of fungus spores and bacteria. The first spore trapping in the upper-air currents with the aid of airplanes seems to have been done in the United States in connection with investigations on the spread of cereal rusts by Stakman et al. (1923). They found that Alternaria spores that were caught at altitudes of 10,500 feet and less were viable, and urediospores and aeciospores of *Puccinia graminis* Pers., caught at elevations of 7,000 feet and 1,000 feet, respectively, also germinated. Following these investigations a great deal of airplane spore trapping has been done and spores have been found at much higher altitudes. Once these light bodies arrive at such heights, they would unquestionably, under favorable wind conditions, be blown great distances before again settling to earth. Davidson (1924b) is probably the only one who has Conducted airplane spore-trapping tests in connection with white-pine blister-rust studies. Over a heavily infected area in British Columbia, aeciospores were collected at each 1,000-foot level up to 5,000 feet, the highest elevation at which trap exposures were made.

That living things may occur in the stratosphere has been demonstrated by Rogers and Meier (1936). In connection with the flight of the balloon "Explorer II," viable fungus spores and bacteria were found above 36,000 feet. Also in connection with the flight of this balloon, which reached an altitude of 72,395 feet, spores of six out of seven fungi carried aloft and down again survived the trip (Meier 1936).

The long-distance dissemination of dust is so well known that further mention of it seems unwarranted. However, of interest is a paper by Ehrenberg published in 1872, in which there is reviewed a total of 536 reports dealing with dust storms and the long-distance air-transport of plant parts. The oldest of the reports dates back to II54 B.C. **It** therefore seems evident that knowledge of the fact that minute objects are carried long distances by winds has been known for centuries.

Pollen grains, which are larger and heavier than fungus spores, have been found in the atmosphere over .the Atlantic Ocean several hundred miles from the nearest land (Erdtman 1937).

The distribution of smoke is another example of long-distance spread. Lyman (1918) summarized the observations on the paths of smoke clouds from Minnesota forest fires in 1918 and found that they were blown from Minnesota to New York and along the Atlantic Coast to South Carolina in two days.

The time required for the wind transport of fungus spores over long distances is also quite short in some instances. That they may be carried several hundred miles in a few days has been demonstrated in connection with the wheat rust studies mentioned in the first paragraph of this section, also in studies on the atmospheric transport of vegetable allergens by Durham (1938, 1942).

The aeciospores of *Cronartium ribicola* are well suited for wind dissemination. ,They are dry, dusty, powdery, not easily wet, and retain their viability for several weeks or longer. They are produced in great abundance and often many feet from the ground where wind currents may readily pick them up. A slight jar of a heavily infected tree will cause clouds of these orange-colored spores to become evident. Spore clouds are shown in Figure 14.

As previously mentioned, no evidence has ever been found of spread of the rust from its single introduction point near Vancouver, British Columbia, prior to 1913. **In** that year, however, aeciospores from this point evidently were wind-borne to ribes over distances ranging from a few to approximately 120 miles. Since distances in this case have been determined from the distribution of the known pine infection centers that had their inception in 1913, it is possible spores may have been carried even farther that year and may have infected ribes not in association with pines. Hence, no future evidence would be left of such spread. By 1917 the cankers on the pines at these new infection centers were producing aeciospores in abundance. **In** that year the rust was widespread on ribes for the second time and became established on pines at a number of additional places. The easternmost and southernmost of these were approximately 265 and 325 miles, respectively, from Vancouver. From the nearest-known 1913 infection centers the distance in

FIGURE 14

A small *Pinus monticola* infected with *Cronartium ribicola.* The tree has been tapped gently so as to jar loose the aeciospores. Two clouds of these spores are plainly visible. (Photograph by Bureau of Entomology and Plant Quarantine, U.S.D.A.)

each case is about 25 miles less. As measured by present-day rust conditions in the West, the volume of aeciospores produced in 1913 and 1917 was extremely small. It is therefore evident that under favorable conditions relatively few of these spores are required for spread over long distances to ribes.

In 1923 it was observed that an extensive spread of blister rust to ribes had occurred to the eastward of the infected pine area in the coastal region. Later findings have shown it was in that year that the fungus first invaded northern Idaho where it then became established on western white pine at a known total of 16 points scattered over an area approximately 100 miles long and 45 miles wide. All evidence obtained to date indicates that this invasion is traceable to wind-borne aeciospores and that the pine infection area in the coastal region of British Columbia was the source of these spores. The distance from that area to the most easterly of these original pine infection centers in Idaho is approximately 400 miles.

In 1927, which was another very favorable year for long-distance spread, the rust was found on ribes in the coastal region of British Columbia over 300 miles beyond the northern limits of western white pine there, and in the Queen Charlotte Islands where the most northerly diseased bushes observed were also over 300 miles from the range of western white pines.

The evidence thus accumulated indicates that in favorable seasons spread from pines to ribes may occur over distances of 300 to 400 miles and possibly farther. Spread over distances of 100 to 200 miles has been common.

RELATION OF WEATHER TO SPREAD AND INTENSIFICATION OF THE RUST

CERTAIN factors must be contributing agents to the development of blister rust and it appears that extensive spread and intensification are the result of a progressive series or a combination of conditions favoring spread and development. The more important of these are: (I) ribes of a species fairly high in susceptibility to the rust in association with susceptible pines; (2) winds favorable to the distant dissemination of aeciospores and occurring at the time of their main period of production; (3) moisture and temperature conditions favorable for the germination of aeciospores and subsequent infection of ribes; (4) environmental conditions suitable for optimum development of the parasite and host, together with conditions favorable for the secondary and succeeding generations of urediospores; (5) environmental conditions favorable for maximum production of teliospores and the subsequent production of sporidia; and (6) moisture and temperature conditions favorable for pine infection. Unless these conditions are all present and occur in sequence at the proper time in the life cycle of the rust, extensive spread and intensification of the fungus will not result.

Although many phases of the blister-rust problem have been investigated during the past 30 or 40 years few actual tests have been attempted in nature to determine the character of moist periods most favorable for infection of pines. The knowledge of this subject to date is therefore based largely on circumstantial evidence. From this evidence it seems to be generally accepted that moist seasons are favorable to spread and intensification of blister rust and that dry seasons retard it. However, this does not always follow. While it is a fact that little if any infection of pine will result in a year with an exceptionally dry summer, on the other hand, heavy infection has not always occurred in years with almost normal or more than normal summer precipitation, and moderately heavy to heavy infection has occurred in summer seasons with precipitation considerably below normal. Falling in the latter category, for example, is the unusually heavy flare-up of the rust on pine that took place in Idaho during the relatively dry summer of 1937. Evidently therefore the total amount of precipitation during a growing season may be a poor criterion of the amount of pine infection to expect. Of greater importance is the frequency, duration, and character of the moist periods and the time at which they occur. Heavy rains and prolonged moist weather during the period of aeciospore production, such as occurred in British Columbia in 1926 and in Idaho in 1941 and 1942, provide unfavorable conditions for dispersal of the spores. Aeciospores become detached from the sorus as they mature and a succession of these spores often continues through a considerable period of time. The latter happens when temperatures are not abnormally high and moist periods are of rather frequent occurrence in the spring. Such conditions evidently are optimum or nearly so for heavy initial infection of ribes. If, however, warm and dry weather prevails throughout the period of aeciospore production, the period of their dispersal is shortened considerably. The majority of the aeciospores evidently lose their viability before moist weather occurs, and initial infection of ribes is then light. Abnormally moist summers with frequent rains may result in exceedingly heavy uredial intensification on ribes and the casting of their leaves before telia are produced, while abnormally dry summers result' in but little development of the rust. If the summer moist periods are not too frequent and are of sufficient duration for uredial intensification an abundant crop of telia maybe produced. A moist period of sufficient duration is then needed for the germination of the teliospores, the production of sporidia and their germination, and the infection of pines. If the moist period is not of sufficient duration for this entire sequence of events but only for the production of sporidia the latter may then be dissipated. If all the available teliospores produced during the summer germinate in the fall during a single prolonged and heavy downpour of rain it is probable that very little pine infection will result, as was the case in parts of California in 1938. On the other hand, heavy pine infection is to be expected in the event of very gentle rains and prolonged mists, or fogs. It therefore should be evident that blister rust, with its various spore stages maturing at different periods during the growing season, is delicately adjusted to climatic conditions. Consequently, any condition unfavorable to it at anyone period prevents any significant number of pine infections for that year.

Spaulding (1929), who has given much consideration to the influence of climate on the virulence of blister rust, found that while rainfall in Europe is less than in North American infection areas the higher relative humidity of the air and greater cloudiness of western Europe apparently more than make up for any deficiency in actual rainfall. According to him, on the whole, the climate of western Europe is as favorable for the progress of the disease as is that of American infection areas, or more so. His findings provide additional evidence indicating that high relative humidity and cloudy weather are more favorable for pine infection than an abundance of rain. Hirt (1942) has also found a relationship between the character of moist periods and the amount of pine infection resulting.

If aeciospores are to be air-borne over long distances from their source to ribes, winds favorable for this are necessary at the time these spores are being produced. In the analysis of long-distance spread wind data are therefore highly important. With the exception of pilot balloon records at Camp Lewis, Washington, the only wind records available in the West at the time Pennington (1925) conducted studies in 1922 and 1923 on the relation of weather to spread of blister rust, were those for surface stations. Although he utilized records of surface winds, it was recognized by him that the topography of the earth's surface causes variation in the direction of such winds and that this would be particularly marked in a mountainous country such as the West. It was accordingly obvious that surface wind records were of limited use. While they proved to be of certain value in the determination of wind movement in the lower elevations adjacent to and paralleling the coast, they apparently could not be satisfactorily used in the analysis of the rust's spread over long distances from the coastal region of British Columbia eastward across the Cascade Mountains into the dry belt and even beyond it. The prevailing winds of the north temperate regions of the earth's surface are from the west or southwest and Pennington attributed the spread that was noted to the eastward to these winds.

Because of the limited value of surface wind records and because no other suitable wind data were available until a number of years after Pennington conducted his investigations, there elapsed a period of time during which no further consideration was given to winds in relation to spread of blister rust. Between 1928 and 1931 the United States Weather Bureau established a number of stations in the western States equipped for obtaining information on the direction and velocity of winds in the upper air. The assembled data are recorded on what are known as upper-air charts. Therefrom the direction and velocity of movement of upper-air winds may be noted at a glance. By the time these data became available, however, no attempt was made to use them for the rust was then advancing over the western States at a very much slower rate than had previously been the case, and this was particularly true for the spread southward through Oregon.

As previously mentioned, blister rust was found for the first time in California in 1936, being observed there only in the northwest corner of the State a few miles from the Oregon line. Recognizing that winds would be one of the chief factors in the further extension of the rust in California, a study of the Weather Bureau upper-air charts for Pacific Coast States for the months of April, May, and June of 1937 was made with special reference to the occurrence of wind periods during those months favorable for the long-distance transport of aeciospores from northern areas where the rust was already well established. It was found that a period of strong northerly winds had occurred between May 29 and June 4, inclusive. Precipitation records showed that this windy period was closely followed by rains in southwestern Oregon and northern

California. Based on these findings it was predicted that weather conditions had been favorable for a wide spread of the rust to ribes over northern California and, as already noted, this was confirmed by subsequent scouting, which showed that the limits of the fungus had been extended about 120 miles south in the State and coincided closely with the southern limits of the rainstorm that occurred a few days after the windy period.

The evidence obtained in 1937 was regarded as an indication that reasonably reliable forecasts of the rust's annual spread might be made. Accordingly, early in July 1938 an examination was made of the upper-air charts for the three spring months of that year and it was found that a period of northerly winds had occurred over the Pacific Coast States from May 16 to 21, inclusive. Precipitation records showed that rains of somewhat patchy occurrence fell over the sugar pine region of northern California between May 27 and 29. These weather conditions were at the time regarded as favorable for the transport of aeciospores from northern pine infection centers southward into California and the infection of ribes there. The results of scouting conducted later in the season showed the fungus to be more prevalent and widespread in the Sierra Nevada than in 1937, but to be quite scarce in the coastal mountains. This distribution of the rust may possibly be attributable to the patchy occurrence of the precipitation that followed the windy period or more likely to the path of spore drift from the north.

The charts for the spring months of 1939, 1940, 1941, and 1942 showed no periods of northerly winds in either of those years regarded as favorable for the air transport of aeciospores from Oregon southward into California. In all of those years except 1942, however, spring moisture conditions in northern California were favorable for initial infection of ribes by aeciospores. The spring of 1942 was late and abnormally cold with much of the precipitation in the form of snow and thus unfavorable for either infection of ribes or their early growth. Before scouting commenced each year it was forecast that a significant spread of the rust such as had occurred in 1937 and 1938 was not expected. During 1939 to 1942, inclusive, no infected ribes were found except in the immediate vicinity of diseased pines bearing sporulating cankers.

The forecasts made during the past six years have therefore proved to be quite accurate. Accordingly, the value of the Weather Bureau upper-air charts as a reliable aid in connection with studies on the long-distance spread of blister rust is believed fairly well established. A short note regarding their use for that purpose for the first time in 1937 was published (Bur. of Pl. Ind. 1938). Also in 1937, Humphrey (1938) considered their importance in epiphytological investigations of stem rust, but did not correlate these wind data with the spread of that fungus. Durham (1938, 1942), however, in allergy studies conducted in 1937, found a correlation between upper-air movement and the dissemination of Alternaria spores over long distances. More recently mention was again made of the use of the upper-air charts in forecasting probable spread of blister rust into California by means of wind-borne aeciospores from distant northern sources (Bur. of Pl. Ind. 1941). These five brief reports constitute the only published records of the use of the upper-air charts in connection with studies on the dissemination of fungus spores.

As the result of certain observations and studies in the West, Lachmund (1934b) reported that the degree, extent, and direction of spread are largely governed by the stage of susceptibility of ribes leaves at the time the main body of aeciospores is produced. A brief summary of the basis he gave for his conclusion follows.

The spring of 1926 was exceptionally early over the entire western white pine region. Ribes leaf development and vegetative activity generally commenced a full three weeks earlier than normaL The production of aeciospores by the rust was not correspondingly advanced, however, and the period of maximum spore production occurred at about the usual time, which in this case was about a month after ribes growth in the same localities had commenced. At this time most of the leaves had attained full size. Aeciospore production was as heavy and moisture and other climatic conditions appeared to be as favorable for infection as in any preceding year. Regardless of these conditions, however, the infection of ribes was light in the immediate vicinity of infected pines in 1926. Also, spread of the rust to ribes that year occurred only in a northerly direction. The light local infection and character of spread were difficult to explain. An examination of weather records and actual observations throughout the region indicated that wind and moisture conditions were as favorable for long-distance spread to the south as to the north. Previous observations had provided evidence that the period of maximum susceptibility of ribes leaves occurred at any early stage of their development. The beginning of general growth activity, including ribes leaf development, was later in more northern latitudes than in the localities of aeciospore production. Lachmund therefore concluded that in 1926 the leaves of these hosts were in a more favorable stage of development for infection to the north than in latitudes of aeciospore production and southward, and the direction of spread that year was explained on this basis.

It was also reported by him that observations had shown that the time of aeciospore production is less subject to variations in seasonal conditions than is the commencement of growth activity in ribes. More recent findings have shown, however, that while this does happen for some unknown reason in some years it is not the rule.

As a check on the observations regarding the age at which ribes leaves are most susceptible to infection by aeciospores, field tests were conducted by Lachmund in 1928. The results, which were included in the report in question, showed that in the case of three species *(Ribes petiolare, R. inerme,* and *R. lacustre)* the youngest leaves (between the ages of 2 and 16 days) were considerably more susceptible to aeciospores than were older leaves. Forty-day-old leaves, the oldest age class of the first two species mentioned that were tested, were still susceptible, but no rust developed on leaves of *R. lacustre* (a relatively resistant species) over 34 days old. In the case of the fourth species *(R. viscosissimum),* however, there was no uniform correlation between age class and susceptibility. Instead, there seemed to be a slight upward trend in susceptibility throughout the range of age class with 44-day-old leaves evidently as susceptible as, if not more so than, those but 4 days old. According to Lachmund, for some unexplainable reason these results were at variance with those of other investigators who found that under eastern conditions ribes leaves are immune or resistant in the beginning and that they reach their most susceptible stage when they have attained full size but have not yet hardened off.

As the result of his observations and tests, Lachmund arrived at the following conclusions: "The most favorable period for spread of the disease by aeciospores occurs when the period of maximum spore dispersal from a given center synchronizes with that in which the largest proportion of the leaves lying within the long-distance range of the spore showers are in their most susceptible stages. The time of ribes leaf development seems to be more affected by variations in seasonal condition than is the time of aeciospore production. An early spring at the aecial source advances the development of the ribes leaf until it is beyond the stage of maximum susceptibility during the period of maximum aeciospore production. This restricts infection at the aecial source, and lessens spread to lower elevations and to the south, where leaf development is still more advanced, but favors spread to higher elevations and to the north, where spring is naturally later and ribes are in more favorable stages of development. A late spring has the opposite effect, lessening spread northward and to higher elevations, where the leaves may not yet have broken from the buds, and favoring spread south and to lower elevations."

The contention that a late spring favored spread to the south was a deduction, and no actual evidence had been obtained at that time to support it. In the light of present-day knowledge it would appear that this supposition might be abandoned, for the results of studies on annual spread of the rust, conducted from 1922 to 1942, inclusive, show no correlation between late springs and southward spread to ribes. In addition to this, there are certain of Lachmund's arguments that might be questioned. To begin with, only four species of ribes were tested by him. The results from one of these showed no correlation between leaf age and susceptibility; consequently, it would seem logical to expect that at least some other species may react similarly. In the case of three of the species the oldest leaves tested were found susceptible. How long susceptibility might be retained is not known. Pierson and Buchanan (1938a) found 74-day-old leaves of *Ribes petiolare* to be susceptible to aeciospores. They did not test older ones. Following the appearance of the first leaves on ribes in the spring, new ones may continue to form upwards to two months or longer. Leaves of different ages are therefore present during the period of aeciospore production. Because of this condition, combined with the fact that relatively old leaves are susceptible, some infection from aeciospores should occur providing weather conditions are favorable. Actually, this is what has happened in the West regardless of the advent of spring or the time when the period of maximum aeciospore dispersal occurs.

Furthermore, Lachmund stated that wind and moisture conditions were as favorable for long-distance spread to the south as to the north in 1926. However, during the main period of aeciospore production) which occurred between mid-April and late May, there were relatively few days that some rain did notfall. Observations on the ground showed that dispersal of these spores was greatly inhibited as a result of the excess moisture.[9] No mention was made of these conditions. With regard

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[9] Heavy precipitation and moist weather as factors inhibiting aeciospore dispersal have been previously mentioned herein.

to wind conditions, the only wind records available were those from surface stations. Since it has been found that these cannot be relied upon for the determination of direction of general wind movement in the West, it would appear questionable if winds were favorable for southward spread in 1926. Following the introduction of the rust near Vancouver in 1910 its spread has been considerably more intensive to the north and east than to the south. All evidence available indicates that prevailing winds have favored this. Consequently, it would seem possible that the northward spread in 1926 might be explained on this basis. Lachmund outlined the limits of spread that year, but did not mention the degree of intensity within those limits. Actually the rust was found on ribes outside the range limits of white pine at only six points. One of these was on the coast and five were in the Cariboo District in the interior. This is an exceptionally light distribution when compared with that found over the same territory in the Cariboo District from 1927 to 1930, inclusive. In each of those years spring was not abnormally early and the rust was found there on ribes at practically everyone of the numerous places where a search was made for it.

Accordingly, it would seem obvious that conditions were not particularly favorable for spread to the northward in 1926. For this reason, and the others mentioned, it would seem that Lachmund's conclusion that "the degree, extent, and direction of spread are largely governed by the stage of susceptibility of ribes leaves at the time the main body of aeciospores is produced" is not too well founded. Evidence accumulated since 1926 strongly indicates that a wide spread of the rust may be expected in any direction in any year that moisture and wind conditions are favorable for such spread.

WAVELIKE CHARACTER OF SPREAD OF THE RUST

THE failure of locally heavy pine infection to occur every year, in conjunction with the absence of appreciable long-distance spread of the rust to ribes and subsequent establishment on pines in new localities, has already been mentioned. In fact, the history of progress of the fungus in the West has shown that seasons characterized by heavy intensification and spread have been infrequent. Thus, in the 32 years that have elapsed since the introduction of the rust, only 5 or possibly 6 have been outstanding in these respects: 1917, 1921, 1923, 1927, and 1937, with

1913 as a possible addition because of the spread that took place that year, though the basis for judgment on the comparative rating of the season is meagre. In the intervening years the amount of pine infection occurring locally and the progress of the rust into new areas have ranged from almost negligible, as in 1924, 1929, and 1936, to moderately high as in 1920 and 1938, with varying intergradations in other years.

In the early years after the introduction of the rust into British Columbia and in later ones following its initial establishment in Idaho a principal cause of this wavelike irregularity was the three-year period or more that must elapse between infection of pines and the production of aeciospores by the resulting cankers. Accordingly it was not until 1917 that aeciospores were available in sufficient abundance at the infection centers established in 1913 to make possible any significant local intensification of the rust or further spread to a distance. In turn, the crop of cankers arising in 1917 did not furnish aeciospores in quantity until 1921. It happened that weather conditions in that year, as in 1917, were favorable for the rust and another wave of advance took place.

Similarly, in Idaho there was no appreciable increase in the rust from the initial 1923 infection centers until 1927, when the first abundant crop of aeciospores in that region and favorable weather conditions combined to provide heavy pine infection in the vicinity of the older cankers and the establishment of the fungus on pines at numerous additional points. The next wave of pronounced increase, based on the addition to the spore supply provided by the 1927 cankers, should have come in 1931, but, though spores were produced that year in great quantities, the summer proved to be very dry and little infection occurred, either of ribes or pines. In the succeeding years the lapse of time between establishment of new waves of cankers and their sporulation became less and less a factor in determining waves of spread while the influence of weather grew conversely preponderant. From 1934 on, aeciospores were produced in abundance annually in Idaho but unfavorable weather prevented much pine infection until the very favorable season of 1937.

The progress of the rust southward through Oregon and into California has been even more sporadic than over other parts of the West. Though the fungus was established on pines in the Cascade Mountains of northern Oregon as early as 1917 or 1918 it did not spread southward from there to any extent until 1927 and it was not until 1937 that it became widely distributed on pines over southwestern Oregon and northern

California. Though several factors, such as host distribution, have contributed to this more erratic progress, the chief cause for it appears to lie in the less frequent occurrence of combinations of conditions, and particularly of winds, favorable for long-distance spread as one proceeds southward.

So far, in a broad sense, the character of individual years with respect to their influence on rust development has been rather consistent over the entire range of the fungus in the West; that is, there appear to have been no years in which conditions have been very favorable for intensification and spread of the rust in one part of its range and adverse in other parts. This relative consistency is no doubt correlated with the fact that seasonal weather tends to show the same characteristics over the entire Pacific Coast so that a cold, late spring or a dry fall in British Columbia will also be likely to be cold and late or dry respectively in California. However, with the range of the rust as extensive as it has now become, some variation in relative favorableness for rust development in different parts in any particular season is to be expected and in a year that is generally unfavorable there are likely to be local areas where appreciable increase in pine infection will occur or the converse.

From what is known of the history of progress of the disease in the two regions it seems evident that the wavelike character of spread has been much more pronounced in the West than in the East, as would be anticipated from the fact that spread in the latter region took place from a number of centers of origin rather than from a single one and from the much more uniform distribution of precipitation over the year in the. East. However, even there some years, notably 1919 and 1927, have been outstanding for heavy infection of pines, at least in part of the region, while other years have been definitely unfavorable, apparently because of the factor of weather (Pennington 1927, 1928; Pennington et al. 1921; Snell 1928, 1929). In the northeastern States, according to Fracker (1936), after the disease has passed through its early years of establishment on a few trees, and thus has developed its basic supply of aeciospore-bearing cankers "its progress is steady and its increase inevitable, with little regard for the vagaries of humidity, rainfall and wind velocity." As indicated, other evidence does not fully bear out this conclusion and there are still greater doubts of its applicability in the West, except in a very broad way. With regard to characteristics of spread it should be pointed out that Fracker was dealing with the increase in per cent of trees infected in individual areas and not with the spread of blister rust to previously uninfected territory, a process much more likely to show wavelike characteristics, particularly under the conditions prevailing on the Pacific Coast.

RATE AND DIRECTION OF SPREAD OF THE RUST

AS the result of studies conducted in 1922 and 1923, Pennington (1925) concluded that the rust was practically certain to spread southward at a much slower rate than to the north and east. This he believed would happen because prevailing westerly winds favor aeciospore dispersal from the coast toward the east, and because summer precipitation diminishes southward.

Actually, however, the rust has not spread faster to the north and east than to the southward. With the introduction point near Vancouver as a center for measurement of distances the following is now known to have occurred. By 1917 blister rust became established on western white pine to the northward about 140 miles or practically to the northern limits of that species in the coastal region of British Columbia, to the eastward 265 miles in the interior of the Province, and to the southward 325 miles in the Cascade Mountains in northern Oregon. In 1923 it spread to pines somewhat farther to the eastward than to the southward. In 1925, however, it had advanced southward on pines approximately 465 miles to a point in southwestern Oregon, but to the eastward it is not known to have advanced farther than about 400 miles by that time. This easternmost point is a pine infection center in Idaho that had its inception in 1923. By 1941 the rust was known to have spread to pines about 450 miles to the eastward and 700 miles to the southward. The easternmost point at which the rust has been found on ribes to date is approximately 630 miles from Vancouver and the southernmost about 725 miles.

The present known limits of distribution on both pines and ribes therefore extend farther to the southward than to the eastward of Vancouver. This, however, applies only to the distance and not to the intensity of spread. By far the heaviest blasts have occurred to the eastward. In general much heavier pine infection exists to the eastward in the Inland Empire than at a similar distance to the southward or in northern Oregon. The limits of eastward spread are actually to the southeast of Vancouver. A point an equal distance due east would be just outside the range limits of white pines in that direction. Also, the northern range limits of white pines in British Columbia do not extend nearly so far to the north there as the present southern limits of the rust in the United States. For that reason it is not possible to compare the rate of spread to the northward with the rates to the eastward and southward at the present time.

In the coastal pine region of British Columbia spread was much more rapid in a northerly than in an easterly or southerly direction. Early-season rains in that region usually follow periods of southerly winds and this condition would be favorable for the wind transport of aeciospores to the northward and the subsequent infection of ribes. The pine stands first invaded were those situated near sea level along the coast and on the floors of the larger valleys extending inland. From these lower-elevation infection areas the rust very slowly worked upward into the higher elevations. The rapid spread and intensification that occurred provided ample evidence of susceptible hosts and climatic conditions favorable for the development of the fungus. White pines are more or less patchy in their occurrence over the region, but wild ribes are common almost everywhere and several of the eight or more species are highly susceptible. Practically all of the older pine infection centers found were in association with wild ribes. The European black currant was of relatively little importance in the distribution of the rust on pines and its subsequent intensification on that host because there were so few plantations of it in close association with white pines. Based on all the evidence accumulated, it is believed that there would have been very little difference in the rate of spread over the coastal pine belt than that which occurred had the European black currant not been present there at all.

In the interior white pine belt of the Province, however, the European black currant played a highly important rôle in the establishment of the rust on pines and its subsequent intensification on that host. Three of the four oldest infection centers found there, i.e., those dating from 1917, were in association with *Ribes nigrum*. This species was also responsible for the establishment of a few centers in 1920 or 1921 and several in 1923. Wild ribes were relatively unimportant in this regard for several reasons. Within the known range of the rust on pines only three species were observed. The most common of these generally is *R. lacustre,* a species quite low in susceptibility and particularly so in telial production. The next most prominent species is *R. viscosissimum*. It is not nearly so widely distributed as *R. lacustre,* but ranks somewhat higher in susceptibility. The third species, *R. sanguineum,* is highly susceptible. It, however, is limited in its occurrence to an area of but a few square miles in extent in the Arrow Lakes region. The interior pine region in general is very sparsely settled and for that reason the European black currant has not been extensively planted there. Also, white pine is, for the most part, patchy in its occurrence. It is mainly because of the very limited distribution of highly susceptible ribes species, however, that the rust has spread and intensified much more slowly in the interior than in the coastal region. It was about 10 years after blister rust became established on pines in the interior that it first became noticeable at a few places on this host in association with one or the other of the two most common of the wild ribes. The comparatively slow rate of spread in the interior cannot be attributed to a deficiency of moisture necessary for the development of the rust. The average monthly precipitation during the growing season in the interior and coastal regions of British Columbia, and in certain other parts of the West, is shown in Table 4.

TABLE 4. AVERAGE MONTHLY PRECIPITATION DURING THE GROWING SEASON IN VARIOUS REGIONS OF THE WEST.[1]

Regions	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*
British Columbia, coastal[2]	2.67	2.14	2.05	1.39	1.22	2.87
British Columbia, interior[3]	1.43	1.58	2.64	1.40	0·99	1.87
Idaho, northern[4]	2.36	2·99	1.94	1.04	1.09	1.90
Montana, western[5]	1.15	2.06	2.08	0.98	0.85	1'43
Oregon, north Cascades[6]	5.15	4·39	2.83	0.84	1.05	3·43
California, northern[7]	2.85	1.55	0·73	0.13	0.15	0·73

1. From British Columbia and United States Weather Bureau Records.
2. Three selected stations-Vancouver, Garibaldi, Pemberton Hatchery.
3. Three selected stations-Revelstoke, Fauquier, Nelson.
4. Five selected stations-St. Maries, Avery, Priest River Experiment Station, Pierce, Wallace.
5. Four selected stations-Haugan, Kalispell, Missoula, Helena.
6. Four selected stations-Zig Zag, Cascadia, Detroit, McKenzie Bridge.
7. Twelve selected stations-Happy Camp, Weaverville, Ruth, Mt. Shasta, Canyon Dam, Quincy, Lake Spaulding, Tahoe, Lake Eleanor, Yosemite, Big Creek, Springville.

No attempt has been made to control blister rust in British Columbia except by the removal of cankers from diseased trees at three of the oldest (1917 origin) infection centers in the interior white pine belt in 1924 (Davidson 1924b). This, however, was soon given up as a hopeless task. Other than that the spread of the fungus over the Province has not been hampered by man.

In 1923, or 13 years after its introduction at Point Grey, blister rust invaded the Inland Empire. Most of the pine infection centers dating from that year are in the southern portion of the western white pine belt and practically all of them occurred in association with the highly susceptible *Ribes petiolare,* a species frequenting the stream courses particularly in the lower elevations. On the other hand, there was no 1923 invasion of the extreme northern part of the white pine belt, where *R. lacustre, R. viscosissimum,* and *R. inerme* are the principal species, although this area is much closer to sources of the rust in British Columbia (see Figs. 10 and II). Once established in the southern portion of the white pine belt the fungus spread over the Inland Empire at about the same rate of speed as it did over the coastal white pine belt of British Columbia. By 1933 centers of pine infection had become established over almost the entire region. Also by that time the rust was widespread on pines in the uplands in association with the less susceptible *R. viscosissimum* and *R. lacustre.* Western white pine is much more abundant and general in the Inland Empire than in either the coastal or interior regions of British Columbia. The general occurrence of this host, together with the abundance of ribes over the region and favorable moisture conditions (Table 4) for the development of the fungus, had much to do with its rapid rate of spread. That the rate of spread and intensification there is being slowed up annually, however, is without question. This is being brought about mainly by the destruction of ribes in control operations that have been in progress since 1924. These plants have now been removed from extensive areas in the uplands and from practically all the stream courses. Other factors of importance in slowing up the progress of the rust are the natural suppression of ribes by competing vegetation, particularly with the closing in of young coniferous stands (Davis and Moss 1940), and the reduction in volume of aeciospores brought about by the natural dying out of cankers and the death of infected pines on areas over which the ribes have been removed.

As has been pointed out, although blister rust became established on pines in northern Idaho in 1923 and in extreme northwestern Montana in 1927, it was not observed on this host in the adjacent Rocky Mountain region to the eastward until 1941. No plausible explanation seems to exist at the present time as to why the rust has been so slow in its eastward progress on pines from northern Idaho and western Montana. Susceptible hosts are not lacking from that portion of the Rocky Mountain region in question. There are several species of ribes, some of which are highly susceptible. The white pines, although quite patchy in their occurrence, are represented by three species *(Pinus monticola, P. albicaulis,* and *P. flexilis),* all of which rank high in degree of susceptibility. Moisture conditions appear to be favorable for the development of the fungus (Table 4). There is no evidence of a dearth of winds necessary for the carriage of aeciospores eastward from the pine infection areas in Idaho. On the basis of present knowledge, therefore, conditions for the eastward extension of the rust appear favorable and it seems that there must be some epiphytological aspect of the situation that is not yet sufficiently understood to account for the lack of continued spread in that direction. Over the West in general blister rust has been very slow to spread from the lower into the higher elevations, and this has been particularly noticeable in connection with the invasion of stands of the highly susceptible *Pinus albicaulis.* Once the fungus becomes established in the higher elevations, however, there does not appear to be anything abnormal about its development there except that the rate of canker growth is slower and fewer generations of the rust develop on the ribes owing to the shorter growing seasons as compared with lower elevations. Why the rust has spread so slowly from the lower into the higher elevations is notwell understood. If it were, it might provide the answer to the slow progress of the disease eastward into the Rocky Mountain region.

Although blister rust early advanced southward into northwestern Washington it did not become widespread on pines there until 1923. By that time, however, the intensity of pine infection was greater and more general to the northward in adjacent British Columbia. Prevailing winds evidently had much to do with this. In most years during the period of aeciospore dispersal in British Columbia there is a greater amount of wind movement from the southward to the northward than vice versa. Once the rust became well established on pines over northwestern Washington, however, its rate of intensification was fairly rapid. Favoring this were an abundance of highly susceptible wild ribes and moisture conditions favorable for the development of the fungus. In amount, precipitation does not differ markedly from that in the adjacent coastal region of British Columbia. Although the rust became established on white pines at one outlying point in the southern Cascades of Washington evidently in 1920, its general progress from the Canadian line southward through that mountain range towards Oregon has been comparatively slow. This is partly attributable to the patchy occurrence of white pines and to precipitation, the latter diminishing somewhat to the southward. Evidently the most important factor in this connection, however, is the prevailing winds during the period of aeciospore dispersal. There is relatively little wind movement from north to south in the Cascades at that time. The destruction of wild ribes in western Washington has not been a factor of any consequence in retarding the intensification of the rust there because they have been destroyed over only a few relatively small areas, mainly in Mount Ranier National Park.

The rate of southward spread of *Cronartium ribicola* on both pines and ribes in the Cascade Mountains of Oregon has been much slower than in the Cascades of Washington. Relatively little rust has been found on either host to date in the southern half of that Range in Oregon even though it became established on pines in the northern portion as early as 1917 or 1918, probably in the former year. In the northern portion moisture conditions are quite favorable for the development of the fungus (Table 4), western white pine is fairly common, and highly susceptible ribes are generally abundant. As a result, intensification has been fairly rapid and an abundance of aeciospores has been produced annually for a number of years. In the southern portion of the Cascades there are no weather stations within the main area of western white and sugar pines. Consequently a direct comparison in the amount of precipitation occurring there with that to the northward is not possible. However, it is known that precipitation diminishes somewhat to the southward. But, it is not so dry there as to preclude intensification and spread of the rust once it becomes established on pines. Moreover, white pines are more common than to the northward, with the highly susceptible sugar pine fairly abundant over extensive areas. Also, there are a number of highly susceptible ribes species in association with both western white and sugar pines. It would seem therefore that the slow southward spread cannot be attributed to a deficiency of moisture or a scarcity of susceptible hosts. Nor has there been an inadequate 'supply of aeciospores to the northward. There is, however, very little wind movement from north to south in the Cascades during the main period of production of these spores. It would appear evident therefore that unfavorable wind conditions are responsible for the slow progress of the rust southward in the Cascades of Oregon. In the Cascade Mountains from the Canadian line to southern Oregon north winds diminish with latitude. The much slower spread of the rust southward in the Cascades of Oregon as compared with that in the same Range in Washington is attributed to this factor. Wild ribes have been destroyed over rather extensive areaS in the southern Cascades and this no doubt has been a factor of some importance in retarding spread southward. However, the rust has advanced very slowly towards these areas.

White pines are much less common in the Coast Range than in the Cascades of Oregon, yet the rust extended southward much earlier in the former than in the latter. It became established on sugar pines in the extreme southwest corner of the State as early as 1925 or 1926, but did not invade the southern Cascades until 1937. There is a greater amount of wind movement from the north along the coast than in the Cascades and this probably accounts for the earlier advance down the coast. Following the initial establishment, the rate of spread and intensification in southwestern Oregon was very slow because of the scarcity of ribes in association with white and sugar pines in that region. For this reason and also because of unfavorable wind conditions, spread from there southward into California was retarded. The prevailing winds in that region are westerly.

Cronartium ribicola has not yet been established on sugar pine in California long enough to permit judgment as to how rapidly it will spread and intensify there. Moisture conditions in the sugar pine region are less favorable for the fungus than in other parts of the West where it is well established (Table 4)' This advantage may be offset at times, however, by the high degree of susceptibility of sugar pine and its main ribes associates, *Ribes roezlii* and *R. nevadense*. A survey, made by Zentmyer and Wagener (1940), of weather records at 18 U.S. Weather Bureau stations representing typical climatic conditions for sugar pine sites indicates that, as a general rule, moisture conditions in California in May are adequate for ribes infection. The other months important in blister rust development are less moist and, on the basis of moisture conditions in the past 25 years, an average of one out of every five years may be expected to be favorable for spread and intensification of the fungus. Rains sufficient for pine infection usually occur relatively late, as a rule not before late September. This tendency becomes more noticeable in the southern Sierra Nevada. The destruction of wild ribes in the commercial stands of sugar pine in the Sierra Nevadas has been under way for a number of years. The removal of these plants undoubtedly will retard the spread into and intensification of the rust in the Sierras.

Recording of upper-air winds in the western States was started by the U.S. Weather Bureau in 1928 and has continued up to the present time. Analysis of these records with special reference to opportunities for the southward transmission of aeciospores indicated that favorable periods for the long-distance transport of these spores into the sugar pine region of California from northern pine infection areas are infrequent, and that, when they do occur, they are not always followed by moisture conditions suitable for infection of ribes. During the 15 years that these records have been available a favorable sequence of winds and moisture has occurred in but two. years, 1937 and 1938-the only ones in which the rust is known to have been widespread on ribes over northern California. Precipitation records show that years with suitable moisture conditions in the spring occur with greater frequency than do years with favorable wind conditions. A common characteristic of winds moving south over Washington and Oregon is a change in their direction to the eastward as they approach the California line. When this happens they are met at that point by winds moving to the northward over California. The meeting of these air masses evidently forms what might be termed a "wind·wall" so far as transport of aeciospores farther southward is concerned. Accordingly, it is believed that the main factor inhibiting a more frequent long-distance spread of the rust to ribes over northern California is the infrequency of north winds into the State. If it were not for this the disease possibly would have become established on sugar pine in California much earlier than has been the case. Also, it possibly would be more widespread.

SOME RELATIONS OF RIBES SPECIES IN THE SPREAD OF THE RUST

EASTERN experience had shown that the European black currant was the ribes species most important in establishing and spreading the rust there. Because of this a program for its eradication from western States was started in 1922. By the fall of 1927 this work had been finished in Montana, Idaho, Washington, and Oregon, and nearly finished in California. Thus, the highly susceptible *Ribes nigrum* was early eliminated from a large area of the West as a factor in the spread of the rust. Mention has previously been made that it has not been destroyed in British Columbia, that it was of but relatively little importance in the spread and intensification of the rust over the coastal region as compared with the native ribes, and that it was the ribes host primarily responsible for the establishment of the disease in the interior pine belt of the

Province evidently because of the scarcity of highly susceptible wild species. Although blister rust was commonly found on *R. nigrum* in British Columbia and Washington, the fact must be emphasized that in practically all cases the plantations of this currant occurred at distances ranging from a mile or two to over a hundred miles from white pines. Had this situation not existed *R.* nigrumundoubtedly would have been a much more important alternate host in the spread of the rust to pines than it actually proved to be.

The invasion of pine stands in Washington and Oregon occurred prior to the inauguration of the program of eradication of *Ribes nigrum.* In Washington 23 pine infection centers have been found that were determined to have had their inception in 1922 or prior thereto. Of this total only 3 occurred in association with *R. nigrum*, the remainder being in association with wild ribes. *R. nigrum* was not responsible for the establishment of the rust on pines anywhere in the State after 1922. In Oregon not a single pine infection center found there was in association with *R. nigrum,* although the rust became established on pines at several places in the State prior to and during the period in which that ribes host was being eradicated. In no instance have infected pines in Idaho been found in association with *R. nigrum.* Nearly all of the oldest centers of pine infection in the State, i.e., those having their inception in 1923, are in Clearwater and Shoshone Counties in association with the native *R. petiolare.* Between 1922 and 1927, or during the course of the work of destroying *R. nigrum,* a total of but 155 plants of that species was found in the two counties. None of these were observed to be diseased. Certainly this number of cultivated plants is insignificant when compared to the wild species, for it was common experience during the course of extensive ribes removal operations in these same counties to find along stream courses many more than 155 *per acre* of the highly susceptible *R. petiolare* alone.

Accordingly, *Ribes nigrum* was of relatively very little importance in initiating blister rust on pines at outlying points in the western States. Evidently this came about because the plant was not cultivated in large numbers, except in a few areas, and was seldom grown in close association with white pines but mainly in cultivated areas and in cities and towns outside the natural limits of those hosts. Considering the available evidence it seems possible that had *R. nigrum* not been destroyed the rate of spread would have differed little from that which has occurred to date. The abundance of highly susceptible wild species generally as compared with the relatively few *R. nigrum* that were found in close associations with white pines argues strongly in favor of this.

Species of wild ribes that have been of importance in the long-distance spread of the rust and its establishment on pines in new localities are: *Ribes bracteosum*, *R. sanguineum*, *R. divaricatum*, *R. petiolare*, *R. inerme*, *R. nevadense*, *R. roezlii*, and *R. cruentum* Greene. These are all highly susceptible. Less susceptible species have not been a significant factor in long-distance spread. Despite the fact that *R. nigrum* is the most susceptible ribes known, no evidence has been found to indicate that the rust has spread any farther to it than to certain of the most susceptible of the wild species. Although the cultivated red currants were quite often found in association with western white pine in British Columbia, they have been of no importance whatever in the spread and intensification of blister rust. Snell (1941a, 1941b, 1941c, 1942) has presented considerable evidence to show that these plants, which are very low in susceptibility and particularly low in telium production, are not of importance in transmitting the rust to *Pinus strobus* in the East.

PIÑON RUST: ITS COMPLICATION IN THE SPREAD OF BLISTER RUST

PIÑON blister rust (*Cronartium occidentale* Hedgc., Bethel, and Hunt) is a native disease of piñon and singleleaf piñon pines (*Pinus edulis* Engelm., and *P. monophylla* Torr. and Frem.) and, like its close relative *C. ribicola*, it has as its alternate host species of *Ribes* (Hedgcock et al. 1918). On pines there is no difficulty in distinguishing between the two fungi for piñon rust does not attack five-needle (white) pines nor does white pine blister rust attack piñon pines. In addition there are marked differences in the pycnial and aecial stages of the two rusts (Colley et al. 1927; Hedgcock et al. 1918). On ribes, however, *C. occidentale* is indistinguishable macroscopically from *C. ribicola*.

This fact is important because of the necessity of determining which fungus is present on ribes in the case of advance infections on these hosts. The need for a method of distinguishing between the two rusts on ribes was early recognized and it was determined that in the uredial stage the two fungi could be separated in most cases biometrically on the basis of differences in the average lengths and wall thicknesses of the urediospores (Colley 1925). This method is fairly good but fallible because some specimens are so near the biometric border line separating the two species that their identity becomes dubious (Hahn 1930). Physiologically the two Cronartiums can be differentiated in the uredial stage by inoculations on ribes, since a large number of horticultural varieties of the common garden currant *Ribes sativum* Syme. (*R. vulgare* Jancz.) are immune to *C. occidentale* and susceptible to *C. ribicola* (Hahn 1930). Disadvantages of this method are that it requires viable urediospores for the inoculations and several weeks of waiting before the results become apparent. Urediospores are frequently lacking from field specimens since most of the scouting is done in the fall of the year at which time the rust may be entirely in the telial stage. It was not until recently that a method was worked out for differentiating the telia of *C. ribicola* and *C. occidentale* (Acree and Goss 1937). It employs a microchemical colorimetric procedure and is much more rapid than any of the other methods.

Pinon rust was first found in California in 1919 when it was observed there on both ribes and singleleaf pinon pine (Bethel and Posey 1921). Since then in the State the disease has been noted on ribes at varying distances outside the range limits of the pine host almost annually. In 1937 the range limits of the two Cronartiums on ribes overlapped for the first time. Pinon rust was found scattered over northern California and into southern Oregon and blister rust spread southward into California about 125 miles. Overlapping in the range of the two occurred again in 1938.

Although pinon rust overwinters on ribes in the warm coastal climate of southern California (Posey and Bethel 1921), no evidence of this has been found in the Sierra Nevadas where leaves are rarely retained the year around.,.

Pinon rust, like blister rust, spreads long distances to ribes by means of air-borne aeciospores. Some of the ribes in southern Oregon on which *C. occidentale* were found in 1937 were nearly 300 miles from the closest pinon pines, except for one small stand of a relatively few acres about 265 miles distant in which the disease does not occur. Spread over distances of 100 to 200 miles has not been uncommon. In 1940 pinon rust was again

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10. In April, 1939, Frank A. Patty of the Division of Plant Disease Control, Bureau of Entomology and Plant Quarantine, found on *Ribes roezlii* mature and green leaves in good condition that had overwintered under snow in Yosemite National Park at an elevation of 6,500 feet. It is possible therefore that either pinon or white pine blister rust might occasionally overwinter under such conditions in high elevations, a possibility hitherto not given consideration.

widespread on ribes, occurring over northern California nearly to the Oregon line.

Most of the ribes species native to California are known to be susceptible to pinon rust either as a result of the finding of bushes naturally infected or through inoculations. None of those inoculated have been found to be immune. The species most commonly found infected in northern California is *Ribes roezlii.* Numerically it is much more prominent than any other occurring there.

SOME BIOLOGICAL FACTORS UNFAVORABLE *TO* DEVELOPMENT OF THE RUST

IN the West a few biological factors are unfavorable to *Cronartium ribicola* and have reduced infection to some extent locally, but generally they have been of little significance. The fungus *Tuberculina maxima* Rostr. is parasitic on the pycnia and prevents the production of aeciospores. It was first found on blister rust in the West in 1926 at a few places in British Columbia (Mielke 1933b). Since then its appearance there has been more or less sporadic, and only in an occasional year has it been observed as fairly common over a few local areas. To the southward in the United States it has been noted as occurring naturally on blister rust only in the Inland Empire region where it is now rather generally distributed, but neither common nor abundant. Attempts made to spread this parasite among white pines infected with blister rust in that region in 1932 and 1933 met with little success (Hubert 1935). Several other fungi have been observed on blister rust lesions, but they are infrequently encountered as a rule and appear to invade the diseased tissues after the lesions have become well developed. Like *T. maxima,* they evidently hasten somewhat the death of the bark over the cankered area. Tests have shown that the fungus *Fusarium bactridioides* Wr. (Wollenweber 1934), which was found on the cone rust *Cronartium conigenum* Hedgc. and Hunt in Arizona and introduced into Oregon in 1932 and Idaho in 1933, will rapidly destroy the blister rust fungus on *Pinus monticola* once it attacks the cankered tissues. However, since its introduction into those two States it has spread exceptionally slowly to cankers on adjacent trees.

Rodents, particularly squirrels and mice, gnaw the bark from blister rust lesions for food, and in some instances the volume of aeciospores is thus considerably reduced (Mielke 1935). The extent of bark removal is much greater on some areas than others and in some years than others. The rodents responsible are somewhat slow to discover the existence of this food supply in new localities, and as a rule 8 to 12 years may elapse after the first appearance of the rust on pines before rodent gnawing becomes evident. By that time, however, the new infection centers are well established and spread to new localities probably has occurred.

It is doubtful if anyone of these biological factors, or even all of them combined, have had any effect on the rate of spread of the rust in the West though they may locally reduce intensity of infection.

No biological factors have been noticed that have had a significant effect on the development of the rust on ribes.

STRAINS OF WHITE PINE BLISTER RUST

NO evidence has yet been presented to show that there is more than one physiologic race of *Cronartium ribicola.* According to Spaulding (1929: 43), whether races or strains have yet arisen in Europe or North America is unknown. Rather extensive tests designed to show this have been unsuccessful. He is of the opinion that the European countries became infected from a common source. As previously mentioned the introduction of the rust into western North America is traceable to a single shipment of diseased pines from Europe in 1910, and no field evidence has been found of any other introduction since then by spores or otherwise. It therefore seems likely that but one race was involved in the introduction of the rust into the West and that if additional ones are now present they have arisen there. No indications of this have been observed, however.

SUMMARY

WHITE pine blister rust, a fungus disease of white pines, is of Asiatic origin. It was first introduced into the northeastern States about 1898. The pathogen was first found in western North America. at Vancouver, British Columbia, in the fall of 1921, and it has been ascertained that it was introduced near there directly from France in 1910 in a single nursery shipment of eastern white pines. All evidence indicates that this was the only introduction in the West.

The fungus is the cause of the most serious disease attacking forest trees in western North America. There are seven species of white pines in the West and all have been found to be susceptible. Within their natural stands only three of the species (western white, whitebark, and sugar pine) are known to have become naturally infected. Present evidence indicates that they are more susceptible than the other four species (limber, foxtail, bristlecone, and Mexican white pine). In its present distribution the rust is by far more common on western white than on whitebark or sugar pine.

The epidemic development of blister rust is affected by a great many factors. Included among those that have been given consideration in connection with the infection of and development of the rust on pines are mode of infection; incubation period, the length of which is influenced by age of tree, character of seasonal weather, locality, altitude, and length of the growing season; the function of the pycniospores and time of their production; the time of aeciospore production and the influence of size of part attacked, thickness of bark, temperature, length of growing season, and character of seasonal weather on the production and dispersal of these spores; canker growth rate as affected by size of the infected part and regional site conditions; the rate of intensification and damage, together with time element and manner of killing of pines and the number of cankers required to seriously injure or kill trees of different sizes; the time required for pine infection; rain, fog, and dew in relation to pine infection; receptivity and susceptibility; vigor of the host; size of tree in relation to infection; relative virulence and abundance of sporidia on different ribes species in relation to intensity of infection on pines; the influence of foliage screens on the infection of pines; and distance and intensity of spread from ribes to pines.

Ribes (currants and gooseberries), the alternate host plants of the rust, are common in the West and are represented by about 60 species. Most but not all of them have been exposed to infection by the rust either naturally or by inoculations. Of those exposed, all were found to be susceptible, the different species ranging from highly so to resistant. The more important factors, which have been given consideration in connection with the infection of and development of the rust on ribes, are relative susceptibility and telium-producing capacity of the species that are the most common associates of western white and sugar pine; incubation period and the influence of temperature on it; the function of the uredial stage and the time of its production as influenced by weather and other conditions, together with the number of generations that may be produced during a season; the function of the telial stage, the time of its production as influenced by host, weather, and other conditions, together with number of generations that may be produced during a season; the longevity of the aeciospores, the time, temperature, and moisture requirements for their germination, and the relative susceptibility of ribes in relation to infection by these spores; the longevity of the urediospores, their germination as influenced by moisture, temperature, and other conditions, and the susceptibility of ribes in relation to infection by these spores; the intensity of infection on ribes as affected by the distance these plants are situated from the aeciospore source; annually repeated heavy infection and its effect on ribes; and the time of telial development on some western ribes as a factor in the infection of pines.

The early history of the rust in the West, as it was determined during the course of field investigations in 1922 and 1923, is reviewed. It was during those years that the introduction point near Vancouver was found, also that circumstantial evidence was obtained indicating that the rust could spread from pines to ribes for distances of 100 miles or more by means of wind-borne aeclospores.

An account is given of the spread of the rust from year to year for the period 1910 to 1942, inclusive. Weather conditions favoring or inhibiting spread and intensification each year are considered. Illustrations are presented showing the spread that occurred during most of the years that were favorable for advancement of the rust into new regions. Also, the present-known limits of distribution of the rust on pines and ribes, which now extends over hundreds of thousands of square miles, is illustrated.

Long-distance spread of blister rust occurs by means of wind-borne aeciospores. Evidence accumulated during the course of 20 years of study shows that, under favorable conditions, these spores may be wind-transported from pines to ribes over distances of 300 to 400 miles, and possibly farther. Records of surface winds have been of little value in connection with studies on spread of the rust because the direction of these winds is strongly influenced by local topography. On the other hand, records of upper-air winds have proven most valuable, and with the aid of upper-air charts it has been possible to forecast, with a high degree of accuracy, the southward spread to ribes in California from pine infection areas situated to the northward.

Moisture is a highly important factor in the spread and intensification of the rust. The character of weather conditions favoring or inhibiting aeciospore dispersal, the infection of ribes, and the infection of pines are discussed. A wide spread of the rust may be expected in any direction in any year that wind and moisture conditions are favorable for such spread.

The spread of rust has been wavelike in character with the waves irregular in the time of their occurrence. This has resulted because weather and other conditions have not been favorable for heavy pine infection locally together with long-distance spread to ribes and the subsequent establishment of the fungus in new localities. In the 32 years since the introduction of the rust there have been but five outstanding years in this regard, viz., 1917, 1921, 1923, 1927, and 1937.

From the introduction point near Vancouver the present-known limits of the rust's distribution on both pines and ribes in the western States extend somewhat farther to the southward than to the eastward. However, the intensity of spread has been heaviest to the eastward.

As compared to the native wild ribes, the European black currant, which is the most susceptible of all species, played a very minor rôle in the spread and intensification of the rust on pines, except in the interior of British Columbia where a number of plantings were found in association with pines. The rust has not spread from pines to *Ribes nigrum* any farther than it has to certain of the highly susceptible wild species.

Pinon blister rust, which also has as its alternate host ribes species, is indistinguishable by ordinary methods in the uredial and telial stages from white pine blister rust. It is now possible, however, to readily distinguish between these two rusts in the telial stage by a microchemical colorimetric procedure. This is of importance because of the necessity of determining which fungus is present on ribes in the case of advance infections since the range limits of the two have now overlapped.

There are a few biological factors that are unfavorable to development of the rust, but they have had little effect on the rate of spread in the West, though they may locally reduce intensity of infection.

No evidence has yet been presented to show that there is more than one physiologic race of white pine blister rust.

ACKNOWLEDGMENTS

THE writer wishes to express his appreciation to Dr. J. S. Boyce of Yale University (formerly in charge of the Portland, Oregon Branch of the Division of Forest Pathology) and to Dr. W. W. Wagener of the Division of Forest Pathology, Bureau of Plant Industry, Soils, and Agricultural Engineering, for criticism and advice in the preparation and presentation of the data. Grateful acknowledgment is also made for coöperation of the Division of Plant Disease Control, Bureau of Entomology and Plant Quarantine, by granting permission to use their records covering the distribution of blister rust in the western United States as determined by their scouting results. Several members of that Division, particularly Messrs. E. L. Joy and D. R. Miller, have generously given their time in providing valuable advice and information. Acknowledgments are also made to Dr. H. T. Giissow of the Dominion Department of Agriculture, Division of Botany, and various members of the British Columbia Forest Branch for their friendly cooperation in the work carried out in British Columbia, and to present and former members of the Portland Branch of the Division of Forest Pathology, Bureau of Plant Industry, who participated in the collection of some of the data presented.

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