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METHOD OF DETERMINING AGE OF BLISTER RUST INFECTION ON WESTERN WHITE PINE[1]

By H. G. LACHMUND[2]

Pathologist, Division of Forest Pathology, Bureau of Plant Industry, United States Department of Agriculture

INTRODUCTION

Blister rust (*Cronartium ribicola* Diet.) was discovered in western North America in the fall of 1921. In 1922 it was found that the disease ranged over a wide area in southwestern British Columbia and adjacent Washington. Apparently it was originally introduced near Vancouver in 1910.[3] Its range now extends practically from Alaska to California and from the Pacific coast in Washington east into Montana. The chief aecial host within this range is native western white pine (*Pinus monticola* Doug.). Investigations of the rust in this great new range have been carried on by the Division of Forest Pathology since 1922. One of the first essentials in these investigations was to establish a method of determining the age of infection on pines. In the present paper this problem is discussed and a solution offered.

Pinus monticola occurs in two distinct geographic belts. One of these belts extends between the Pacific coast and the eastern slopes of the Coast Range in British Columbia, from about 150 miles north of the international boundary, southward into northwestern Washington, and thence mainly along the Cascade Mountains of Washington and Oregon into the higher elevations of the Sierra Nevada of California; the other belt extends from about 200 miles north of the international boundary, in the interior of British Columbia, southward into the main commercial range of the species in northern Idaho and adjacent Washington and Montana. Until 1929 the known range of pine infection by the blister rust was confined chiefly to the coastal belt in British Columbia and northern Washington and to a small portion of the interior belt 120 to 135 miles north of the boundary, in British Columbia. The range of infection is now known to extend, in the coastal belt, south in the Cascade Mountains to central Oregon, and, in the interior belt, into the main commercial pine region of Idaho. The results reported here are mainly from studies made within the earlier known portions of the range, which constitute the area of longest established and heaviest infection, but they are also

[1] Received for publication Aug. 19, 1932; issued May 1933.

[2] The writer was assisted in the collection of data on which this article was based by J. L. Mielke, T. S. Buchanan, A. A. McCready, J. W. Kimmey, and W. F. Cummins, of the Division of Forest Pathology, and C. N. Partington, formerly of that division, and by W. V. Benedict, of the Division of Blister Rust Control.

[3] PENNINGTON, L. H. RELATION OF WEATHER CONDITIONS TO THE SPREAD OF WHITE PINE BLISTER RUST IN THE PACIFIC NORTHWEST. Jour. Agr. Research 30:598. 1925.

based on data from the newer sections of the range. The data from the two areas are in such close agreement as to indicate that the results will be applicable to the entire range of *P. monticola* in the Pacific Northwest.

CONDITIONS GOVERNING INFECTION OF WESTERN WHITE PINE

Cronartium ribicola infects its aecial hosts through the needles.[4] The needles of *Pinus monticola* are regularly held for three full growing seasons. Although some needles fall at the end of the third season, a great many are generally held through the fourth season, and some are commonly held to the end of the fifth season. If the growth rates of the needle-bearing parts and the environmental conditions are favorable, a few needles may be retained through the sixth or even the seventh season, and very exceptionally a needle bundle or two may persist through the eighth season. Thus infection may conceivably find entrance to the bark on internodes of any age up to eight seasons. It is obvious, on the other hand, that the best chances for entrance are on the younger growth and that the dropping of the needles prevents much infection from entering on internodes more than 4 seasons old.

Infection of the needles may occur at any time that moisture conditions are favorable during the period in which sporidia are produced. For all practical purposes, in the range of *Pinus monticola* this may be considered as limited to the period during which teliospores are produced; or, roughly, from about June 1, when these spores first begin to form, until about November 30, when Ribes plants have lost their leaves and most of the fungus spores have germinated.

Ordinarily the majority of the teliospores are produced within a relatively short period. This concentration of telial sporulation is particularly marked, and comes earliest in the pine-infection centers where Ribes plants are plentifully infected by aeciospores early in the season. Under these conditions the teliospores are usually produced in maximum quantities, and their production reaches its height in July or August.

Any favorable moist period during the time when teliospores are abundant results in the production of great numbers of sporidia and, if other conditions are favorable, in extensive infection on pines. On the other hand, if conditions are not favorable, the delicate sporidia, through ineffective germination or loss of viability, soon lose all power to infect, and thus the pine-infecting potentialities of the fungus on Ribes are largely dissipated for the season. The present investigations have shown that for the range of *Pinus monticola* in general conditions are favorable for heavy pine infection on an average of one season out of three.

DEVELOPMENT OF THE CANKERS

Infection is followed by an incubation period during which the rust grows through the needle into the bark, where its further development causes sufficient discoloration or swelling to permit of an accurate macroscopic diagnosis.[5] This period varies for individual infections.

[4] CLINTON, G. P., and MCCORMICK, F. A. INFECTION EXPERIMENTS OF PINUS STROBUS WITH CRONARTIUM RIBICOLA. Conn. Agr. Expt. Sta. Bul. 214: [428]-459, illus. 1919.
[5] CLINTON, G. P., and MCCORMICK, F. Op. cit., p. 449-455.

Observations of the rust through its western range on *Pinus monticola* indicate that the first discoloration or visible swelling of the bark that marks the incipient canker appears only under exceptional circumstances in the first season following that of infection, that it appears principally in the second season, to a lesser degree in the third season, and to a negligible degree, if at all, later than the third season.

The period required for production of the fruiting stages varies also.[6] When the incipient canker makes its appearance early or during the middle of the season, pycnia are generally formed upon it the same year. Cankers appearing toward the end of the season usually do not produce pycnia until the next year. On the majority of the cankers aecia are formed in the year following that in which pycnia are produced, but on many not until the second year.

For young cankers it is seldom difficult to determine the year's growth (wood [7]) on which they originated, and on thrifty trees the internodes of entrance can usually be determined for cankers of much greater age. The age of the growth on which the canker originated readily establishes the maximum possible age of the canker, since it is obvious that infection can not occur prior to the formation of the part infected. Considered in relation to the general appearance of the canker, this affords a rough index of its age. But in the great majority of cases it is impossible to determine accurately the year of infection for the individual canker. Only by considering large numbers of cankers classified according to the year's growth upon which they occur and to their stage of development can the year of infection be determined.[8]

CANKER PRODUCTION

Since the teliospores in pine-infection areas are usually produced within a relatively short period during any season, the occurrence of heavy infection of the pines will necessarily be correspondingly restricted in point of time, possibly to a few days toward the end of the period of teliospore production, or immediately following it. As might be expected, therefore, incipient canker formation in the infection centers generally occurs in definite waves, and usually the majority of the cankers of the individual waves show a marked tendency to form simultaneously.

Heavy waves of canker formation occurred in most of the infection-study areas of the coastal section in 1922 and 1923, in the interior section in 1924, and more or less generally throughout the range in 1929. In 1922 most of the cankers appeared in midseason, during late July and August. In 1923 the greatest numbers appeared in June and July. Most of those produced in the interior study areas in 1924 developed from midseason until September, although some continued to form until the end of the season. In 1929 concentrated production generally occurred toward the end of the season and in some places started up for a time the following spring.

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[6] SPAULDING, P. INVESTIGATIONS OF THE WHITE PINE BLISTER RUST. U. S. Dept. Agr. Bul. 957:24–27. 1922.

[7] The term "wood" has been used by others in a sense similar to that for which the present writer prefers the term "growth," to designate internodes of given years.

[8] PENNINGTON, L. H. Op. cit., p. 596.

Most of the heavy waves of canker formation and some of less intensity have stood out distinctly, in some cases strikingly so. For example, at an infection area near Revelstoke, British Columbia, where the rust was discovered on pines in 1922 and had clearly been present on them for a number of years, no more than 48 cankers, incipient or otherwise, could be found on them until 1924. In June of that year a wave of incipient canker formation began, reaching such proportions in July and August that by September incipient and juvenile cankers could be counted in the area by the thousands. At another area near Revelstoke, where infection had been present on the pines since 1922, the number of cankers increased more than 1,000 per cent during the latter part of the growing season in 1929 and the spring of 1930.

DISTRIBUTION PATTERN OF CANKERS IN INCIPIENT CANKER WAVES

The incipient cankers of the waves of canker formation that occurred in 1922 maintained a highly regular numerical arrangement in their distribution on the internodes of different years. The youngest growth on which these cankers occurred was that of 1920. Most of the cankers, however, were concentrated on the growths of 1919 and 1918, the greatest number being on 1919 growth. Their occurrence was relatively light on 1917 growth, infrequent on 1916 growth, and very exceptional or lacking on older growths. Since these incipient cankers had appeared almost simultaneously, it seemed probable that the majority, at least, had resulted from a common infection year.

Inasmuch as some of the cankers occurred on 1920 growth, it was evident that the majority must have resulted from an infection not earlier than that of 1920. Since none was present on growth younger than 1920, this year was evidently the infection year. If the infection had occurred in 1921 some of the cankers would undoubtedly have been present on 1921 growth; if the infection had occurred in 1922, there would not have been sufficient time for even incipient cankers to develop, or assuming incubation to have taken place, the cankers would have appeared on the growth of 1922 as well as on that of other years.

The waves of canker formation that occurred in 1923 showed a distribution closely analogous to that of the 1922 waves. No cankers were found on 1923 or 1922 growth. Relatively few were found on 1921 growth; the great majority occurred on 1920 and 1919 growth, and the greater number of these on 1920 growth; 1918 growth had relatively few, and older growths were very little affected. The same general relations have characterized the distribution of cankers of each distinct wave of canker formation since then.

It is evident that this characteristic numerical distribution of the cankers, combined with similarity in stage of development, provides a means of ascertaining the infection years for groups of cankers in more advanced stages, thus making it possible to determine the main years of infection and to work out the history of the rust from analyses of older classes of cankers.

For convenience in presenting and summarizing the observations and data the following symbols are used:

a, youngest growth upon which cankers of the infection wave were found.
b, growth 1 year older than *a*.
c, growth 2 years older than *a*.
d, growth 3 years older than *a*.
e, growth 4 years older than *a*.
f, growth 5 years older than *a*.
g, growth 6 years older than *a*.
h, growth 7 years older than *a*.

Figure 1 shows diagrammatically these symbols and the normal occurrence of needles for several successive years.

Most of the needles on *d* in A are dropped at the end of the season, and the remainder are generally dropped at the end of the season the following year. The chances of infection through the needles on

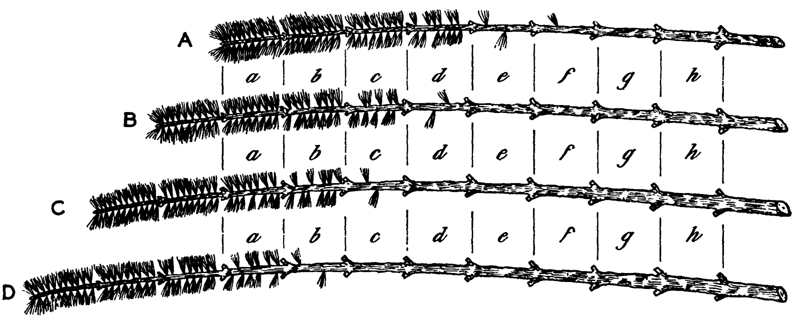

FIGURE 1.—Needle retention in *Pinus monticola* infected with *Cronartium ribicola:* A, Branch after completion of internode *a;* B, branch one year later; C, branch two years later (when most of the cankers appear); D, branch three years later (when the majority of the remaining cankers appear); *a*, youngest growth, or internode, on which cankers of the infection wave were found; *b* to *h*, growths, or internodes, 1, 2, 3, 4, 5, 6, and 7 years older than *a*, respectively

older growths are obviously small. Undoubtedly this accounts for the small representation of cankers on such growths shown in the characteristic pattern of the cankers of the distinct waves of canker formation, which is summarized below:

Growth	Cankers	
a	Relatively few.	
b	Greatest number	large majority.
c	Considerable numbers	
d	Relatively few.	
e	Very few.	
f	Exceptional.	
g	None.	
h	None.	

Sample counts of cankers from these waves are presented in Table 1; the number on each year's growth is expressed as a percentage of the total.

The individual records consistently show the same general relationships. The percentage of cankers on *a* is normally relatively small, averaging about 10; *b* and *c* together have consistently the largest percentage (80–90), with much the largest percentage (usually more than 50) on *b;* the percentage on *d* is generally relatively small (averaging about 5); and that on older growths is practically negligible.

TABLE 1.—*Canker records from distinct waves of canker formation*[a] *in various areas*

COASTAL REGION, BRITISH COLUMBIA

No.	Elevation	Location	Youngest growth showing cankers (*a*)[b]	Year of canker formation	Number of cankers	Percentage of cankers on— *a*[c]	*b*	*c*	*d*	*e*	*f*	*g*
1	Near sea level	Thurston Bay	1920	1922	77	17	52	23	7	1	0	0
			1920	1922	53	10	58	28	4	0	0	0
			1920	1922	68	6	50	43	1	0	0	0
			Total or average		198	11	53	31	4	1	0	0
			1921	1923	76	12	63	13	9	3	0	0
			1921	1923	81	14	60	20	6	0	0	0
			1921	1923	136	7	57	34	2	0	0	0
			Total or average		293	10	59	24	5	1	0	0
			1922	1924	123	19	61	17	3	0	0	0
			1924	1926	115	9	55	34	1	1	0	0
			Total or average		729	12	57	26	4	1	0	0
2		Pender Harbor	1921	1923	134	5	54	37	4	0	0	0
3		Chee Kye	1920	1922	40	8	41	35	8	0	0	0
			1921	1923	417	8	49	37	6	0	0	0
			1921	1923	302	10	53	32	5	0	0	0
			Total or average		719	8	51	35	6	0	0	0
			1922	1924	48	17	64	19	0	0	0	0
			1923	1926	45	16	60	22	2	0	0	0
			Total or average		852	9	52	33	6	0	0	0
4		Sperling	1921	1923	91	7	55	31	7	0	0	0
5		Qualicum Beach	1923	1925	56	11	57	30	2	0	0	0
			1924	1926	112	7	68	21	4	0	0	0
			1927	1929	40	12	55	30	9	0	0	0
			Total or average		208	9	63	25	3	0	0	0
			Total or average		2,014	10	55	30.2	4.6	.2	0	0

COAST MOUNTAINS, BRITISH COLUMBIA

No.	Elevation	Location	Youngest growth showing cankers (*a*)[b]	Year of canker formation	Number of cankers	*a*[c]	*b*	*c*	*d*	*e*	*f*	*g*
	Feet											
6	1,300	Daisy Lake	1921	1923–24	98	10	56	24	10	0	0	0
7	800	Owl Creek	1923	1925	145	2	53	43	2	0	0	0
			1924	1926	123	4	60	33	2	0	0	0
			1927	1929	52	8	48	34	10	0	0	0
			Total or average		320	4	55	38	3	0	0	0
8	1,300	Mile 72, P. G. E. Ry	1920	1922	121	14	42	33	10	1	0	0
			1921	1923	124	13	46	34	4	1	0	0
			Total or average		245	13	44	35	7	1	0	0
			Total or average		663	8	51	34.5	6	.5	0	0

[a] From main body of wave where possibility of admixture of cankers of two successive years was least in each case. Samples were taken indiscriminately through the stand from trees that could be examined from the ground or easily climbed. Cases indeterminate in regard to age of growth infected or stage of development of the canker were not included.

[b] From sample records of the Division of Blister Rust Control.

[c] For definition of symbols *a*, *b*, *c*, *d*, etc., see page 679.

TABLE 1.—*Canker records from distinct waves of canker formation*[a] *in various areas*—Continued

OTHER AREAS

No.	Elevation	Location	Youngest growth showing cankers (*a*)[b]	Year of canker formation	Number of cankers	Percentage of cankers on—						
						a[b]	*b*	*c*	*d*	*e*	*f*	*g*
9	1,500	Revelstoke, British Columbia.	1922	1924	296	7	52	31	8.5	1.5	0	0
			1922	1924	307	3	51	34	10	2	0	0
			1922	1924–25	180	14	52	27	6.5	.5	0	0
			Total or average		783	7	52	31	8.7	1.3	0	0
10	2,000	Columbia River, 8 miles north of Revelstoke.	1927	1929–30	1,805	12	54	30.12	3.5	.33	.05	0
11	1,700	Arrow Park, British Columbia.	1927	1929	135	8	53	36	3	0	0	0
12	3,100	Apex, British Columbia, experiment plot.	1928	1930	144	5	52	32	10	1	0	0
13	2,500	Mount Hood, Oreg., near Rhododendron.	1927	1929	92	9	42	37	12	0	0	0
14	500	Eagle Creek, Oreg	1927	1929–30	243	14	42	36	7	1	0	0
			Total or average		3,202	10.2	52.3	31.3	5.5	.67	.03	0
			Total or average		5,879	9.8	53.2	31.3	5.21	.47	.02	0

See footnotes on p. 680.

DETERMINATION OF YEAR OF INFECTION

The typical distribution pattern of the incipient cankers, their simultaneity of appearance, and the conditions governing infection of the pines may be taken as conclusive evidence that the majority of the cankers of each wave are approximately the same age and of common origin; i. e., that they resulted from an infection of the same year. On this basis, the year of infection for each of these waves is determined by the youngest growth affected. In most cases this is the growth that formed two seasons before the appearance of the cankers. In the waves that became apparent in 1922, for example, the youngest growth showing cankers was that of 1920; in the waves of 1923, it was the growth of 1921; in the 1924 waves, it was the growth of 1922, etc.

Since there may be some doubt as to these conclusions, however, the analysis of the 1922 waves may be carried somewhat further. It may be assumed that infection occurred in 1921. Since none of the cankers were present on 1921 growth, it would follow either that the needles of 1921 were immune to infection or that a longer time was required for incubation in the needles and bark of 1921 than in the needles and bark of older growths, and that the infection on 1921 growth had not yet become apparent. Since relatively few of the cankers occurred on 1920 growth, it would be necessary to assume either that the needles of 1920 were resistant to infection in 1921 or that incubation was slower for this growth than for older growths. In accordance with the regular habit of needle retention in *Pinus monticola* (fig. 1), 1919 growth (*b*), which was in its third season of development in 1921 (fig. 1, B), lost some of its needles at the end of the season in 1921. Most of the needles that remained on 1918 growth (*c*) fell at the same time. Yet the great majority of the cankers occurred on 1919 and 1918 growths. Therefore, for 1918 growth at least, the rust must have grown through the needles and into the bark with extraordinary rapidity. The growth of 1917 (*d*) was practically devoid of needles in 1921. (Fig. 1, B.) Yet the number of cankers on this growth, although small in comparison to the number on 1919 and 1918, growth was actually very considerable. Since most of the few needles remaining on this growth were cast in the fall of 1921, the only possible explanation would be that some of the infection on this growth occurred directly through the bark, which was then 4 seasons old. Certainly this explanation is too improbable to merit further consideration, and it is obvious that to assume that infection occurred in 1922 would require an explanation still more improbable.

If it is assumed that the cankers of the 1922 waves resulted from the combined infection of two or more years, it would be necessary to conclude, since these waves exhibited the typical arrangement of distinct canker-formation waves generally, that this arrangement characterized the distribution of cankers of two or more infection years forming simultaneously and that all the distinct waves arose from similar combinations, for the typical arrangement is too consistently maintained to be accidental. On this basis, for example, if it is assumed that the 1922 waves resulted half from 1919 infection and half from 1920 infection, then the 1923 waves must have originated from equal proportions of infection of 1920 and 1921, the 1924 waves from equal proportions of infection of 1921 and 1922, and the 1929 waves from equal proportions of infection of 1926 and 1927. In other words, the infection years would necessarily bear a regular proportional relationship toward one another, which is obviously beyond probability.

Evidently, then, it is reasonable to accept the typical arrangement as evidence that the majority of the cankers of any one of these waves resulted from infection in a single year and that the youngest growth affected (*a*) marks the infection year; i. e., it is the growth formed the year infection occurred. Thus Table 1, column 4, gives the infection year for each of the waves of which the cankers were counted.

The dates of the infection as determined by the foregoing methods have been further confirmed by observations of weather conditions. In the years shown by the analyses of cankers to have been heavy infection years, conditions have been favorable for heavy pine infection; and when analyses have shown that the infection was light, conditions have been unfavorable for infection.

The method of age determination is thus supported by a complete chain of evidence comprising the following series of phenomena found occurring repeatedly and uniformly throughout a wide range of representative areas over a period of nine years of observations:

(1) Evidence or actual observations of outstanding favorable seasonal conditions for infection of the pines.

(2) Two seasons later a heavy wave of canker formation, sometimes extending into the third season.

(3) Distribution of these cankers in accordance with a characteristic distribution pattern.

(4) Only one acceptable explanation of the canker distribution, namely, that most of the cankers in each wave were the same age; i. e., that they resulted from an infection of the same season.

(5) Date of the infection season fixed by the distribution of the cankers as a favorable season two or three seasons before the appearance of the majority of the cankers.

Since, however, before the appearance of the canker the infection year is indicated only by its outstandingly favorable conditions in sporidia production and moisture, the evidence for the hypothesis herein advanced is primarily circumstantial. It is desirable, therefore, to consider cases where there could be no doubt in regard to the year of infection. The opportunity to do this occurred recently in a case in which the infection year was definitely known before the cankers appeared. In this case two Ribes plants, the only specimens standing in a small isolated area of sound pine, were infected artificially in 1928. Ribes infection was not present in the area in 1927 or in 1929. In the growing season of 1930, 144 incipient cankers appeared only on trees within a short distance of the Ribes and in greatest profusion on those in the immediate vicinity of the Ribes. There can be no doubt that these cankers resulted from the infection on the Ribes plants in 1928. The record of these cankers (Table 1, area No. 12) follows closely the general trend and average of the other records.

It has been stated earlier in this paper that cankers are rarely found on trees in the first season after the year of infection. This is the case with most trees. On trees more than 3 feet high and 8 years old the writer in nine seasons of observations has never seen an incipient canker on growth younger than that formed two years before the year of examination. On the youngest seedlings and on those up to about 5 years old, however, the writer has positive proof that a great many if not most of the cankers appear in the season following that of infection. In determining the heavy infection years, therefore, cankers on such seedlings must not be included with the records of infection on the older trees, which generally constitute most of the growth in any natural infection area and therefore have the great majority of the cankers.

Variation in needle retention is another factor that must be taken into account in investigations of the history of infection in any pine area. The normal period of needle retention described earlier in this paper does not apply absolutely, for in areas where growth is relatively slow, usually at higher elevations, the needles are commonly held for a somewhat longer period than is normal; and where growth is particularly rapid they are actually held for a somewhat shorter period than is normal. This is especially noticeable on the faster growing parts such as the leaders and upper branches of thrifty trees, where the needles are commonly shed a full year earlier than is normal.

Since infection occurs through the needles, it is clear that the distribution of the cankers on growths of different years will be influenced by differences in needle retention. It may be assumed, for example, that areas 8, 9, 12, and 13, in Table 1, represent conditions of high altitude and slow growth and that areas 1 and 5 represent conditions of lower altitude and particularly rapid growth. Table 2 shows the two scales of arrangement for the two types of conditions separately. The arrangement for the grand total of Table 1 may for all practical purposes be considered normal; the data are given as approximate percentages for comparison in Table 2.

TABLE 2.—*Percentage of cankers found on growths of different years under conditions of low altitude and rapid growth and of high altitude and slow growth*

Growth affected	Percentage of cankers under indicated conditions			Growth [a] affected	Percentage of cankers under indicated conditions		
	Low altitude (rapid growth)	High altitude (slow growth)	Normal		Low altitude (rapid growth)	High altitude (slow growth)	Normal
a [a]	10+	7+	10−	*f*	0	0	Trace.
b	60	49+	53+	*g*	0	0	0
c	26−	34−	31+	*h*	0	0	0
d	3+	9+	5+	*i*	0	0	0
e	0.5	1−	0.5−				

[a] Growth of season of infection; i. e., youngest growth showing cankers of the wave.

As might be expected, the high-altitude group shows a greater spread of the infection to older growths, *c* and older growths having more than the normal amounts and *a* and *b* growths less; whereas the low-altitude scale shows more infection than normal on *b* growth and less than normal on *c* and older growths. As a rule, the differences are small, and the same general relationships prevail in all the scales.

TECHNIC FOR DETERMINING AGE OF CANKERS

The application of the foregoing scales of arrangement is simple. On encountering a new infection area the investigator first determines the general span of needle retention in order to decide what scale to apply in determining the infection years. The normal scale or even the typical distribution as expressed in descriptive terms alone (p. 679) will usually suffice for general application. Records should then be made of the cankers classified according to stage of development. The following classification has been found most useful:

Young cankers:
- *First symptoms.*—First signs of infection on the bark; incipient cankers indicated by discoloration less than one-half inch in length on the smaller, slower-growing twigs and branches and up to about three-quarters inch in length on the larger branches and leaders, usually showing little or no swelling.
- *Juvenile.*—Small infections that have developed beyond the stage of first symptoms but have not yet produced pycnia.
- *First pycnia.*—Infections that at the time of the count or earlier in the same season were bearing pycnia for the first time.
- *Pycnial scars.*—Infections that had borne pycnia for the first time the preceding year but failed to produce aecia in the spring of the year in which the count was made.
- *First aecia.*—Infections that bore aecia for the first time in the spring of the year in which the count was made.

Old cankers:
- *Aecia produced twice.*—Cankers that bore aecia for the second season in the spring of the year in which count was made.
- *Aecia produced several times.*—Cankers that had borne aecia for several seasons.
- *Dead.*—Old cankers in which death prevented further development.

From first to last, these headings represent normal progressive steps, following incubation, in the development of the individual infection.

In order to apply this scheme of classification it is necessary to consider two facts: (1) That cankers grow longitudinally at an average rate of approximately 2.5 to 3 inches per year on twigs and branches less than one-quarter inch in diameter, and (2) that this rate increases up to an average of about 7 or 8 inches a year on parts 3 inches or more in diameter. It is also necessary to be familiar with the normal development of fruiting stages described on page 677. Where fruiting has obviously been retarded, the plan of classification may be enlarged to include such cankers.

In Table 3 an illustration is given of the application of the distribution pattern to the analysis of the history of the rust in a typical infection area near sea level. Table 3 gives a count taken indiscriminately on April 27, 1924, from the cankers found on thrifty trees ranging from approximately 10 to 30 years of age. The count included only cankers for which it was possible to determine definitely the age of the growth on which the canker started and the stage of development of the canker.

TABLE 3.—*Canker tabulation, Chee Kye, British Columbia, April 27, 1924*

Growth affected	Number of cankers at indicated stage of development							
	Young					Old		
						Aecia produced		
	First symptoms	Juvenile	First pycnia	Pycnial scars	First aecia	Twice	Several times	Dead
1	2	3	4	5	6	7	8	9
1924	0	0	0	0	0	0	0	0
1923	0	0	0	0	0	0	0	0
1922	0	0	0	0	0	0	0	0
1921	12	9	0	4	19	0	0	0
1920	19	21	0	23	162	3	0	0
1919	2	10	0	16	126	20	0	0
1918	0	0	0	0	27	14	2	0
1917	0	0	0	0	0	3	2	0
1916	0	0	0	0	0	0	0	0
1915	0	0	0	0	0	0	2	0
1914 and older	0	0	0	0	0	0	0	0

The count did not include cankers of the first year of infection on pines in this area. Special search for older cankers showed, on growth ranging from that of 1910 to that of 1913, a few very old cankers. The arrangement of these old cankers and the fact that weather records indicate 1913 to have been an outstandingly favorable year for infection of both Ribes and pine, showed that the cankers probably resulted from infection in 1913. The analysis of the older cankers, not included in Table 3, showed considerable intensification in 1917 and 1918, particularly in the latter year. A comparison of the normal distribution pattern with the tabulation in Table 3 shows that much intensification occurred in 1920 and a very large amount in 1921. From the distribution relationships of the cankers listed in columns 2 and 6 of Table 3 it is evident that the great majority are of 1921 origin. The proportion of these cankers to older cankers, in view of the fact that the number recorded represents but an infinitesimal fraction of the number present, indicates that a great wave of intensification occurred in 1921. Practically all the cankers in column 7, from their arrangement, are clearly of 1920 origin.

Table 4 gives a tabulation for the same area from November 15 to 16, 1924, the year in the spring of which the tabulation in Table 3 was made. The same rules applied in making the tabulation given in Table 3 were observed in making the tabulation given in Table 4.

TABLE 4.—*Canker tabulation, Chee Kye, British Columbia, November 15 to 16, 1924*

Growth affected	Number of cankers at indicated stage of development							
	Young					Old		
	First symptoms	Juvenile	First pycnia	Pycnial scars	First aecia	Aecia produced: Twice	Aecia produced: Several times	Dead
1	2	3	4	5	6	7	8	9
1924	0	0	0	0	0	0	0	0
1923	0	0	0	0	0	0	0	0
1922	6	1	3	0	0	0	0	0
1921	22	8	21	0	29	0	0	0
1920	4	5	24	22	137	8	0	0
1919	0	0	2	14	83	19	0	0
1918	0	0	0	1	16	7	3	2
1917	0	0	0	0	0	0	13	0
1916	0	0	0	0	0	0	6	0
1915	0	0	0	0	0	0	1	0
1914	0	0	0	0	0	0	1	0
1913 and older	0	0	0	0	0	0	0	0

A comparison with the normal distribution pattern shows clearly that considerable additional intensification of infection on pines occurred in 1922. The cankers in columns 2 to 4 of Table 4 are mainly of 1922 origin. Their number is small in proportion to the number of 1921 cankers (columns 5 and 6), but they seem to exceed the number in 1920 (column 7). It must be remembered, however, that as the cankers grow older they are increasingly difficult to classify exactly according to stage of development and year of origin. Therefore, since doubtful cases are not included in the counts, some allowance must be made to balance this difference. Observations indicated that cankers of the 1920 wave were slightly more abundant than those of the 1922 wave. In view of the fact that aecial sporulation and the opportunities for the infection of Ribes were much better in 1922 than in 1920, owing to the development of sporulating cankers between these years, it was evident from the count, together with the observations, that 1920 was a considerably more favorable year than 1922 for infection in this area.

As already indicated, canker formation in *Pinus monticola* takes place chiefly in the second year after the year of infection and to some extent in the third year. The cankers generally begin to form in the spring of the second year and are produced in the greatest numbers during the summer and fall of that year. In the winter, growth practically ceases in the rust as well as in the host. Consequently, if all the cankers have not made their appearance in the second year, the remainder do not ordinarily develop until after active growth is resumed the following spring.

Normally the proportion of cankers produced in the third year is small and the period of formation is confined to the first months of spring. Frequently, however, a considerable number, sometimes many, are produced, and the period of formation continues until well into the summer.

Where successive infection years occur, the third-year production of cankers frequently results in an overlapping in the formation of the cankers of one infection year with that of the next and the intermixture of incipient cankers of two infection years. Since the proportion of cankers produced in the third year is usually small and production is generally limited to spring, the overlapping and intermixture are correspondingly slight and limited to spring; but when third-year production is considerable and prolonged the overlapping and intermixture may be extensive.

Besides occurring at incipiency, intermixture of cankers normally takes place during the later stages because of variation in rate of development and production of fruiting stages and the consequent impossibility of classifying the cankers according to the year of origin after they have passed the early stages. Thus, cankers formed in the fall of one year do not produce pycnia until the following summer. Meantime cankers resulting from the next infection year are formed in the spring and produce pycnia at the same time as do the cankers formed the preceding fall. The result is an intermixture of the cankers of the two consecutive infection years in the "First pycnia" column. If the count is taken shortly before the formation of pycnia, there will be an intermixture of the two sets under the "Juvenile" classification.

The frequency of intermixture increases with increasing age. For example, not all the cankers that produce first pycnia one year produce aecia the following spring; some cankers normally produce their first aecia the second spring after the production of pycnia. Where successive infection years occur this will result in considerable intermixture under the classification "First aecia." The extent and complexity of intermixture will obviously be still greater among the older cankers.

This intermixture, whether it occurs at incipience or later, tends to obscure the actual distribution relationships of the cankers. Fortunately, the infection years in the earlier stages of the epidemic are generally separated by periods of one to several years during which little or no infection occurs; if later they become successive they usually are highly unequal, so that the years of heavy infection stand out. But even if intermixture is extensive the infection years may be differentiated by use of the typical distribution relationships.

The application of the relationships in these cases may be best illustrated by a hypothetical example. Assuming that 100 cankers of each of two successive infection years, 1922 and 1923, represent a single stage of development and that in both cases the distribution of the cankers is identical with the normal scale, it follows that the distribution of each set and of the sums of the two sets, the latter constituting the numbers recorded, would be approximately as given in Table 5.

TABLE 5.—*Hypothetical distribution of cankers in a case of intermixture of 100 cankers from each of two infection years*

Growth affected	Number of cankers		
	From 1923 infection	From 1922 infection	Total
1923	10	0	10
1922	53	10	63
1921	31	53	84
1920	5	31	36
1919	1	5	6
1918	0	1	1
1917	0	0	0
Total	100	100	200

Application of the scale to the combined totals in this case would permit an almost exact segregation of the two sets. Obviously such an equal combination and exact agreement of the individual components with any distribution scale is not to be expected in nature. But as already shown, there is consistently a sufficiently close adherence to the general relationships of the typical distribution pattern to permit analysis where intermixture occurs.

The detailed data collected by the Division of Blister Rust Control on the Long Meadow Creek and Three Bear Creek infection area, Idaho, in July, 1930, represent an extensive admixture caused by overlapping of canker formation and by variation in development, and illustrate a practical application of the distribution pattern to actual conditions. In this case the overlapping of canker formation and consequent intermixture in the cankers of the younger stages were extreme. (Table 6.) The area may be classified as normal in general conditions. But since most of the trees were of considerable height and the majority of the cankers were situated on the slow-growing branches of the lower crowns, which formed the major portion of the substratum for infection in close proximity to the Ribes, the scale of arrangement for slow-growing conditions was used in the analysis of the data.

TABLE 6.—*Canker tabulation, Long Meadow Creek and Three Bear Creek infection area, Idaho, July, 1930*

Growth affected	Number of cankers at indicated stage of development							
	Young					Old		
	First symptoms	Juvenile	First pycnia	Pycnial scars	First aecia	Aecia produced: Twice	Aecia produced: Several times	Dead
1	2	3	4	5	6	7	8	9
1930	0	0	0	0	0	0	0	0
1929	0	0	0	0	0	0	0	0
1928	60	127	2	4	1	0	0	1
1927	111	750	35	61	65	0	0	3
1926	125	1,328	123	232	248	2	2	2
1925	39	578	73	146	304	6	7	2
1924	4	88	16	54	101	24	10	7
1923	0	12	1	10	11	4	7	3
1922	0	1	0	1	0	0	4	4
1921	0	0	0	0	0	0	0	1
1920 and older	0	0	0	0	0	0	0	0

A detailed analysis of the data in Table 6 gives the following results: The distribution of the cankers in column 2 indicates that they are primarily of 1928 origin, although the inclusion of a certain proportion originating from 1927 infection is suggested by the relatively large representation on 1926 growth. Column 3 contains the majority of all the cankers counted. A superficial examination of the figures indicates that many of the cankers originated from infection in 1928 but that the greatest number originated from infection in 1927. This may be seen by comparing the great numbers of cankers on 1926 and 1925 growths with the typical distribution pattern as expressed in descriptive terms alone (p. 677). A more critical analysis may be made by trial and comparison of assumed values on the basis of the relationships shown in the scale. In column 3 the 127 cankers on 1928 growth are obviously of 1928 origin. Assuming the occurrence of cankers of this year on older growths in this column to be approximately 610 on 1927 growth, 500 on 1926 growth, 100 on 1925 growth, and 10 on 1924 growth, a total of 1,347 cankers is obtained, leaving a remainder of 1,537 distributed as follows: 140 on 1927 growth, 828 on 1926 growth, 478 on 1925 growth, 78 on 1924 growth, 12 on 1923 growth, and 1 on 1922 growth. In terms of percentage the distribution for the 1928 group becomes: *a*, 9; *b*, 45; *c*, 37; *d*, 8; *e*, 1; and for the 1927 group: *a*, 9; *b*, 54; *c*, 31; *d*, 5; and *e*, 1. The figures show that about 82 per cent of the cankers in the 1928 group and 85 per cent of the cankers in the 1927 group occurred on *b* and *c* growths, which compares well with the normal pattern and at the same time balances the variations from the values of the high-altitude scale as closely as is necessary for practical purposes. The conclusion is the same as that derived from the superficial analysis; i. e., that many of the cankers originated from infection in 1928 but that the greater number originated from infection in 1927.

In column 4 of Table 6 it is evident that the great majority of the cankers originated in 1927, although a few of 1928 origin are included also. Since 2 of the cankers occur on 1928 growth, this column, in accordance with the high-altitude scale of arrangement, should contain about 14 cankers of 1928 origin on 1927 growth, 10 on 1926 growth, and 2 on 1925 growth. This makes a total of about 28 cankers of 1928 origin, leaving a balance of 222 distributed as follows: 9+ per cent on 1927 growth, 51+ per cent on 1926 growth, 32+ per cent on 1925 growth, 7+ per cent on 1924 growth, and less than 1 per cent on 1923 growth. A comparison of the high-altitude scale with the distribution pattern of these cankers shows an almost exact agreement of the figures with the scale and definitely determines 1927 as the infection year for the group.

In column 5 of Table 6 is found a class of cankers that made their appearance and produced pycnia in the year preceding that of the tabulation but failed to produce aecia in the tabulation year, 1930. It will be noted that four cankers in this column were found on 1928 growth. These cankers, therefore, originated from 1928 infection and made their appearance in the following season, 1929. Since this is extremely unusual, except on young seedlings up to about 5 years old, it is presumed that these cankers were recorded from such seedlings, of which undoubtedly there was a certain representation on the area. The distribution of cankers resulting from a given year's infection on such young trees differs somewhat from the normal distribution on older trees and averages about 15 per cent on *a* growth, 69 per cent on *b*, 14 per cent on *c*, and 2 per cent on *d*. According to this relationship, since 4 of the cankers occur on 1928 growth column 5 should contain about 18 such cankers on 1927 growth and 4 on 1926 growth, making a total of about 26 cankers that may be considered to have originated from infection of 1928. There remain 482 cankers, distributed as follows: 9 per cent on 1927 growth, 47+ per cent on 1926 growth, 30+ per cent on 1925 growth, 11+ per cent on 1924 growth, 2+ per cent on 1923 growth, and less than 1 per cent on 1922 growth. Comparison of the arrangement of these cankers with the high-altitude scale shows that the infection year was 1927.

The majority of the cankers in column 6 of Table 6 are of 1927 origin, although a few are of 1928 origin, and there is evidently a very considerable proportion of 1926 origin on 1926 and older growths in this column. This is clear not only from the arrangement of the cankers but from the fact that in general the production of aecia occurs only in part of the cankers in the year following that of their appearance, aecial production on most of the remainder occurring in the following year.

The distribution of the cankers in column 7 of Table 6 indicates infection in both 1926 and 1925. The number of 1926 cankers in column 7 is only a fraction of the number in column 6. Evidently, then, most of the cankers that originated from 1926 infection either failed to produce aecia in 1929, following the production of first pycnia in 1928, or did not reach the stage of pycnial production until 1929, or both, and did not arrive at the stage of aeciospore production until the spring of 1930.

The distribution of the cankers in column 8 of Table 6 indicates infection in both 1926 and 1925. If the 1926 cankers in column 8 had actually produced aecia more than twice it would appear that they must have formed and produced pycnia at least by 1927, the year following infection. As already stated, this is a rare occurrence except on very young trees. Since the proportion of such cankers in this case appears to be rather large and since at the time of year the count was made cankers that have produced aecia only twice may easily appear to have produced aecia more than twice, it is more probable that part of the 1926 cankers in column 8 had actually produced aecia only twice and should have been included in column 7.

The prevalence of cankers on 1924 growth, as shown in columns 7 and 8 of Table 6, indicates that the larger proportion originated from infection in 1925. The number of 1926 cankers recorded in column 6, however, is greater than the total of all cankers in columns 7 and 8 and, together with the 1926 cankers in these two columns, indicates a decidedly heavier infection in 1926 than in 1925.

From a recapitulation of the foregoing analyses and from a broader consideration of the data in Table 6, two years—1927 and 1928—stand out as years of very heavy infection, 1927 showing much the heavier infection. In considering the degree of infection indicated by the record for the year 1928, however, it should be remembered that part of the cankers do not become apparent until the third year after the infection year. The tabulation was made in 1930. The incidence of cankers of 1927 origin in the youngest classes in stage of development indicates that in the Long Meadow and Three Bear

Creek area there is a considerable lag in incubation and that relatively large proportions of the cankers may not make their appearance there until the third year after the infection year. On this basis, a considerable proportion of the cankers of 1928 origin might not appear until 1931. Therefore, since the record was made in 1930, the indications of the degree of infection in 1928 must necessarily be considered incomplete.

In addition to the infection of 1927 and 1928, the analysis shows a certain amount of infection in 1925 and 1926, the greater amount in 1926.

The earlier infection history of the area had to be studied by means of special counts of the oldest cankers that could be found. The arrangement of these cankers and their situation on the area indicated that an appreciable amount of infection occurred in several local foci in 1923. No cankers were found that could be assigned to any earlier infection year. The infection in 1923 and that in 1925, when the 1923 cankers were just making their appearance but had not yet produced aecia, was considerably heavier and more profusely distributed than is normal through infection of Ribes by the long-distance spread of aeciospores from the outside. The usual ratio of Ribes infection to that on pines indicated that at least one or two sporulating cankers were present in the near vicinity at the time. It seems probable, therefore, that the original invasion of the locality by the rust must have occurred some years earlier than 1923.

From the data secured by these special counts and from the analysis of the tabulation in Table 6 the infection history for this locality may be summarized as follows:

(1) Original invasion probably a few years before 1923.

(2) 1923.—Very few aeciospores; favorable infection season; infection of pines at several points in the area.

(3) 1924.—Very few aeciospores; unfavorable infection season; negligible intensification on pines.

(4) 1925.—Very few aeciospores; favorable infection season; appreciable intensification of infection on pines.

(5) 1926.—Great increase of aeciospores resulting from sporulation of the cankers of the infection of 1923; unfavorable infection season; considerable intensification on pines.[9]

(6) 1927.—Great majority of 1923 cankers produced aeciospores; aeciospore production probably doubled or trebled that in 1926; very favorable infection season; great intensification on pines.

(7) 1928.—Another large increase of aeciospore production as a result of beginning of sporulation on cankers of 1925 origin; favorable infection season; further heavy intensification on pines.

From the foregoing analysis it is evident that the application of the relationship of arrangement is essential to any determination of infection years where cankers of successive infection years are mixed. Pennington [10] has stated that—

when a large number of cankers of approximately the same stages of development are found distributed through the internodes of three or four successive years, it is practically certain that infection resulted from exposure in the last of these years.

[9] As a result of the beginning of sporulation of the cankers of 1923 origin the number of aeciospores produced on the area must have been increased many hundredfold over that in 1925. Although the intensification of infection of pines in 1926 was about five or six times greater than that of 1925, the fact that it was much less than might have been expected from the increase of aeciospores and the opportunities for infection of Ribes on the area indicates that infection conditions in 1926 were unfavorable.

[10] PENNINGTON, L. H. Op. cit., p. 596.

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The application of the method of determining the age of the cankers, as reported in this paper, to similar distributions shows that in general this is true; but one would be at a loss on this basis to determine the infection years when, as is commonly the case, the distribution normally covers internodes of five years or when the cankers of two infection years are mixed. Even when the cankers found are confined to growths of only four years, such mixtures may occur, as is indicated from the analysis of column 7 of Table 6. A comparison with the distribution pattern is therefore necessary for accurate diagnosis in any case. Where the infection years are as badly mixed as those in Table 6, such a comparison constitutes the only means of differentiation. With its aid it is possible, even in such cases, to obtain a good picture of the heavy infection years and of the history of the progress of the rust on pines.

SUMMARY

Pinus monticola, in its natural range in the Pacific Northwest, generally casts most of the needles of any one year at the end of the fourth season, although some are held five seasons and a few may persist for as long as eight seasons. Since *Cronartium ribicola* infects its aecial hosts through the needles, infection in any season may conceivably find entrance to the bark on internodes up to 8 seasons of age but will necessarily enter chiefly on those of the last four seasons.

Conditions favorable for heavy pine infection in the Pacific Northwest are generally limited to a short period in any season and occur, on an average, about one season out of three. Heavy infection of pines in any year and locality usually becomes manifest in a more or less distinct wave of incipient canker formation in the second season following the season of infection. The cankers of any year of infection show a highly characteristic numerical relationship in their proportional distribution on the growths, or internodes, of different years. The characteristic relationship may be summarized as follows:

Growth affected	Number of cankers
a. Growth of the season of infection	Relatively few.
b. Growth 1 year older than *a*	Greatest number } large majority.
c. Growth 2 years older than *a*	Considerable number } large majority.
d. Growth 3 years older than *a*	Relatively few.
e. Growth 4 years older than *a*	Very few.
f. Growth 5 years older than *a*	Exceptional.
g. Growth 6 years older than *a*	None.
h. Growth 7 years older than *a*	None.

Thirty-two sample counts, totaling 5,879 cankers from distinct infection waves of five different years in 14 different places, showed the following scale of distribution for the total:

Growth	Percentage of cankers
a	10−
b	53+
c	31+
d	5+
e	0.5−
f	Trace.
g	0
h	0

In the individual counts, *b* and *c* together had consistently 80 to 90 per cent of the cankers, with much the largest percentage (usually more than 50 per cent) on *b*. The percentages on *a* and *d* were relatively small, *a* generally having the larger. The percentages on older growth were almost negligible.

A comparison of the typical distribution pattern with comprehensive sample records of cankers classified according to stage of development and year's growth affected will generally permit an accurate determination of the main infection years and provide a reliable guide to the progress of the rust on pines in any infection area.

Although incipient canker formation from a given year's infection is normally concentrated in the second season after that of infection, it may carry over extensively into the third season. This frequently results in an overlapping in the formation of the cankers and the consequent intermixture of cankers of two successive infection years under one classification in stage of development. Since the rate of development of the individual cankers varies, this intermixture of cankers becomes more common as development advances. The application of the distribution pattern is therefore essential for the accurate determination of infection years.