A Study of Puccinia graminis and Cronartium ribicola

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A STUDY OF PUCCINIA GRAMINIS
AND CRONARTIUM RIBICOLA

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CHAPTER I

THE ISSUE

As a result of personal knowledge of wheat rust and white pine blister rust, the writer was interested in learning more about these two related fungi. Knowledge of research concerning both rusts and an understanding of the problem is vital to plant pathology.

I. THE PROBLEM

Statement of the problem. It was the purpose of this study (1) to review the literary history of rusts in the United States and in the Northwest in particular, (2) to learn where rusts generally are found geographically, (3) to gain further information regarding the etiology of wheat rust (*Puccinia graminis tritici*), of white pine blister rust (*Cronartium ribicola*) and to become enlightened on other rusts, (4) to learn ways of controlling the two rusts, black stem rust of wheat and white pine blister rust, and to gain an appreciation of the economic importance of rust prevention.

Importance of the study. Wheat production in the Pacific Northwest affects the economy of many areas just as the white pine industry affects parts of Oregon, California, and northern Idaho as well as adjoining areas of Montana and Washington. These rusts are a continuing threat to both lumbering and farming by reducing the yield. A continual search for knowledge of more resistant varieties of wheat and pine, as well as more effective controls, are essential in order to maintain adequate quantities for the future generations.

II. LIMITATIONS

Although this is primarily a study of wheat rust and blister rust in the Pacific Northwest, some information is included concerning rusts in other geographic areas. These two pathogens may appear to be quite different because of their unrelated hosts, but in actuality the pathogens are closely related and an understanding of one enhances the understanding of the other. The area of plant pathology dealing with rusts is too extensive (170 species listed for the Northwest) to be included in a paper of this nature; therefore, two rusts were chosen because of their common occurance and economic importance (10:171-181).

CHAPTER II

BLACK STEM RUST AND WHITE PINE BLISTER RUST

History of black stem rust. Two of the important rusts in the Pacific Northwest are black stem rust which is caused by the organism *Puccinia graminis* and white pine blister rust which is caused by the organism *Cronartium ribicola*. Since these directly affect man and his econimic activity they have been noted in historical writings from time to time. Black stem rust has the longer recorded history and is mentioned in some of the Biblical accounts. Apparently no records of the observed effects of blister rust were recorded until the middle of the nineteenth century.

Because of the separate history of these two rusts and because each of the rusts affects the economy in the Pacific Northwest directly, each history will be considered separately.

From a textbook by Heald (6:774) certain significant facts were derived which show man's increase in knowledge regarding wheat rust. Black stem rust was first mentioned during Biblical times as "Blasting and mildew". It was known to the Romans and they believed it had been sent to them as a curse. Each year on April 25 they held a festival--the Robigalia of Rubigalia--to propitiate the gods Robigus and

Rubigo and thus protect their fields (6:774). There seems to be some doubt as to whether they were appeasing the gods or looking for another chance to have a festival (1:367).

As late as 1733, Tull did not think the disease was of a fungus-like nature, instead he believed it was caused by the attack of insects. The black spots were supposed to be their excreta.

About this time barberry was thought to have some effect on wheat though the disease was still not known to be a fungus, rather it was thought to be caused either by the effect of a noxious effluvium, or by a poisoning caused by the pollen of the flowers, or by the appropriation of the soil nutrients by the barberry in the vicinity. Later, because of the developing awareness of the relationship between barberry and wheat, certain legislation was passed for its extermination and forbidding the planting of barberry. Such laws were passed in Connecticut in 1772 and in Massachusetts in 1775.

In 1797 Persoons recognized the causative factor of wheat rust as a fungus-like organism, but he still believed that barberry rust must be caused by a separate fungus. Persoons was the one who gave the pathogen the name *Puccinia graminis*.

Sir Joseph Banks, in 1805, believed that it was possible that the fungus which infected wheat and that which infected barberry could be the same. He also thought that it was possible that it could be transferred from barberry to corn.

Marshall in England showed by experiment that the organism which caused rust on barberry was the same organism that caused wheat rust. This was done by planting barberry in the middle of a wheat field and observing the results. A Danish schoolmaster, Schoeler, did many experiments to demonstrate the connection between barberry and other grains. One of his most important experiments was rubbing the leaves of rye with the leaves of infected barberry when the leaves were wet with dew. In five days he observed rust on the innoculated rye and no rust elsewhere. Even though his findings were published by the Royal Agricultural Society of Denmark in 1818, the experiments were overlooked for many years (6:774).

In 1954, Tuslane showed the genetic relationship between the uredinal and the telial stage. He also showed that this was a general rule among Uredinales (order of fungi).

The classic works of De Bary in 1864 and 1865 demonstrated the heteroecious nature of the pathogen by innoculating the barberry with black rust then transferring it back to the rye by the seciospores.

Following the demonstration of the relationship of barberry and stem rust, laws were passed by Denmark in 1869, by Prussia in 1880, and by France in 1888 making it possible to exterminate or to restrict the planting of barberry.

In the United States similar laws were passed regarding barberry extermination and in 1917 the Federal Government started a special campaign for the elimination of barberry. By the mid 1920's twenty-five laws had been passed in Germany relating to barberry eradication and control. The 1869 law in Denmark was followed by a more stringent one in 1904. Eradication laws were also passed in Norway in 1916 and Hungary in 1920. England had a voluntary uprooting program which has been successful (6:775).

Between 1917 and 1923 South Dakota, North Dakota, Iowa, Montana, Minnesota, Nebraska, Michigan, Wisconsin, Wyoming, Oregon, and Washington passed barberry elimination laws.

In 1918, Congress began to make annual appropriations for an eradication program. Barberry eradication areas were established as a cooperative enterprise between federal and state agencies in the states of Montana, Wyoming, Colorado, North Dakota, South Dakota, Nebraska, Minnesota, Michigan, Illinois, Indiana, and Ohio (14:630).

Quarantine Law 38 was established by Federal Horticultural Board prohibiting shipment of thirty-one rust susceptible species of Berberis and Mahonia into the area (14:631). In the literature Berberis and Mahonia both listed as several species that serve as alternate hosts, however, a species that can be found in the Northwest is Berberis vulgaris (9:22). For the United States only B. vulgaris, B. fendleri and Mahonia aquifolium related as hosts. Although M. aquifolium is present over much of the Northwest, it has not been found to be an alternate host and has been found to be only of minor importance in other areas (6:790). In 1931 the Federal quarantine was extended to interstate transport of the thirty-one species. Missouri, Pennsylvania, Virginia and West Virginia were included in the eradication program in 1937. Canada started a similar program in Manitoba, Saskatchewan and Ontario in 1917.

In 1942 sixty per cent of the area designated for eradication was considered nearly free of barberry. The other forty per cent of the eradication area had been covered once but was in need of attention a second time.

History of white pine blister rust. White pine blister rust caused by the pathogen Cronartium ribicola is another economically important rust in the Pacific Northwest. It has a different and somewhat shorter recorded history.

Blister rust was first recognized by Dietrich in Western Russia in 1856. He also observed the telial stage in *Ribes*. It was observed in Finland in 1861, in Germany in 1865, and in Denmark in 1883.

In 1888, Klebahn proved that the white pine blister rust pathogen had as an alternate host several species of *Ribes*.

The White Pine, *Pinus strobus*, was introduced in Europe in 1705 and since that time it has been planted extensively. It has been suggested that the pathogen *Cronartium ribicola* is endemic to Asia and parts of Europe. Since the *Pinus strobus* is more susceptible to the pathogen than the native pines, it soon set the stage for a severe outbreak of white pine blister rust. The fact that no recorded observation of *Cronartium ribicola* was made in Europe prior to 1865 could have been because the disease had not been prevalent before, but after 1856 the fungus spread rapidly.

In the United States white pine blister rust was first observed on *Ribes* at Geneva, New York, in 1906. It was first observed on pine in 1909. It was thought to have been introduced from Europe between 1898 and 1910 on seedlings (7:403). One shipment from Germany was distributed to 226 different localities (14:632).

The disease was observed in New Hampshire, Vermont, Massachusetts, Connecticut, New York, Pennsylvania, New Jersey, Ohio and Indiana by 1916. It was also observed in

Michigan, Wisconsin, Minnesota and Ontario, Canada, about this time. In 1921, blister rust was discovered in British Columbia and the Puget Sound area of Washington. By 1925 it had spread to Northwest Oregon (7:404).

Geography of black stem rust. *Puccinia graminis* has been found in nearly every country that grows wheat. England, Denmark, France, Germany and other European countries have in the past had rust in epiphytotic proportions, but since the eradication of barberry, it has become infrequent in these countries. Australia and South Africa have had serious rust infections. It has also been reported in India.

In the United States rust has been most common in the Great Plains hard-winter and hard-spring wheat belts. It has also been found in the states bordering the Ohio River. In some of the Eastern states, such as Maryland and Virginia, it has been reported, but it is by no means common. At times it reaches epiphytotic proportions in the interior valleys of California and on the coast of California it is almost always prevelant.

Rust is also severe in some Southern states, even though here little wheat is grown. As a result, in Southern Texas the growing of wheat is hazardous. In the dryer, northern areas of Texas, rust occurs to a lesser extent (6:776).

The Pacific Northwest is said to be an area where rust is rarely of economic importance as compared with areas such as the upper Mississippi Valley. However in 1961, it reached epipytotic proportions and did considerable damage. During the year 1961, the disease was a serious problem in the irrigated wheat of the Columbia Basin and in the wetter Palouse area, but was of lesser importance in the dry wheat area.

Geography of white pine blister rust. There are eight native species of white pine in the United States. Three of these are important to the lumbering industry. One species is the eastern white pine which is found from Georgia to Maine and west to Minnesota. Another is the western white pine which is found in the panhandle of Idaho and nearby parts of Idaho and Washington. The third is the Sugar Pine which is found in Oregon and California (13:454).

Etiology of black stem rust. The pathogen *Puccinia graminis* and *Cronartium ribicola* are macrocyclic rusts, rusts having at least one binucleate spore in addition to the teliospore (telulospore). Both organisms are heteroecious. In *Puccinia graminis* two-celled teliospores are produced in mid-summer on the leaves of wheat and other grains. The spores either exist in the winter on the straw or drop onto the ground where they must pass a period of dormancy and low temperature before they will germinate. Early in the spring, the spores produce a slender, colorless hypha into which the diploid nucleus migrates, undergoes meiosis, and forms four haploid nuclei. Septa are then laid down separating the nuclei into four cells. Each cell procudes a sterigma on which a basidiospore is formed. The nucleus in each cell then moves through the sterigmata into the basidiospore (sporidium). This entire process of germination and formation of basidium (promycelium) and basidiospores is very rapid and requires only a few hours. The basidiospores are ejected and carried by the wind and must reach the common barberry soon or die. The basidiospores germinate on the barberry and produce a germ tube which penetrates the cutical of the plant and enters the epidermal cells where it obtains nourishment. Then a branched uninueleate mycelium develops that has a nucleus carrying the factor + or - depending on what its parent carried. Several basidiospores usually infect the same barberry plant so + or - mycelium will develop side by side (1:377).

After infection the hyphae of the fungus nearest the upper epidermis develops spermagonia (pycnium).

> Each spermogonium contains numerous spermatiophores which cut off a succession of minute spermatia. These are exuded in small droplets of nectar from the opening above the spermogonium. Several periphyses are also formed in the upper part of the spermogonium. Each spermatium contains a large nucleus carrying the + or - factor, depending on the strain of mycelium which produced the spermogonium. All spermatia from a single spermogonium carry the same factor. The same mycelium

> which produces the spermatia also gives rise to receive hyphae with the same genetic make-up as the spermatia. These arise in the spermogonia and protrude through the ostioles. The spermogonial periphyses may also change to receptive hyphae. Since multiple infection is probably the rule in nature, spermatia and receptive hyphae, some of each carrying the + factor and some the - factor, are generally found on infected barberry leaves. Spermatization now takes place through the agency of insects. A fly or some other insect, attracted by the fragrance of the spermogonial mass, visits it and sips the sweet nectar exuding from the ostioles. During this process spermatia in the nectar adhere to the mouth parts of the insect and are subsequently brushed off by the receptive hyphae and periphyses of the next spermogonium which the insect visits (1:378).

If a + is transferred to a - or vice versa, spermatization takes place by the spermatial nuclei passing through the receptive wall via a pore dissolved in the receptive wall.

> Meanwhile the mycelium has penetrated the entire leaf and the hyphae near the lower epidermis have formed a number of aecial primordia. It is presumed that the spermatial nuclei, which pass from the spermatia into the receptive hyphae, travel down the hyphae, pass through the septal perforations of the mycelium, and reach the cells of the aecial primordia, rendering them binucleate (1:378).

This has not been proven but it appears to be the best explanation to the dikarytization of the aecial primordia (1:378). The aeciospores (aecidiospore) are the first binucleate spores produced in the life cycle. These eventually break through the lower epidermis of the barberry and are disseminated by the wind and under favorable conditions germinate.

If the aeciospore lands on a susceptible grass host, infection then results. After infection, the binucleate mycelium in the grain host forms cell masses, the uridia, on which asexual binucleate uridiniospores (urediospore, uredospore) arise on rather long stalks. The pressure from the uridiniospores causes the epidermis to rupture and masses of urudiniospores appear. The rupture of the host's epidermis are elongated streak-like pustules and the urediniospores are a red-rust color which gives rise to the common name "rust". Upon walking through a field that is heavily infected, a person will get the part of his clothes that is in contact with the host covered with the rust-colored spores.

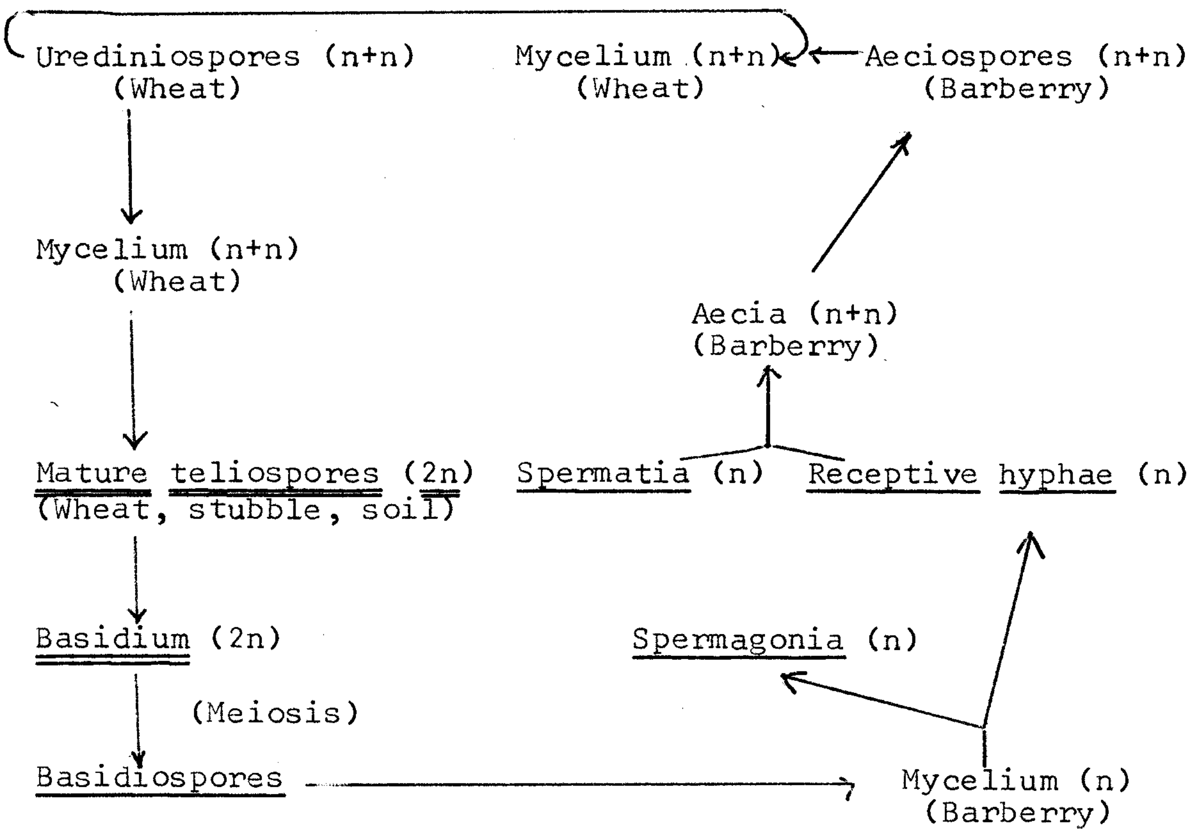
The uridiniospores are capable of germination as soon as they are matured, thus several uridial cycles are produced each spring and early summer if the conditions are favorable.

When the grain begins to ripen, some of the uridia begin producing teliospores and as the season progresses, more and more teliospores are produced. The pustules that produce teliospores appear as black streaks on the straw and constitute the black stage of the rust. Thus the cycle is complete (1:378).

The life cycle of Puccinia graminis can be shown by diagram as set forth on the following page.

Since the barberry has been eradicated in many areas the teliospore can not function as a part of the life cycle in the continuation of the organism. The barberry is of less importance in the South because the teliospore does not germinate in the southern areas of relatively warm winters and because ordinarily new barberry growth in the South does not occur at the proper time.

Life Cycle of *Puccinis Graminis*



(2:207)

In the South the uridiniospores can overwinter and infect grains without the need for an alternate host. These spores are carried north by air currents (4:410).

The exact timing of favorable environmental conditions for reproduction of the uridinic cycle and for the

> dissemination of spores is required. Usually the migration is prevented or retarded by some periods of unfavorable environment (14:410).

It has been found that there is a correlation between the mean temperature and the amount of rainfall during the last two months of the growing season and the severity of the black stem rust in susceptible varieties of wheat.

> When total precipitation fell below 2 in. or when the mean temperature ranged between 66° and 72° and the total rainfall exceeded 215 in. In other words, warm moist weather is necessary for the production of abundant inoculum when susceptible hosts are available (14:410).

Control of black stem rust. Since the uridiniiospores are still able to cause infection in spite of the teliospores it may at first seem that the eradication program has been in vain and has resulted in a tremendous waste of money, however, the barberry eradication program has two main benefits: one is the elimination of early spring primary innoculations, and the second is the prevention of the development of new and nonprevalent physiological races of the fungus through hybridization in the sexual phase that produces the aeciospore (14:631).

The species *Puccinia graminis* contains numerous biological subspecies and races. The subspecies *tritici* affects wheat. This subspecies is made up of a large number of physiological races which differ in their parisitism of different subspecies of the host. *Puccinia graminis tritici* consists of over 200 different races (12:331). New races develop by mutation from time to time. Different races have differing degrees of pathogenity on different races of wheat. Plant breeders are constantly breeding new races of wheat that have a resistance to rusts. They have been able to breed wheats that are resistant to one race or several races of rust but not all races. Since there are usually only a few races of rust that affect a given race of wheat these resistant races of wheat are planted in the area that do not have the pathogenic race which affects it. New races appear from time to time by either importation, mutation, or recombination and infect races of wheat that have not been infected before. Another problem is that a wheat may be highly resistant to the strains of rust in an area but are susceptible to other diseases in the area. These circumstances bring about the need for a continuing breeding program (14:410).

Species and races of grain rusts. The rusts that affect wheat and other grains are:

Puccinia graminis tritici	Stem rust on wheat and barley
Puccinia rubegovera	Leaf rust on wheat
Puccinia glumorum	Stype rust on wheat
Puccinia graminis avenae	Stem rust on oats
Puccinia coronata avenae	Crown rust on oats

Puccinia graminis secolis	Stem rust on rye
Puccinia rubigo-vera	Leaf rust on rye

(12:329)

Wheat stem rusts attack several other hosts. Some of these are barley, rye, squirreltail grasses (*Hordeum* species), certain wheatgrasses (*Agropyron* species), wild-rye grasses (*Elymus* species), battlebrush grasses (*Hystrix* species), and some broomgrasses (12:329).

Varietal resistance to black stem rust. The following is a list of some varieties of wheat and the races of *Puccinia graminis tritici* that infect them.

Races of subspecies Tritici	Variety
T. compactum	Little Club
T. vulgare Vill.	Marquis
T. Vulgare	Reliance
T. vulvare	Kota
T. durum Desf.	Arnutka
T. durum	Mindum
T. durum	Spelmer
T. durum	Kubanka
T. durum	Acme
T. monococcum L.	Einkorn
T. Dicoccum Schrank	Vernal
T. dococcunm	Khapli

The resistance of the pathogen from race to race of the host involves three different biological principles. One type of resistance is a protoplasmic resistance. This type of resistance is explained by Walker.

> When a resistant variety of wheat is exposed to uridiospores or seciospores, germination and formation of appressoria proceeds in the same manner as on the susceptible host. More stomata may be entered in the very susceptible than the very resistant plant. In the congenial host the mycelium arising from the sub-stomatal vesicle proceeds intercellurarly, forms haustoria and gradually retard growth and productivity of the host. In the resistant host the same process occurs up to the formation of a small haustorium. Then the latter collapses, as does the haustorial mother cell, and in turn the host cell dies. In the highly resistant host, then, little damage is done. The type of resistance just mentioned is based upon the interaction of the protoplasts of host and pathogen (14:413).

A second type of resistance of stem rust is related to the stomata opening and closing. Black stem rust of wheat finds more favorable conditions for entering the plant during daylight. Since humidity is usually highest in the morning, the critical time for infection then is when the dew is on and the stomata are open. The stomata open later in some varieties than in other varieties and thus if the opening of the stomata is delayed until after the dew is dried the conditions for infection are reduced. This kind of resistance is known as functional resistance (14:413).

A third type of resistance is related to the amount of collenchyma, and the amount of parenchyma in the host.

Rust fungus does not equally invade collenchyma as it does parenchyma and if a minimum amount of parenchyma is present at the time of invasion then the damage from the fungus is reduced accordingly (14:414).

It has been suggested by Caldwell, Schofer, Compton and Patterson that rather than breed for varietal resistance, what we really should be breeding for are varieties of grain that are tolerant of the rust pathogen. They suggest that this would give a more stable approach since new races of rust are constantly developing and affecting varieties of grain that it has not affected in the past.

The authors did some experiments with *Puccinia coronata* which is the pathogen that causes crown-rust in certain varieties of oats and found that certain oat varieties, in spite of a high rate of infection, maintained both good yield and good quality (3:714-715).

Effect of black stem rust. Wheat rust is not a serious problem every year in the Northwest although it does show up in local areas from time to time (12:329). In 1961 it reached epidemic proportions in the irrigated areas of the Columbia Basin and in the dryland areas of Eastern Washington. Many of the irrigated farms in the Columbia Basin which normally produce a yield of from 50 to 80 bushels of wheat got a 25 to 35 bushel yield. Losses have reached 85 to 90 per cent in some areas of the world at times in the past. This would make the crop a complete loss and not worth harvesting.

The actual effect on the wheat itself is that the kernels from the plant that is infected may be shrunken one-half or two-thirds normal size. Because of the "pinching" affect, the kernels are very light and are blown out with the chaff in the harvesting process (12:329)

Etiology of white pine blister rust. White pine blister rust is caused by the pathogen _Cronartium ribicola_. It is a macrocyclic heteroecious rust which affects various species of white pine (five needles) and has as an alternate host various species of _Ribes_ (1:383).

The species of pine and the alternate hosts that are found in the Northwest are:

Pine in Northwest Affected	Alternate Host in NW
Pinus albicaulus	_Ribes acerifolium_
Pinus flexilis	_Ribes cereum_
Pinus lambertiana	_Ribes cruentum_
Pinus monticola	_Ribes inerme_
	Ribes irriguum
	Ribes lacustre
	Ribes laxiflorum
	Ribes lobbii

Ribes oxycanthoides

Ribes sanguineum

Ribes triste

Ribes viscosissimum

(1:74-76)

To discuss the life cycle of the blister rust pathogen on white pine, it is well to start with the basidiospores (sporidium) that are produced from teliospores (teleutospores) germinating and producing promycelium (basidium) and basidiospores. The basidiospores infect pine needles and produce mycelium which infect the twig. The pathogen may overwinter as mycelium of the infected pine. Aecia form in the spring and may discharge aeciospores (aecidiospores) for about a month (1:383). The aeciospores may remain viable for about four weeks.

The aeciospores, like the other spores in the life cycle, have minimum and maximum temperature limits at which they germinate. The aecia are on the pine host. These form prominent, white or cream-colored flaring peridial lips which are clearly visible and give the disease its characteristic name.

The aeciospores are carried to the Ribes leaves by wind and the spores may be carried up to seven miles. Ribes leaves must be moist for infection to occur and are more susceptible when they are young. The infection occurs through the stomata. Uredia appear after a short incubation period. Several generations of uredia may be produced in one season. Wind is the chief disseminator and viable urediospores (uridiniospores, uredospores) have been found 3,200 feet from their origin. Both uredia and telia are produced on the various species of Ribes (14:433). The uredia are minute and are found on the underside of the leaf. They have the appearance of brown, dome-shaped igloos. The telia are also produced on the underside of the leaf and are elongate, often curved, horn-like columns of teliospores which are united both laterally and terminally (1:383).

The teliospores germinate in place the season they are produced from promycelium each with four basidiospores. These are disseminated by the wind and have been known to be carried 600 feet.

These germinate immediately and the germ tube enters through the stomata of pine. Thus the life cycle of the pathogen is completed (14:433).

Different species of white pine vary in resistance. *Pinus albicaulis*, *P. lambertiana* and *P. monticula* are more susceptible than *P. strobus* and *P. flexilis* while *P. aristata* and *P. peuce* are somewhat resistant. Resistant species are *P. armandi*, *P. griffithi* and *P. korainsis*.

From time to time *P. strobus* is found to be highly resistant and these resistant individuals are being used in a breeding program to develop resistant strains (14:434).

Blister rust is controlled by removing the alternate host *Ribes* from the white pine areas. Man has the advantage over this fungus because the repeating (uridinal) stage is not on an economically important host as the case with the repeating (uridinal) stage of the pathogen *Puccinia graminis*.

Ribes is removed both mechanically and with chemicals. The herbicides 2,4D and 2,4,5-T are the most widely used chemicals. In the control areas the *Ribes* are removed throughout the area and in the surrounding zone for at least 1,000 feet. This prevents the production of basidiospores and teliospores which might infect pine. Twenty-eight million acres had been included in the blister rust control area in 1942. Of this part of the area has been rechecked at least once. The area has since been extended in the Western States (14:632).

Effect of white pine blister rust. In the white pine belt of Idaho, Montana, and Washington the western white pine represents about three-fourths of the value of the forest products in the white pine region. The other forest products in the white pine belt could not be profitable, however, if the white pines were not present in large numbers.

The other five species grow in the high mountains and are of little economic value but are valuable for protection of watersheds (13:454).

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