Epidemiology of Stripe Rust of Wheat, 1961-1968

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Gregory Shaner and R. L. Powelson

ABSTRACT

Epidemics of stripe rust occurred in Oregon during 1960, 1961, and 1964 and continue to be a threat to wheat production. The primary source of inoculum for epidemic development in the spring came from early-sown wheat that had become infected the previous fall. Spread of rust during the winter was slow and occurred mostly by plant-to-plant contact. Only a small amount of overwintering inoculum was required to start an epidemic. From April through June stripe rust increased at apparent infection rates of 0.1 to 0.25 per unit per day. Disease development at these rates would require only one infected leaf per acre in mid-February for an epidemic to develop, given favorable weather.

The minimum period of foliage wetness for infection to occur was three hours and the optimum was eight hours. Mean daily temperatures of 6 to 22° C were favorable for infection.

Key words: **Stripe rust *(Puccinia striiformis)*, wheat, epidemiology, Oregon, oversummering, overwintering, moisture, temperature, mathematical models.**

INTRODUCTION

Stripe rust, caused by *Puccinia striiformis* West., has become a serious disease of wheat in Oregon. The epidemic of 1961 cost wheat growers 15 million dollars. During the two decades prior to 1960 stripe rust was of little significance and drew no attention from pathologists. Earlier studies were inspired not by the seriousness of the disease but because the rust had only recently been discovered in the United States and its importance was undetermined (*4, 5*).[1] Since these initial studies new varieties and changes in cultural practices have evidently affected the epidemiology of stripe rust, so new studies were undertaken in 1964.

Most of the wheat in Oregon is grown along the northern edge of the state from Wasco County in the west to Wallowa County in the east (Figure 1). Wasco, Sherman, Gilliam, Morrow, and Umatilla counties comprise the Columbia Basin of Oregon. One-third of Oregon's cultivated cropland is in this area, most of which is devoted to wheat (*9*). The area is bordered on the west by the Cascades and on the east by the Blue Mountains. The wheat land slopes upward to the

[1] Numbers in parentheses refer to Literature Cited, page 31.

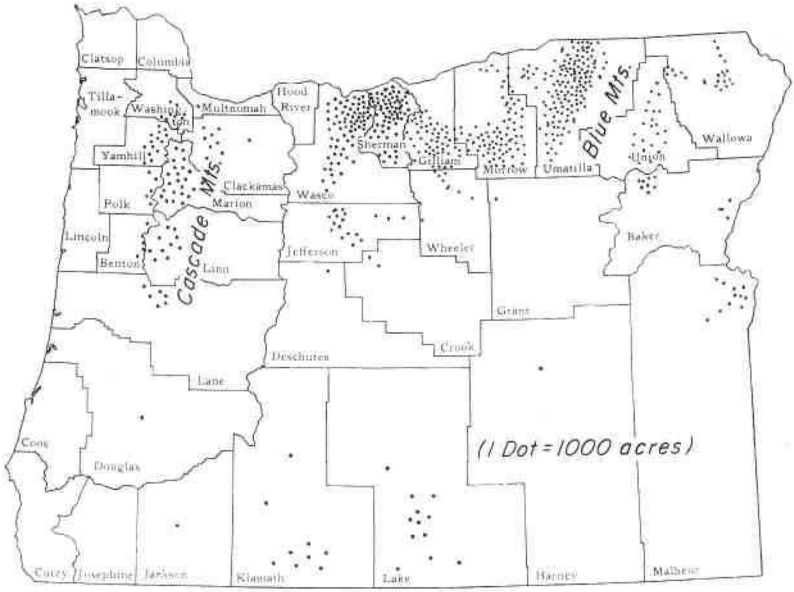

Figure 1. Wheat-growing areas of Oregon.

south and finally gives way to forest. Except for a part of Umatilla County, the Columbia Basin is bordered on the north by the Columbia River. The wheat land is an area of rolling hills with many shallow valleys. Wheat is grown mostly on plateaus at elevations of 1,500 to 2,000 feet.

Precipitation in the Columbia Basin is 10 to 20 inches annually, mostly between November and March. The summers are dry. Winds in the Columbia Basin are usually southwesterly during the day and easterly at night.

Wheat in Union County is grown in the Grande Ronde Valley, which lies between the Blue Mountains and the Wallowa Mountains. The mean annual precipitation in the Grande Ronde Valley is 21 inches.

Wheat is grown in Wallowa County on the low hills north of the Wallowa River. This area is at a higher elevation than the Columbia Basin and the Grande Ronde Valley. The mean annual precipitation is 14 inches. Wheat matures later in this valley than in Union County and in the Columbia Basin.

Because of the low annual rainfall in most of the Columbia Basin, wheat is grown on a summer-fallow rotation program. Land is not summer-fallowed in eastern Umatilla County, but wheat is commonly rotated with peas. Fields are cropped annually in the Grande Ronde Valley. Wheat is often fallow-rotated in Wallowa County.

Where summer fallowing is practiced, the stubble is left standing until the following spring for wind and water erosion control. Wheat is sown from late August through November, depending on soil moisture conditions. Because of the dry summers, volunteer wheat does not emerge any earlier than fall-sown wheat. The only green wheat remaining after harvest of the crop is an occasional plant which failed to head with the rest of the crop.

Wheat is also grown in the Willamette Valley, situated between the Coast Range and the Cascades. Average annual rainfall is about 38 inches. The summers are dry. Wheat fields in the Willamette Valley are scattered and are smaller than the ones in the Columbia Basin. In both western and eastern Oregon nearly all the wheat grown is the soft white winter type.

MATERIALS AND METHODS

Field Surveys

During the four years of this study, wheat fields and adjacent areas in the Columbia Basin were surveyed frequently, noting rust severity and reaction type. Severity was recorded using the International Scale (*13*), which is given for reference in Table 1. The severity rating is referred to as the degree of attack (DA); when translated into the corresponding percentage of leaf surface attacked, this is called percentage of attack (PA). During 1964, county extension agents made regular rust severity readings of selected fields. Development of stripe rust on wheat in the Willamette Valley was observed at the Hyslop Agronomy Farm near Corvallis.

Table 1. INTERNATIONAL SCALE OF STRIPE RUST SEVERITY*

Degree of attack (DA)	Severity
0	No symptoms observed
1	One lesion to 10 meters drill length (0.001%)
2	One lesion to 1 meter drill length (0.01%)
3	One lesion to 0.1 meter drill length (0.1%)
4	At least one lesion to the tiller, but not more than 1% of leaf surface infected (1%)
5	5% of leaf surface infected
6	10% of leaf surface infected
7	25% of leaf surface infected
8	50% of leaf surface infected
9	75% of leaf surface infected
10	100% of leaf surface infected

* From article by J. C. Zadoks, 1961 (*13*).

Dew Treatments

To provide moisture for infection of wheat by *P. striiformis* in greenhouse studies, a dew chamber was constructed using a 32-gallon metal garbage can. The can was placed in a walk-in cold room maintained at 3 C. Water in the bottom of the can was heated to 25 C with a heating cable, resulting in an air temperature within the can of 12 C. Under these conditions a fine layer of moisture formed on wheat leaves within a half hour after being placed on a rack above the water in the can.

RESULTS

Descriptive Epidemiology

Although detailed observations of the 1961 epidemic were not made, monthly field reports of R. L. Powelson, then extension plant pathologist, provided a general outline. When stripe rust was first observed in the Willamette Valley in March, prevalence was low. By April the rust was severe on susceptible winter wheat and was described as "epidemic" in May. The first mention of stripe rust in the Columbia Basin was in the February report. About 75% of the wheat acreage in the Columbia Basin in 1961 was planted with Omar, a susceptible variety. On the basis of the May survey, wheat in the Columbia Basin was divided into three severity classes (Table 2). Warm weather in June compounded losses by desiccating diseased plants.

Table 2. SEVERITY OF STRIPE RUST IN THE COLUMBIA BASIN (1961)

County	Percentage of acres in each severity class		
	Severe*	Moderate†	Light‡
	%	%	%
Wasco	3	47	50
Sherman	3	67	30
Gilliam	2	6	92
Morrow	2	28	70
Umatilla	5	80	15

* Severe: flag leaf rusted.
† Moderate: no rust pustules on flag leaf.
‡ Light: some rusted leaves present.

Again, in 1964, stripe rust caused losses to wheat growers in Oregon. Stripe rust was prevalent in the early spring in the Columbia Basin, but high temperatures and low rainfall suppressed further disease development, particularly in Gilliam and Umatilla counties. Disease continued to increase in Sherman County. A brief period of rain in late May and early June increased the disease severity, but a subsequent dry period retarded further development. Surveys in the

Columbia Basin during the summer of 1964 failed to reveal stripe rust on any of the rare late wheat tillers or grasses which were still green. Rust was present on the later maturing wheat in Wallowa County in late August. Conditions for rust were favorable throughout the growing season in the Willamette Valley, and all leaves of susceptible plants were severely rusted.

The winter of 1964-1965 was particularly severe in northeastern Oregon. By mid-March, when wheat is normally stooling, much of the wheat had not yet tillered. Because of winterkill, growers reseeded many fields. No stripe rust was found in March. Weather was favorable for disease during the spring, on the basis of comparisons with years in which the disease had developed, but rust failed to appear in most areas. Some early rust developed in Union County where wheat was protected by snow cover. By July 9, susceptible wheat in early stages of ripening had a severity of DA 9 at the Eastern Oregon Experiment Station (Union). Stripe rust was found on maturing wheat and late-season tillers throughout northeastern Oregon in mid-July of 1965. A nearly mature field of Omar south of The Dalles (Wasco County) had a DA of 4. Winter in the Willamette Valley was milder, and stripe rust developed rapidly there.

The first reports of stripe rust on wheat of the 1966 crop were from Wasco and Umatilla counties in December 1965. The winter of 1965-1966 was mild. By March, stripe rust could be found in most fields in the Columbia Basin. Initial infection foci were still evident. In several fields where rust was confined to the lowest leaves, the leaves in contact with the moist soil surface bore the pustules. The warm soil surface and higher humidity probably created a more favorable environment for infection and incubation than that to which the upright leaves were exposed. After March, stripe rust development retarded. As the wheat grew, severity decreased in most fields. Only traces of rust were evident in June. However, rust on late tillers was found, especially in Union and Umatilla counties. Late tillers and grasses throughout northeastern Oregon were inspected in late September, and rust was found only on an experimental plot of wheat in the Blue Mountains near Tollgate.

During a survey in the western Columbia Basin on December 30, 1966, stripe rust was found in the wheat cover crop of some orchards south of The Dalles (Wasco County). The cover crop's stage of growth indicated that the cover crop had been planted earlier than the regular wheat crop. Rust was found on upper leaves, and the focal pattern of disease showed that the rust had spread within the cover crop during the fall.

Cover cropping is an old practice in The Dalles orchard area (T. Thompson, personal communication). Rye was used initially, but wheat (variety Golden) has been used since 1958. Golden is an old commercial variety of northeastern Oregon. It was resistant to stripe rust in 1961, but is susceptible to the present races of the disease. Very little Golden is still grown by wheat producers. Prior to 1965, irrigation was available for only a small portion of the total orchard acreage; therefore, the cover for most orchards was sown when the commercial wheat crop was sown—any time from September through November. Since 1965, irrigation water has been available to most of the 5,000 acres of orchards in the area and the cover crop has been sown in August. Thus, only in the last few years have these orchards been an area of extensive, early sown, stripe rust-susceptible wheat.

During the same survey (December 30, 1966) when stripe rust was found in the orchards, stripe rust was also found (DA 2) in an advanced wheat border around a stubble field in western Sherman County. The wheat evidently had been seeded in August or September as an erosion control measure. In wheat fields to the south and east of this border, small rust foci were found. Snow cover prevented examination of fields in the vicinity of the orchards. By the end of January, however, rust could be found in most wheat fields in Wasco and Sherman counties. These observations and those from subsequent surveys are summarized in Table 3.

Table 3. Development of Stripe Rust in the Columbia Basin (1967)

	Jan. 28		March 23		May 3		June 29	
County	Prevalence*	Mean DA	Prevalence	Mean DA	Prevalence	Mean DA	Prevalence	Mean DA
Wasco	3/3	1.0	9/11	2.2	......	......	2/2	4.0
Sherman	11/13	1.2	9/9	3.6	3/3	6.3	5/5	3.5
Gilliam	0/2	0	5/5	1.3	5/5	3.6	2/2	6.5
Morrow	0/3	0	4/4	1.3	7/7	3.9	1/1	1.0
Umatilla	4/12	0.5	13/13	1.8	10/10	5.6	3/3	3.0

* Prevalence is the fraction of fields with stripe rust of those inspected.

Early August was the latest time that active stripe rust was found. It was observed on a few rusted culms in Wasco County, in an irrigated field of spring wheat in Sherman County, and in a maturing field in Wallowa County. Rust was also seen on grasses near the rusted wheat.

Stripe rust was found on December 7, 1967, in orchards where it had not been observed in September and October. By late February stripe rust still could not be found in most of northeastern Oregon, in contrast to the previous year. The disease was spreading within the orchards but was still distinctly focal. Single foci were seen in only two wheat fields, one in Wasco County a few miles south of the orchards and the other in western Sherman County. Each focus involved three plants. By late March foci in the orchards were merging. The cover crop was plowed under in April, but tillers which had not been turned under still bore active rust pustules. The focus in the Wasco County field increased in size during March, but no new foci were seen in that field or in any other during April. The stripe rust epidemics of northeastern Oregon from 1961 through 1968 are summarized in Table 4.

Quantitative Epidemiology

Of the four years of this study, stripe rust was most severe in 1964. In that year, detailed notes were taken on stripe rust development in selected fields in all northeastern Oregon counties but Wasco. Only in Sherman County did the disease reach epidemic proportions; data from there were used for a quantitative examination of stripe rust's ability to spread in the field, using van der Plank's equations (*11*). One field in Gilliam County, where disease did not become severe, was included for comparison.

Van der Plank's basic parameter for describing an epidemic is the apparent infection rate (r). The greater the value of r, the faster the disease increases.

The apparent infection rate (r) was calculated (Table 5) for six fields in Sherman County and one field in Gilliam County in 1964, using the equation:

$$r = 1/t \log_e x/(1\text{-}x) \qquad (1)$$

Time (t) is measured in days; the proportion of disease (x) is the percent of severity divided by 100. The apparent infection rate (r) is the regression coefficient of $\log_e x/(1\text{-}x)$ on t.

The overlapping of confidence intervals for apparent infection rates of the Sherman County fields indicated that disease increased at the same rate in all of them (Table 5). Gaines and Omar were equally susceptible. Field G was the only field examined in Gilliam County in which disease increased. In the other fields, infection just kept pace with the growing host so that severity remained constant; therefore, the amount of infected foliage actually increased with time.

With one exception (field B), stripe rust in Sherman County was at the 0.25% severity level (DA 3) at about day 137 (May 17). By late June (about day 175) maximum severities had been reached.

Van der Plank defines the basic infection rate (R) by the expression:

$$R = r\ x_t/x_{t-p} \qquad (2)$$

The proportion of infected tissue at time (t) is denoted by x_t. The proportion of infectious tissue at time (t) is denoted by x_{t-p} where p is

Table 4. Summary of Northeastern Oregon Stripe Rust Epidemics

	1961	1964	1965	1966	1967	1968
First observed						
Date	Feb.	April 9th-15th*	May 11	Dec. 1965	Dec. 1966	Dec. 1967
Location	Umatilla Co.	Col. Basin	Umatilla Co.	Wasco and Umatilla cos.	Wasco and Sherman cos.	Wasco Co.
Highest DA						
Date	May 15	June 24	July 9	March 22	May 3	July 3
Location	Col. Basin	Sherman Co.	Union Co.	Wasco and Umatilla cos.	Sherman and Umatilla cos.	Union and Wallowa cos.
Last observed						
Date	Unknown	Aug. 26	July 14	July 15	Aug.	
Location		Wallowa Co.	Wasco, Umatilla, Union and Wallowa cos.	Umatilla and Union cos.	Wasco, Sherman and Wallowa cos.	

* Observation not begun until April 9th.

Table 5. Development of Stripe Rust in Seven Fields of Winter Wheat in Northeastern Oregon (1964)

Field and variety	County	Time given severity was reached, days*		Apparent infection rate (r)	95% confidence limits for r		Coefficient of correlation
		DA 3	DA 6				
A. Omar	Sherman	141	170	0.138	0.198	0.078	0.9360
B. Omar	Sherman	119	147	0.146	0.165	0.127	0.9908
E. Omar	Sherman	141	165	0.163	0.197	0.129	0.9644
C. Gaines	Sherman	134	157	0.175	0.236	0.114	0.9317
D. Gaines	Sherman	131	151	0.193	0.227	0.159	0.9816
F. Gaines	Sherman	137	162	0.163	0.242	0.084	0.9215
G. Gaines	Gilliam	181	235	0.074	0.144	0.004	0.7279

* January 1 = day 1. Wheat ripens between days 196 and 211 (July 15 to July 30).

the length of the latent period in days. If the length of the latent period is known, one can determine the value of x_{t-p} by solving Equation (1) for x using the appropriate value of r and $(t\text{-}p)$ in place of t.

To determine latent periods throughout the year, seedlings of Gaines or Omar were inoculated, put in a dew chamber overnight, and then placed in the field near Corvallis. The time required for the first pustules to appear was noted. During the period of greatest disease increase on wheat (March through May), latent periods ranged from 26 to 16 days (Figure 2). The shortest latent period (11 days) occurred in July and September. After the middle of September latent periods lengthened rapidly, reaching 40 days by December.

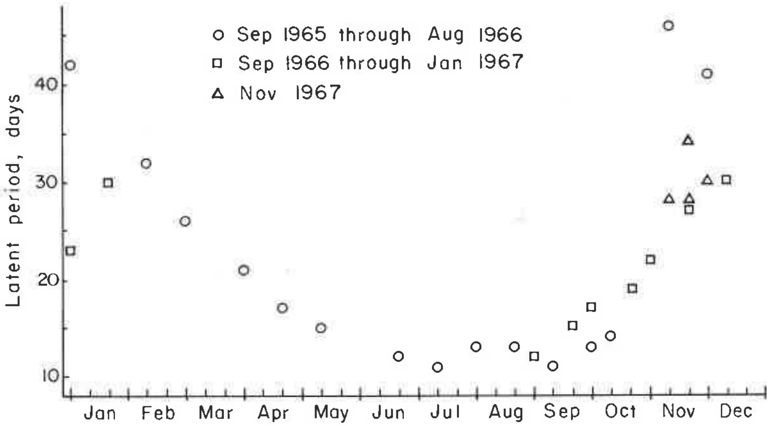

Figure 2. The relation between the latent period and the time of the year.

If r and p remain constant, R will steadily decrease as x increases (*11*). But p is not constant throughout the period of stripe rust development in Oregon. The latent period becomes progressively shorter from January through July. Using field B as an example, because the regression line of logit x on t has the highest coefficient of correlation, the influence of a decreasing latent period on the value of R when r is constant has been determined (Table 6). For comparison, values of R have been computed using a constant latent period of either 12 or 24 days. In an epidemic characterized by a constant apparent infection rate (r), the basic infection rate (R) diminishes more rapidly as the epidemic progresses if p also diminishes with time rather than remaining constant.

Since R accounts for the latent period, it is a more accurate description of the epidemic than is r. When r remains constant while p

Table 6. Effect of a Changing Latent Period on the Value of R at Various Times in the Epidemic When r is Constant*

Time (days)	logit x_t	x_t	p†	R (basic infection rate)		
				p variable	$p = 12$ days	$p = 24$ days
109	–7.516	0.00078	24	5.694	1.138	5.694
129	–4.596	0.010	19	2.317	0.973	4.867
149	–1.676	0.158	15	1.153	0.732	3.845
169	1.244	0.776	13	0.331	0.301	1.205
189	4.164	0.985	12	0.157	0.157	0.218

* r equals 0.146 per unit per day.
† Determined for the date of each time (t) from Figure 2.

decreases, conditions favorable for disease development deteriorate more than they do when r and p are both constant. Although throughout spring and summer the pathogen is able to produce spores in less and less time following infection, other factors (perhaps those controlling penetration or the number of spores resulting from each infection) mitigate against the pathogen.

Development of Stripe Rust in the Willamette Valley

The development of stripe rust was followed in plots of Omar wheat at the Hyslop Agronomy Farm in the Willamette Valley. The disease progress curves for four years appear in Figure 3. At Corvallis the apparent infection rates decreased abruptly during the season. The change in r occurs between logit $x = 0$ (DA 8) and logit $x = -1$ (DA 7). This point was reached earlier at Hyslop than in the northeastern Oregon wheat fields. A change in the apparent infection rate also was detected during an epidemic in a spring wheat planting at another farm near Corvallis (Figure 4). Rust severity rapidly increased until June 16, when logit $x = 1$ (DA 9), but then changed little for the remainder of the epidemic. This decrease in the apparent infection rate occurred two months later than the decrease in the rate in winter wheat at Hyslop in 1967 (Figure 3).

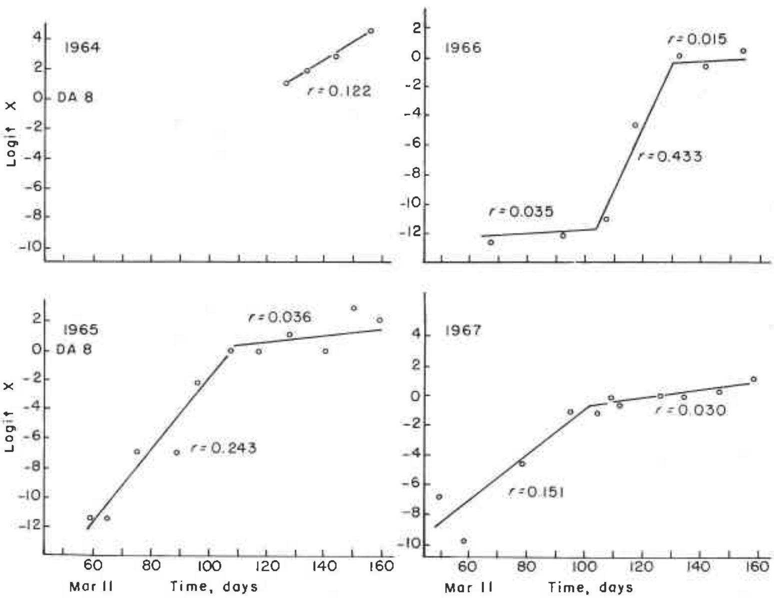

Figure 3. Apparent infection rates (r) of stripe rust of Omar wheat.

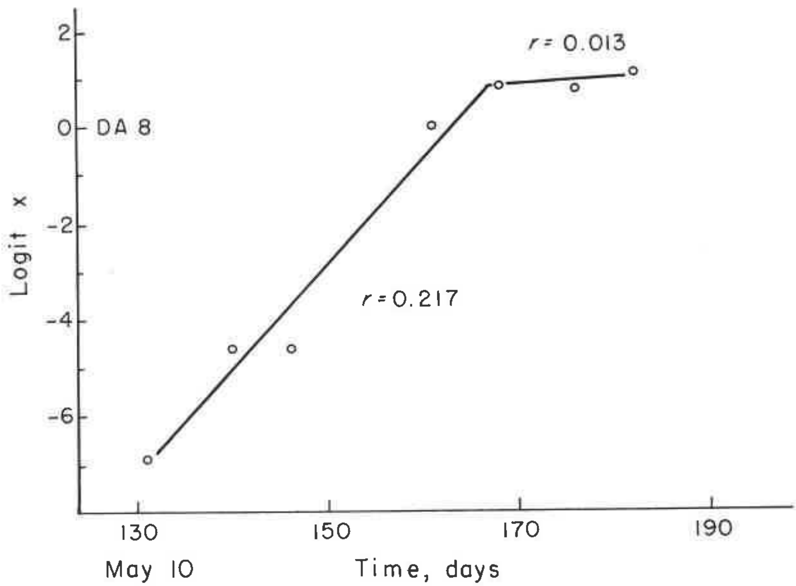

Figure 4. Apparent infection rates (*r*) of stripe rust on Baart spring wheat.

The curves of Figure 3 indicate the length of time that rust is active on wheat in the Willamette Valley. The first points for the years 1965 and 1966 represent the first observations of rust. Rust was seen first on December 31, 1966, in the 1967 crop year. Severity remained near DA 1 until the middle of February when activity of the fungus increased. Evidence for fall infection is difficult to find in the Willamette Valley.

To study overwintering of *P. striiformis* in the Willamette Valley, wheat at Hyslop Farm was inoculated in the fall of 1965 by rubbing rusted seedlings along the rows of wheat. The level of rust remained low throughout the winter (Figure 5). Symptomatic tissue was nearly eradicated by late February, but rust rapidly increased with the advent of warmer weather in March.

Wheat was heavily and uniformly inoculated on September 27, 1966, using an atomized freon suspension of uredospores (*6*). Eleven days later stripe rust infection was evident (flecking). Thirteen days after inoculation the reaction type was 3 but the severity had not changed (Figure 6). If mycelium had not grown within the leaves, this initial level of disease would have remained unchanged until a second latent period had passed. But 21 days after inoculation a large increase in the DA was detected. This could only have been from growth of

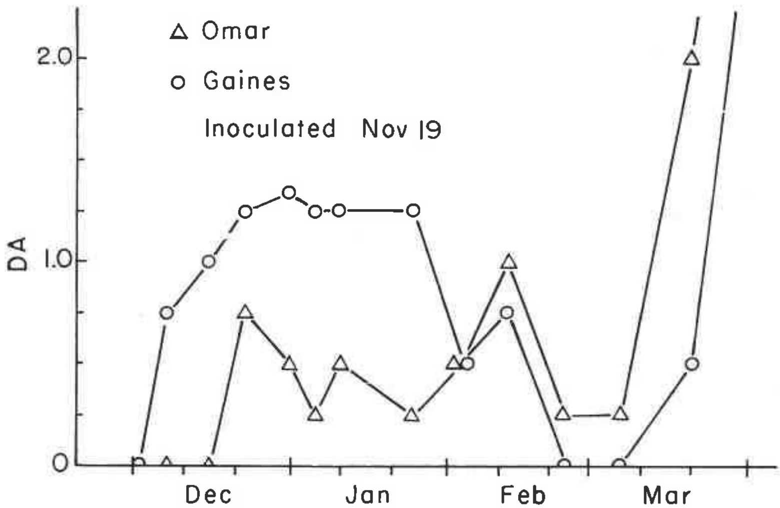

Figure 5. The development of overwintering stripe rust in two varieties of winter wheat, 1965-1966.

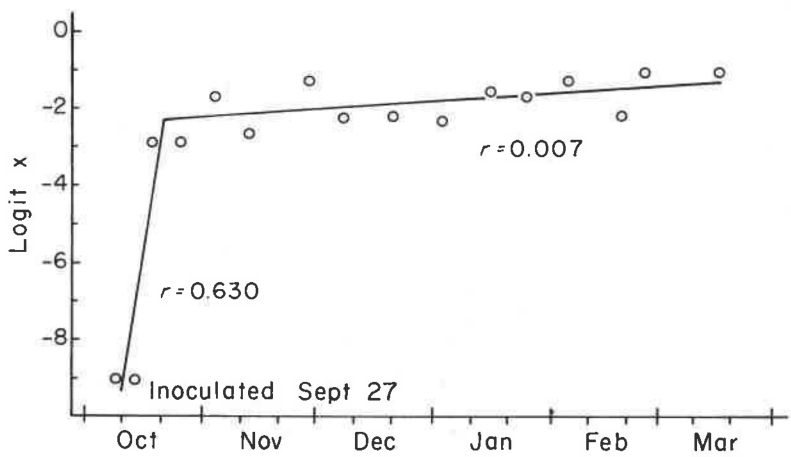

Figure 6. Apparent infection rates (*r*) of overwintering stripe rust on Omar wheat, 1966-1967.

mycelium within the leaves. An outside spore source could be ruled out because a nearby plot of uninoculated wheat remained rust-free. After reaching the level observed at 21 days, the DA increased little for the remainder of the fall and winter. During this time there was some host growth and new infection. But senescence of lower leaves, after they were beaten to the soil by rain, removed infected tissue from the population.

Factors Affecting the Rate of Rust Development

Weather affects the rate of stripe rust development. Experiments were conducted to investigate the influence of weather on particular stages in the infection cycle of the fungus.

The effect of temperature on the latent period. Wheat seedlings (Gaines or Omar) were inoculated periodically throughout the year at a farm near Corvallis. After inoculation they were put in the dew chamber overnight. The following morning half of the plants were placed outside and half were left in the greenhouse as controls. The plants were inspected regularly and the first appearance of pustules was noted. These experiments were conducted for two years, beginning in September 1965.

The variation in the latent period with the time of year is depicted in Figure 2. The relationship between mean daily temperature and the latent period is expressed in Figure 7. There is close agreement between this figure and figures published by other authors relating temperature to latent period *(3, 11, 13)*. This, and the reasonably close fit of the points in Figure 7 to the smooth curve fitted to them, suggests that temperature is the weather factor having the greatest effect on the latent period.

The effect of dew period duration on germination and infection. Moisture on leaves is necessary for infection by *P. striiformis.* Lightly inoculated seedlings were placed in the dew chamber which had been turned on previously to equilibrate. At various times after being put in the dew chamber, some of the plants were returned to the greenhouse. The moisture on the leaves evaporated naturally within a few minutes after the plants were removed from the dew chamber. The prevalence of rust (percent of inoculated plants on which rust developed) was noted for each dew duration treatment. Altogether, 13 such experiments were conducted.

In addition to measuring the prevalence of infection, spore germination was evaluated on agar or leaf surfaces. Slides coated with 1% water agar were inoculated with a freon-spore suspension *(6)* and incubated in the dark in a saturated atmosphere at 15 C. The slides were examined periodically for spore germination.

To measure spore germination on leaf surfaces, a thin film of glue (Testor's Formula B model cement) was spread with a glass rod over the leaves to be sampled. After drying for about a minute, the glue strip was pulled off and placed on a slide over a drop of lactophenol

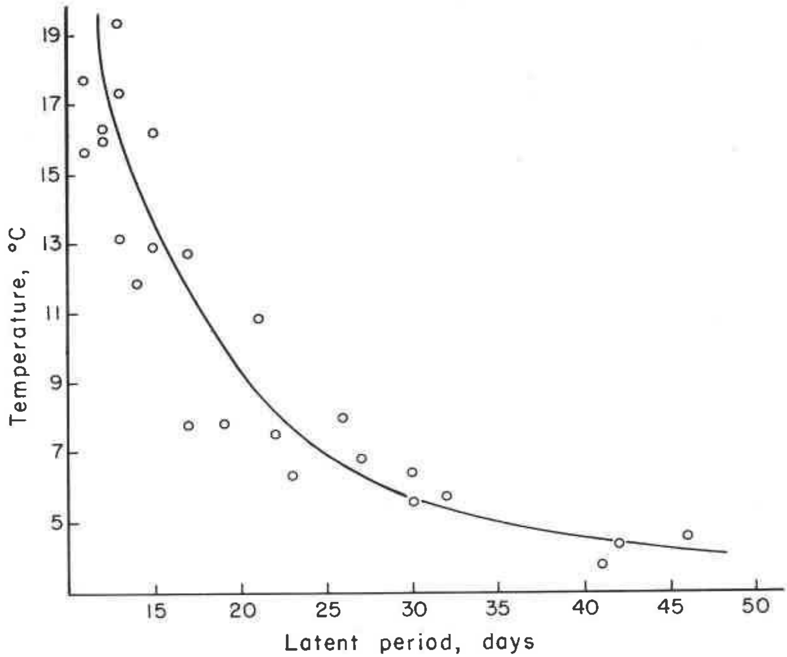

Figure 7. The influence of mean daily temperature on the latent period.

cotton blue. The percentage germination of the spores adhering to the strip was determined.

Germination was detected on agar after one hour of incubation, but the rate was low until after four hours of incubation (Table 7). Most spores germinated between four and eight hours of incubation.

None of the inoculated plants became infected within a dew period of two hours or less. After three to five hours of dew 24 to 46%

Table 7. PERCENTAGE GERMINATION OF *P. striiformis* UREDOSPORES ON AGAR AND WHEAT LEAVES

	Spores examined	Hours of incubation						
		1	2	3	4	5	7	8
	No.	%	%	%	%	%	%	%
Agar	300–900	0.3	0.1	0.4	4.4	12.3		29.8
Wheat (1)..	9–105		33.3	47.2	43.8	42.9		
Wheat (2)..	89–193	8.3	23.0				31.5	
Wheat (3)..	1,200	1.0			3.6		9.6	

infection occurred, but maximum infection (90%) took place only after dew had persisted eight or more hours.

Germination could be detected on plants which had been in the dew chamber for only two hours (Table 7). As with prevalence, the level of germination increased as the duration of dew increased.

Natural infection conditions. The above experiments provided information on the effect of dew duration on infection level when temperature, light, and inoculum were constant. In another group of experiments, plants were exposed in the field where conditions favorable for infection were variable. Dew duration, temperature, and inoculum density during the exposure period were determined.

Wheat seedlings (Baart) grown in 4-inch pots were exposed for 24 hours near a plot of wheat with severe stripe rust at a research farm near Corvallis and then returned to the greenhouse. Nineteen exposures were made, each time with fresh seedlings, from April 20 to June 24, 1967. Only half of the seedlings were inoculated prior to exposure to permit distinction between days when inoculum was limiting and when weather was limiting. The prevalence of rust in each group was recorded. A similar experiment was conducted from October 14, 1967 to January 13, 1968, using Gaines and Omar winter wheats.

The duration of free moisture during the exposure period was measured with a Wallin-Polemus dew recorder (*12*). Temperature and relative humidity were recorded with a hygrothermograph. These instruments were placed on the soil surface near the seedlings. A modified rod-type spore sampler similar to that described by Bromfield and others (*2*) was exposed during the 24-hour period. Cellophane tapes ($\frac{3}{4}$ inch wide) were wrapped around the rod 4 and 9 cm from the base. The rod was then coated with glycerine jelly. After exposure these tapes were peeled from the rod and the total number of rust spores impacted on both tapes (297 mm^2) was determined by microscopic examination.

Of the 19 exposures made during the spring (Table 8), the inoculated group of plants developed rust on 14 occasions. The uninoculated group of plants developed rust on 11 occasions. This suggests that most nights from April to late June of 1967 were favorable for infection. Not only was weather favorable but inoculum was moving.

During the fall and winter of 1967, 16 exposures were made (Table 9). Rust developed on the inoculated plants on 13 occasions. Rust was found on uninoculated plants only three times. Spore-trapping data indicate that the amount of inoculum moving in the air could account for the difference between the results with uninoculated plants in these experiments and those of the preceding spring. In the fall, until December 11. there was no active rust detected in the area of

Table 8. DEVELOPMENT OF RUST ON INOCULATED AND UNINOCULATED WHEAT SEEDLINGS AFTER A 24-HOUR EXPOSURE (Hyslop Farm, spring of 1967)

Date	Spore count	Free moisture period	Prevalence of rust		Mean temperature
			Inoculated	Uninoculated	
		hours	%	%	° *C*
4-20	19	12	50	10	10.9
4-22	92	11	15	2	9.8
4-24	135	10 R*	4	0	12.3
4-27	16	–R†	11	0	7.0
5-1	7	......	92	2	10.6
5-5	......	11	8	2	15.3
5-9	2	13R	6	0	9.3
5-13	5	10	54	4	14.2
5-17	21	5	4	2	18.3
5-20	217	5	0	0	22.9
5-23	81	4	0	0	15.1
5-26	97	4	0	0	13.1
5-29	257	11R	2	4	10.5
6-2	323	7+7R	10	28	13.5
6-6	3,732	0	0	0	15.5
6-9	2,314	8	100	100	12.7
6-14	1,023	9	98	100	19.0
6-19	2,410	0	0	0	20.6
6-24	1,442	7	84	98	20.7

* R indicates the moisture was in the form of rain; otherwise it was in the form of dew.
† –R indicates hours of moisture in form of rain unknown.

Table 9. DEVELOPMENT OF RUST ON INOCULATED AND UNINOCULATED WHEAT SEEDLINGS AFTER A 24-HOUR EXPOSURE (Hyslop Farm, fall of 1967)

Date	Spore count	Free moisture period	Prevalence of rust		Mean temperature
			Inoculated	Uninoculated	
		hours	%	%	° *C*
10-14	0	....	15	0	8.7
10-17	0	18	76	0	7.8
10-24	0	19R*	98	0	6.9
10-26	0	15R	2	0	7.9
10-28	0	19R	90	0	6.2
11- 1	0	6	0	0	5.8
11- 6	0	12R	84	0	8.3
11- 9	67	7R	14	0	9.0
11-17	5	....	94	0	5.6
11-22	0	4	6	0	2.6
11-28	2	–R†	18	2	6.0
12- 7	....	13	10	0	2.5
12-16	0	11R	0	0	0.6
12-19	0	24R	0	0	1.2
12-27	0	14	100	8	7.9
1-13	0	24R	86	12	8.0

* R indicates that moisture was in the form of rain; otherwise it was in the form of dew.
† –R indicates hours of moisture in form of rain unknown.

exposure. From December 11 until the termination of the experiment there were actively sporulating plants within 5 feet of the plants used in the experiment, but spore movement in the air was not detected.

The mean prevalence of rust on all inoculated plants was 28% in the spring and 43% in the fall. So, although weather conditions favorable for infection were more frequent in the spring, when they did occur in the fall, a higher prevalence resulted. In Figure 8 the prevalence of rust on inoculated seedlings is compared with temperature and moisture conditions during the exposure period. For 50% or more of the inoculated plants to become infected, moisture had to persist at least seven hours. These prevalences occurred more often when the moisture was in the form of dew rather than rain, because rain washed the spores from the air and foliage. Good infection resulted when mean daily temperatures were between 6 and 22 C. Beyond these limits the data are insufficient to draw conclusions about temperature and infection. In the case of the one point in Figure 8 where moisture was deemed inadequate and yet some infection occurred (2.5 C), frost had formed on the leaves. The recorder may not have reflected moisture conditions on leaves in these circumstances.

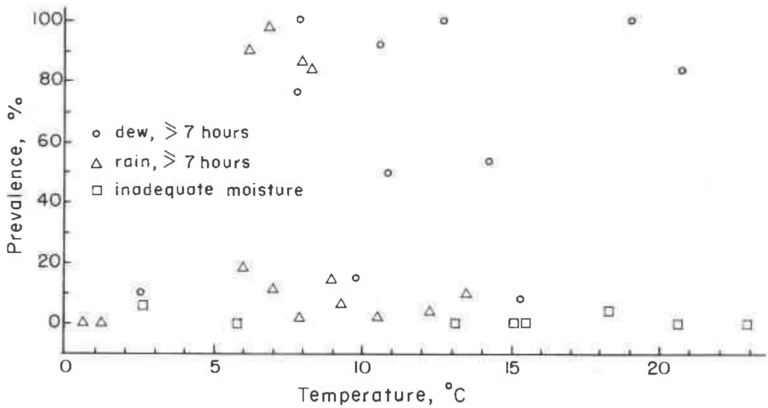

Figure 8. The influence of temperature and moisture on infection of inoculated plants in the field.

These experiments also permit comparison of spore counts on the traps with prevalence of rust. Considering the times when moisture was adequate, there was a sharp difference between prevalences when spore counts were less than 100 and when they were greater than 1,000 (Figure 9). When spore counts were between these two values, moisture conditions were not favorable for infection. On one occasion

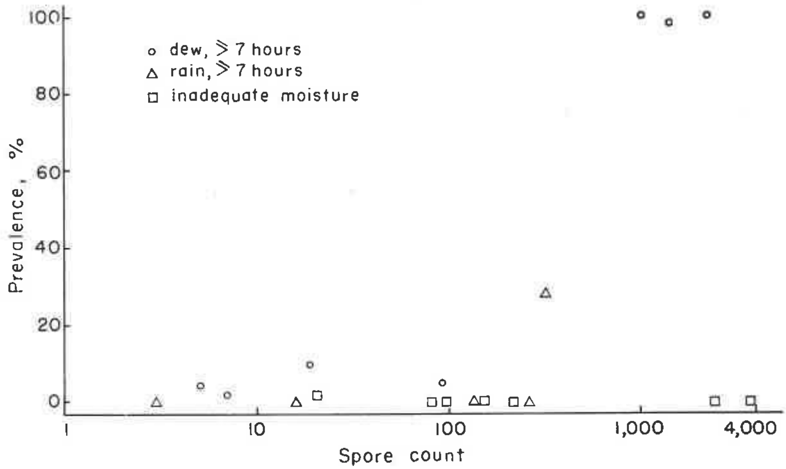

Figure 9. The relationship between spore count and the prevalence of rust.

when rain fell and the spore count was 340, 28% of the plants developed rust. A higher prevalence of rust would probably have resulted if dew rather than rain had provided moisture during that exposure period.

Rate of growth of stripe rust in leaves. Once *P. striiformis* has infected a leaf, the mycelium can grow extensively within the leaf, producing large numbers of uredia. The growth rate of the fungus in leaves was estimated by measuring the increase in length of the sporulating area. The distance between the edge of the visible lesion and the tips of the runner hyphae is fairly constant (*1*). Tests were made in the greenhouse to prevent secondary infection.

In one experiment spores were applied to the middle of the leaf in a band about ½ cm wide with a camel's hair brush; the leaves were then placed in the dew chamber overnight. The length of the sporulating zone which developed on each leaf was measured 15 and 25 days after inoculation. The average increase in length during this 10-day period was 8.9 mm per day. The mean temperature was 21.4 C.

In another experiment growth rates of lesions resulting from single spore inoculations were determined (Figure 10). In this case measurements were made daily for a 10-day period beginning 12 days after inoculation. A chlorotic region could be seen at either end of the sporulating region of the leaf. Measurements were made from one edge of the chlorotic zone to the other. The length of the sporulating

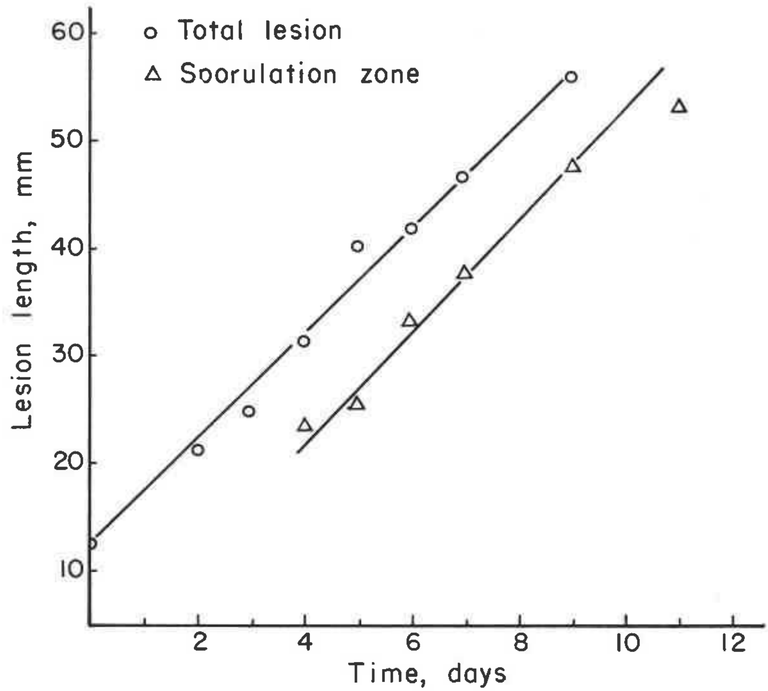

Figure 10. The growth of lesions resulting from single spore infections.

zone was measured also. Over the interval of the experiment, the increase in the length of the sporulating zone of the lesion and of the total lesion were linear. The rates for both were about 5 mm per day. In this experiment and the one above, lesions were growing in two directions.

Infectious periods of individual leaves. From October 1966 to June 1967 field observations were made at the Hyslop Agronomy Farm on the length of time that individual leaves bore spore-producing pustules. Leaves just beginning to show symptoms of stripe rust were marked with string tags and observed at intervals until senescence. Once tillers began elongating in the spring, the positions of leaves on the tillers were recorded.

During the winter rust was slow to spread within wheat plantings, but spore-bearing pustules could be found at all times. These pustules were of the large, susceptible-reaction type, but there was more necrosis associated with them than there was in the spring. Commonly, rust was first observed at leaf tips before the leaf was fully expanded.

On the infected, emerging leaf there was initially a chlorotic patch in which uredia eventually formed. As the sporulating zone progressed down the leaf, the original zone of sporulation became necrotic. Thus there was continuous rust development along the leaf consisting of pre-pustule chlorosis, an area of active sporulation, and finally tissue that had passed the infectious stage because of necrosis. At any one time sporulation usually occurred over less than half of the leaf. The infectious period of the leaf was terminated when the entire leaf became necrotic. The length of time between the first appearance of pustules on a leaf and its complete necrosis varied, depending upon the time of year when the pustules first appeared (Table 10). This period of time increased from late October until mid-January, then decreased again until mid-March when observations of seedling leaves were discontinued. By then the tillers were elongating, and lower leaves which had overwintered were deteriorating.

Table 10. Period of Rust Development on Individual Seedling Leaves of Winter Wheat at Hyslop Farm

Date of tagging*	Number of days spore-bearing pustules were on leaf†	Corresponding latent periods‡
October 26, 1966......	17	19
November 3, 1966....	17	22
November 29, 1966..	34	27
December 20, 1966....	35	30
January 15, 1967......	42	30
February 18, 1967....	35	32
February 26, 1967....	25	30
March 18, 1967	20	24

* First uredia just rupturing the epidermis.
† This period was terminated when the leaf died.
‡ From Figure 2.

The last column of Table 10 shows some latent periods (determined from Figure 2) for infections that took place on the dates given in the first column of the table. Comparing these latent periods with the infectious periods, one can see that once an emerging leaf was infected, the primary infection could completely ramify the leaf and produce uredia before any subsequent infections could produce pustules.

During the spring, development of rust on the stem leaves of individual culms was observed (Figure 11). The time between the first appearance of pustules on these leaves and their complete necrosis ranged from 19 to 35 days. Owing to multiple infections and shorter latent periods during the spring, much of the leaf surface bore pustules before there was much necrosis.

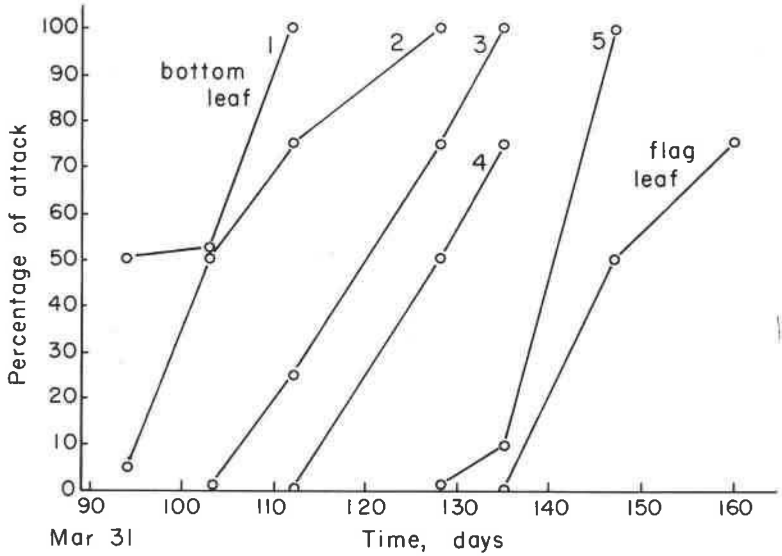

Figure 11. The development of rust on leaves of a single stem of Omar wheat. The leaves are numbered consecutively.

DISCUSSION

By inspecting wheat-growing areas of Oregon throughout a four-year period, information was gathered on the population dynamics of *P. striiformis*. The earliest that rust was seen on wheat in northeastern Oregon was in December. It was most severe at that time on early-sown wheat, such as the cover crops used in orchards in Wasco County. Foci were clearly evident and rust was on the upper leaves of plants, indicating several infection cycles had taken place. Infections may have occurred in early September when the wheat emerged, but escaped detection until December when development of rust was sufficient to make detection more likely. In December of 1967 rust development was not so extensive as in 1966. Single leaves, widely separated, bore pustules. Not until February were foci observed, indicating that conditions in the winter of 1967-1968 were not as favorable for spread of the pathogen as they were in the winter of 1966-1967. During 1967-1968 the orchards were the only area where evidence of infections could be found until March. Although rust usually could be found late in the season in Wallowa and Union counties because wheat matures later there, these areas do not appear to be a source of inoculum in the fall because rust usually is first seen in the western Columbia Basin. Whatever the source of inoculum, the initial level is light.

The rarity of green wheat and the absence of rust on it during the late summer and fall, plus the rarity of stripe rust on other grasses during this same period, raises the question of how much inoculum is required to initiate an epidemic in the early spring, given favorable weather. The quantitative examination of stripe rust development in the Columbia Basin can be used to predict how much infected tissue was present early in the season. The mean apparent infection rate (r) for the fields in Sherman County was 0.163 per unit per day (Table 5). Using this value and the mean time that rust reached a severity of logit $x = -2$ (about DA 6), the level of rust at some earlier time can be calculated using Equation (1). On February 15 the level of rust would have been 7.37×10^{-8} per unit ($7.37 \times 10^{-6}\%$). The amount of foliage in February would be about 10^{7} cm^2/ha (*13*). Thus 0.737 cm^2/ha or 0.3 cm^2/acre would be the area of diseased tissue. Because of the extensive growth of stripe rust mycelium within the leaf, one infected leaf in five acres could bear enough pustules to cause this level of disease.

Infected leaves probably could be more frequent because the calculation assumes an even distribution of inoculum. In a year of little winterkill, the level of disease (in terms of the number of leaves infected) would be nearly the same as the level of fall infection. In a mild winter there would be some increase in the number of infected leaves from the time of fall infection until February 15. The level of rust in February points out the difficulty of adequately determining the level of fall infection. If the expected frequency of infected leaves is only perhaps one leaf per acre, then every plant on several hundred acres of wheat would have to be carefully scrutinized to determine the actual level.

Figure 2 shows that infections evident on February 15 could take place any time prior to the first week in January. Even when mean daily temperatures are near freezing, infection can occur (Figure 8). Burleigh (*3*) reported infection when the mean daily temperature was –8 C, with moisture in the form of snow and frost. Results in the Willamette Valley (Figure 6) indicate that during the winter disease development is limited more by the failure of the spread of inoculum than by unfavorable conditions for infection.

In Sherman and Wasco counties, the orchard cover crop and other early-sown wheat could provide inoculum to nearby wheat fields before winter weather hindered spore movement. The level of rust in February reflects the level of inoculum produced in the fall rather than the amount of oversummering inoculum. In the orchard cover crops there was less than one focus per five acres, indicating that they were infected by a lower level of inoculum than subsequently infected wheat fields in the area. Therefore, only a few infected grasses or late wheat plants, not too far removed from the orchards, might carry enough inoculum through the summer to successfully initiate an epidemic in the spring, with an intermediate stage on early-sown wheat.

The ability of the mycelium to grow throughout the leaf permits the fungus to produce new inoculum without frequent conditions favorable for infection. Pustules may cover an entire leaf as a result of a single infection. The slow growth of mycelium during cold weather results in a long infectious period for an individual leaf (Table 10). Thus, during periods when conditions are not conducive to spore dispersal or infection, the fungus can still produce inoculum. Fewer initial infections are necessary to result in a given severity than is the case with the more local lesion-type diseases.

Van der Plank (*11*), in discussing sanitation as a disease control measure, points out that the value of sanitation diminishes as the product *rt* increases, where *t* refers to the entire period of disease development. The analysis of sanitation can be applied to the analysis of natural survival of inoculum. Both are concerned with the inoculum available to initiate an epidemic. Stripe rust has a moderately high apparent infection rate, and the period of disease development is long. Because of this, the destruction of inoculum, especially prior to infection in the fall, will have little effect on the final outcome of the epidemic unless the destruction is very thorough. Thus, even a summer such as that of 1967, during which much inoculum was certainly destroyed, would not prevent the development of an epidemic the following spring if climatic conditions during the winter and spring were favorable for disease development. But the winter in northeastern Oregon was also unusually dry, so that development of the wheat crop was retarded. The dry conditions would not have been favorable for infection. Unusually cold weather in March, both in northeastern Oregon and in the Willamette Valley, lengthened the latent periods so that existing infections were slow to produce inoculum.

The later in the season that destruction of inoculum occurs, the less thorough it must be to achieve a given setback to the epidemic. A severe winter, in which much fall-produced foliage is destroyed, is more likely to prevent an epidemic than is a hot summer. The events of the 1965 crop year would bear this out. The summer of 1964 was apparently favorable for the oversummering of stripe rust. But the winter of 1964-1965 was severe, and there was much winterkill of fall-infected foliage. The development of stripe rust in northeastern Oregon was retarded that year although climatic conditions in the spring seemed favorable.

Regardless of how favorable the summer and winter are for the survival of the fungus, conditions in the spring must be such that *r* is high in order for an epidemic to develop.

One factor that influences r is the latent period. The latent period decreases from December through July (Figure 2), and this in turn seems mostly due to increasing temperatures (Figure 7, also references *3, 10, 13*). Thus, spread of rust would be retarded in a spring that was cooler than normal.

The influence of a longer latent period can be evaluated by using the basic infection rate (R), which is independent of the latent period, and the relation:

$$p^R = pr_l e^{prl} \qquad (3)$$

In this equation the apparent infection rate (r_l) is the rate when x is so small that r is not affected by it. Using a value of R of 2.317 (from Table 6) and latent periods of 19, 21, and 25 days, three infection rates can be calculated (Table 11). As the latent period increases, other things being equal, the apparent infection rate decreases and the epidemic slows down. When the initial inoculum is low, the effect of the longer latent period is substantial even on June 25th (day 175). It is most unlikely that weather conditions would lengthen the latent period uniformly throughout the season, but an unusually cold or warm spring would certainly affect early stages of the epidemic through the latent period. Under these circumstances, the effect on the final level of disease would not be as substantial as suggested in Table 11. But if a wheat cultivar were developed on which *P. striiformis* took longer to produce spores, the effect of a longer latent period would persist throughout the epidemic and could be a valuable form of general resistance if the latent period extended sufficiently (at least 2 days).

Observations of rust development at Hyslop Farm in the Willamette Valley can be examined with respect to weather. A distinctive

Table 11. INFLUENCE OF EXTENSION OF LATENT PERIOD ON APPARENT INFECTION RATE (r)*

	Latent period (p), days		
	p	$p+2$	$p+6$
Apparent infection rate (r)	0.146	0.135	0.119
Proportion of rust (x) at day 150†	0.169	0.061	0.012
Proportion of rust (x) at day 175	0.886	0.654	0.194

* Basic infection rate (R) equals 2.317.
† Proportion of rust at day 46 (Feb. 15) was 5.07×10^{-8}.

feature of the disease progress curve for 1966 (Figure 3) is the period of slow disease development early in the season, from March 5 (day 64) to April 14 (day 104). The period of January through March 1966 had more precipitation, in terms of both amount and frequency, than the same periods in 1965 and 1967 (Table 12). Precipitation data from January through March were considered when analyzing disease development in the period March through mid-April because disease

Table 12. PRECIPITATION DURING THE PERIOD FROM JANUARY THROUGH MARCH AT HYSLOP FARM

	Year				
	1961	1964	1965	1966	1967
No. of days with precipitation	69	60	37	65	55
Total precipitation, inches	31.95	16.80	13.61	19.20	15.47

seen then was the result of infection and spore dispersal from January on, due to the latent period. High rainfall probably hinders movement of spores through the air. Also, lower leaves bearing pustules are beaten to the soil by rain and rapidly rot there; this was also noted by Zadoks (*13*). The reports of disease development in 1961 indicate that the disease was slow to become evident in the spring. This would be expected because of the heavy winter rainfall that year. Heavy winter rainfall is not deleterious to the epidemic, however. Although early spread of rust is restricted, the additional moisture in the soil probably makes conditions more favorable in the spring by providing moisture for dew formation by the distillation process (*7*).

The disease progress curves for Omar wheat at Hyslop Farm bent sharply downward at about DA 8 (Figure 3). The disease progress curve for a spring wheat planting in 1967 behaved similarly (Figure 4), but the change in rate was two months later than the rate change in the Omar wheat. This time difference suggests that the change in rate was not a response to some adverse change in weather.

A decrease in the infection rate also occurred in California (*10*), when severities of rust rated DA 8 to DA 9. At this rate the balance of an epidemic shifts because more tissue is diseased than is healthy. In the northeastern Oregon fields DA 8 was not reached until late in the epidemic, if at all, and no abrupt decrease in r was noted.

Although weather was apparently not responsible for the deflection of the disease progress curves, weather conditions might have determined how much the curves deflected. Increasing temperatures could hinder disease development. Sharp (*8*) demonstrated that at a constant temperature of 24 C the mycelium of *P. striiformis* could not survive in infected leaf tissue. Therefore, one might expect that when the temperature exceeds 24 C, the development of the fungus would be halted. When the number of days that the temperatures exceeded 24.2 C (75 F) are compared with the magnitude of r after deflection, it

Table 13. NUMBER OF DAYS THAT TEMPERATURES EXCEEDED 24.2 C AT HYSLOP FARM

Month	1964	1965	1966	1967
April	0	1	1	0
May	2	4	9	7
June	6	14	14	19
r*	0.122	0.036	0.015	0.030

* Late-season apparent infection rates for Omar wheat; r-values are from Figure 3.

is seen that the number of such days in May is inversely related to the value of r (Table 13).

Stripe rust has a long period of development on wheat each year in Oregon. Its success in overwintering indicates that very little inoculum is needed to initiate infection in the fall, so attempts to reduce the level of oversummering inoculum would probably be unsuccessful. Early-sown wheat provides an opportunity for multiplication of inoculum in the fall. The more such multiplication occurs, the more likely are fields sown at the normal time to be infected in the fall. Fields infected in the fall will be more severely rusted by harvest time than fields not infected until spring, because when conditions for spread become favorable in the spring, heavy concentrations of inoculum are already present in the fall-infected fields. Therefore, use of other cereals or crops for early planting, such as in the orchards, would prevent this fall multiplication of inoculum. Likewise, the later the wheat crop is sown in the fall, the less likely it is to be infected before the following spring.

SUMMARY

To gather information on factors favoring epidemics of stripe rust, the development of the disease in the field was followed. The earliest time that rust appeared on the new wheat crop in northeastern Oregon was in December. It was most severe then on early-sown wheat, such as the cover crops in Wasco County orchards, indicating that these were the sites of primary infection. Rust persisted in these plantings throughout the winter. In the Willamette Valley, leaves that were infected near their tip during fall and winter produced new uredia for several weeks, as mycelium grew through the leaf. Thus new inoculum could be produced during the winter over a long period even if conditions did not favor infection. During early spring, the appearance of rust in wheat fields near areas of overwintering inoculum suggested that such fall-infected plantings had an important role in the epidemiology of stripe rust.

From April through June, stripe rust increased at apparent infection rates of 0.1 to 0.25 per unit per day. Considering the long period of disease development, it was estimated that at these rates only one infected leaf per acre in mid-February would provide sufficient inoculum for an epidemic, given favorable weather. Moisture is one important weather factor since it is necessary for infection. Eight hours of dew resulted in high levels of infection and three hours of dew were necessary before any infection occurred. Rain also could provide the moisture for infection, but fewer infections resulted than when dew provided the moisture. Mean daily temperatures of 6 to 22 C were favorable for infection.

After maturity of the wheat crop, rust occasionally could be found on late wheat plants or other grasses, but only a small proportion of such plants were infected.

Results of this study indicate that the use of crops not susceptible to stripe rust for early plantings, such as orchard cover crops, would reduce the level of overwintering inoculum, which in turn could reduce the likelihood of severe stripe rust in the spring on the wheat crop.

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