The Oversummering and Dispersal of Inoculum of Puccinia striiformis in Oregon

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Oregon Agricultural Experiment Station Technical Paper No. 3208. This work was supported in part by contract funds from the Department of the Army, Fort Detrick.

The authors express their appreciation to Joanna Pyott for her assistance in examining the spore traps.

Accepted for publication 3 July 1972.

ABSTRACT

Stripe rust (*Puccinia striiformis*) was found on grasses in wheat-growing regions and in adjacent mountains of Oregon during late spring only after the disease was well established on the wheat crop. Disease incidence on these grasses diminished during summer, and approached zero during August. Stripe rust was seen less frequently on grasses in the mountains than on grasses in the wheatland. Most plants of susceptible grass species were free from stripe rust in the field, but became infected when inoculated in the greenhouse. Commercial wheat plantings served as the sources of inoculum for natural infections of wheat in plots located up to 64 km from wheat fields.

Urediospores were trapped on rod spore samplers exposed in the field only after stripe rust was well established on the wheat crop. The number of spores trapped followed closely the development of the disease in wheat fields near the traps. Throughout northeastern Oregon, urediospores moved predominantly from west to east.

The results suggest that urediospores which infect the fall wheat crop come from rust that oversummers on residual green wheat and grasses within the wheatland.

Phytopathology 63:13-17

The source of stripe rust (*Puccinia striiformis* West.) inoculum for fall infection of Oregon's wheat crop has remained undetermined since the discovery of the disease there in 1916 (4). The fungus has no known alternate host, so urediospores must serve as primary inoculum. The critical period in the disease cycle is the period between ripening of the wheat crop in July and the emergence of the new crop in October (12). During this interval, there is very little green wheat in Oregon because of the dry summers. We occasionally found stripe rust on ripening wheat and residual green wheat during July and early August (12). The earliest when stripe rust was found on the fall-sown crop was in December, and then only in early-sown fields. Since apparently little stripe rust oversummers on wheat in Oregon, we conducted investigations to determine whether rust oversummers on hosts other than wheat or whether inoculum moves in from some distant source.

MATERIALS AND METHODS.–Wheat in northeastern Oregon is grown in three areas separated by mountains (Fig. 1). These are the Columbia Basin, consisting of Wasco, Sherman, Gilliam, Morrow, and Umatilla Counties; the Grande Ronde Valley of Union County; and the low hills north of the Wallowa River in Wallowa County. Throughout the years 1964 through 1967, we looked for sources of stripe rust inoculum in these wheat-growing areas and in the adjacent mountains. Observations were also made in the Cascades, which separate western and eastern Oregon, in the Willamette Valley, and in the Coast Mountains.

Stripe rust collected from grasses or wheat was tested in the greenhouse for pathogenicity on Oregon's commercial wheat cultivars and grasses.

To study long-distance spore dispersal, we established wheat plots in the mountains at various distances from wheatland (Fig. 1). Ten wheat cultivars, differing in their susceptibility to stripe rust, were grown at each site (Table 2). Nearly all the wheat grown commercially in northeastern Oregon during this study were the cultivars Gaines, Moro, and Omar. Druchamp was also grown in the Willamette Valley.

Two plots consisting of a 2-m row of each cultivar were established at each location in the fall. Poultry wire cages (2 m X 6 m X 1.5 m), with rodent shields

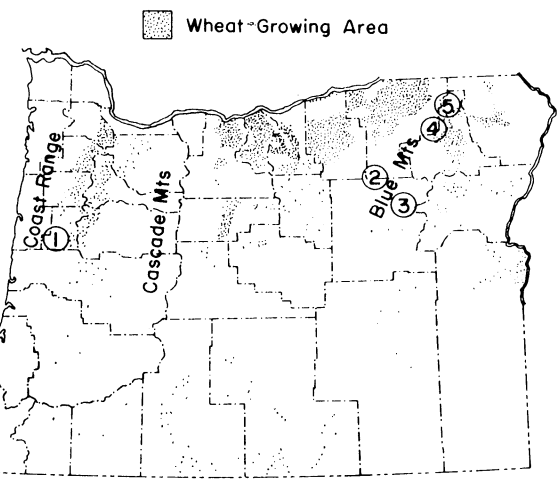

Fig. 1. Wheat-growing areas of Oregon and location of the Mountain plots: 1 = Mary's Peak, 975 m; 2 = Tupper, 1,311 m; 3 = Dale, 1,615 m; 4 = Meachum, 1,219 m; and 5 = Tollgate, 1,524 m.

near ground level, completely enclosed each plot to prevent damage by animals.

Spore trapping was carried out for 4 years in or near wheat fields throughout northeastern Oregon using rod spore samplers (2). The trap consisted of a stainless steel rod fitted permanently to a rubber base. A galvanized metal disc threaded onto the top of the rod protected the trap from rain during the exposure period. Cellophane tapes (19-mm width) were wrapped around the rod 4 and 9 cm from the base. Then the rods were dipped in molten glycerine jelly for provision of a sticky surface. The rods were exposed in the field about 1.2 m aboveground for 24 hr. The tapes were removed after exposure of the trap, and examined microscopically. The number of urediospores trapped on the north, east, south, and west sectors was determined.

RESULTS.–*Rust on grasses.*–We observed stripe rust on eight species in four genera of the Gramineae growing in their natural habitats. Stripe rust was observed on several species of *Agropyron* being grown in grass nurseries, but not at other locations (Table 1). *Elymus cinereus* Scribn. & Merr. and *Bromus marginatus* Nees were the most frequently rusted grasses in eastern Oregon. *E. cinereus* is a large perennial, common along roadsides and streambanks in shallow valleys. *B. marginatus*, also a perennial, grows around wheat fields and in the mountains. During spring, *P. striiformis* sporulated abundantly (reaction type 3) on *E. cinereus*; but during the summer, the reaction type diminished to 2 or 1 and finally to necrotic stripes. We never observed rejuvenation of stripe rust on such foliage during the cool, moist weather of autumn.

Most plants of *E. cinereus* examined were free of rust. To determine whether such plants were susceptible to stripe rust, we collected seed at five locations across northeastern Oregon. Plants grown in the greenhouse were susceptible to a wheat isolate of *P. striiformis* (reaction type 3).

Stripe rust was found on *B. marginatus* near wheat fields, at the Tupper Mountain plot (Morrow County), and considerably south of the wheat-growing area (Malheur and Grant Counties). Rust was on the grass at Tupper in June, but was not found when the plot was examined during August and October.

Other grass species in northeastern Oregon were examined regularly for stripe rust. *Bromus breviaristatus* Buckl. grows in the Blue Mountains between the Columbia Basin and the Grande Ronde Valley. No rust was ever found on this grass, when inspected during summer and autumn. However, when grown and inoculated in the greenhouse, it was susceptible to a wheat isolate of *P. striiformis* (reaction type 2-3; 70% severity).

TABLE 1. Observations of stripe rust on grasses in Oregon, 1965 through 1967

Grass	Location[a]	Months in which stripe rust found
Agropyron cristatum	Nursery, OSU	Apr.
A. cristatum	Hyslop	May
Agropyron elongatum	Nursery, OSU	Apr., June
Agropyron riparium	Nursery, OSU	Apr.
A. riparium	Hyslop	May
Agropyron sibiricum	Nursery, OSU	Apr., June
A. sibiricum	Hyslop	May
Agropyron spicatum	Nursery, OSU	Jan.(2)[b], Feb.(2), Apr., July, Sep., Dec.(2)
A. spicatum	Hyslop	May
Agropyron trachycaulum	Nursery, OSU	Apr.
Bromus marginatus	Malheur Co.	Aug.
B. marginatus	Grant Co.	June
B. marginatus	Union Co.	June
B. marginatus	Morrow Co.	June
B. marginatus	Wallowa Co.	Aug.
Bromus species	Union Co.	July(2)
Elymus canadensis	Nursery, OSU	Apr., June
E. canadensis	Morrow Co.	June
Elymus cinereus	Col. Basin	June(2), Sep.(2)
E. cinereus	Union Co.	Aug.
E. cinereus	Wallowa Co.	June, Aug.
Elymus glaucus	Nursery, OSU	Apr.
E. glaucus	Benton Co.	Aug.
Elymus species	Col. Basin	Mar., July
Hordeum brachyantherum	Union Co.	June
Poa ampla	Nursery, OSU	July
P. ampla	Hyslop	Sep.
Poa sp.	Deschutes Co.	Sep.

[a] Except for the grasses at Hyslop Agronomy Farm or the nursery on the Oregon State University Campus, the grasses listed were in their natural habitats.

[b] Where rust was observed more than once on the species at the given location, the number of observations is given in parentheses.

TABLE 2. Development of stripe rust on the wheat cultivars grown at the mountain plots

	Reaction type for each location and year																	
	Tollgate				Meachum			Dale				Tupper				Mary's Peak		
Wheat cultivars	1965	66	67	68	1965	66	68	1965	66	67	68	1965	66	67	68	1966	67	68
Suwon/2*Omar	0[a]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gaines	+	+	+	0	+	+	0	+	+	+	0	0	+	+	0	+	+	0
Moro	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Druchamp	0	0	NS[b]	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heines VII	+	+	0	0	0	0	0	+	0	+	0	0	0	+	0	+	0	0
Capelle Desprez	0				0			0				0						
Nord Desprez		+	NS	0		0	0		0	+	0		+	0	0	NS	0	0
Omar	+	+	0	0	+	+	0	+	+	+	0	+	+	+	0	+	+	0
Hymar/Orfed	+	+	0	0	+	+	0	+	+	+	0	+	+	+	0	+	+	0
Golden	0	+	0	0	0	+	0	+	+	+	0	0	0	+	0	+	+	0
P.I. 173438/Elgin	0	+	0	0	0	+	0	0	+	+	0	0	+	+	0	+	0	0
Month first observed	Sep.	Sep.	June		Sep.	June		Sep.	June	June		July	July	June		Aug.	June	

[a] 0 = no rust; + = rust present.
[b] NS = no stand.

Agropyron cristatum (L.) Gaertn. is used for pastures in the Columbia Basin and is also common along roadsides and around wheat fields. Even when stripe rust was severe on wheat, *A. cristatum* nearby was free of rust. When *A. cristatum* seed from Umatilla and Wasco Counties was grown and inoculated with *P. striiformis* in the greenhouse, reaction types ranged from 0-3.

Agropyron dasystachyum (Hook.) Scribn., *Agropyron inerme* (Scribn. & Smith) Rybd., *E. cinereus*, *Elymus glaucus* Buckl., and a *Poa* sp. all grew near our mountain plots, but we never observed stripe rust on them there, even when the wheat was infected. Plants grown from seed of these grasses in the greenhouse were inoculated with a wheat isolate of *P. striiformis*. Reaction types varied within each species from moderately resistant to susceptible for all but *E. glaucus* and *Poa* sp. All bluegrasses were immune. The *E. glaucus* from the Meachum plot was immune, whereas that from the Dale plot ranged from resistant (flecking) to fully susceptible.

E. glaucus from other sources was also variable in reaction to *P. striiformis*. The plants on which stripe rust was found in Benton County (Table 1) were resistant to wheat isolates. *E. glaucus* obtained from the Oregon State University Seed Testing Laboratory varied from completely resistant to fully susceptible to wheat and grass isolates of stripe rust.

In addition to determining the susceptibility of certain grasses to wheat isolates of *P. striiformis*, we determined whether collections of rust from grasses were pathogenic on wheat. The rust we found on *E. glaucus* in Benton County (Table 1) was only weakly pathogenic on Baart wheat, which was fully susceptible to all of our wheat isolates. *P. striiformis* collected from *B. marginatus* at three locations (Tupper Mountain plot, Wallowa County, and Malheur County) and from *E. cinereus* throughout northeastern Oregon was virulent to wheat. *P. striiformis* was collected from *Agropyron spicatum* (Pursh.) Scribn., *Agropyron sibiricum* (Willd.) Beauv., *E. glaucus*, and wheat, all growing in a nursery on the Oregon State University campus. All of these isolates infected wheat, *Agropyron desertorum* (Fisch.) Schult., *A. sibiricum* and *E. glaucus* in the greenhouse.

Although we often found stripe rust on *Poa* spp. this rust consistently failed to infect wheat in the greenhouse. We examined *Dactylis glomerata* L. during the 4 years of this study because this grass is susceptible to stripe rust in Europe (7), but never found stripe rust on it.

Mountain plots.–Stripe rust developed on wheat at all mountain plots except in 1968, when no rust was found at any of the locations (Table 2). This correlated with a lack of rust development in the commercial wheat crop in 1968. Gaines, Omar, and Hymar/Orfed were usually infected, and Druchamp, Moro, and Suwon/2*Omar were always resistant. The reactions of the remaining cultivars varied from year to year and from location to location. All of the cultivars grew poorly at Tollgate during 1967, which probably influenced the lack of rust development that year. Also, Heines VII and Nord Desprez were poorly adapted to conditions at the plots, which could account for their inconsistent reaction to stripe rust.

Infection of the wheat at the plots probably occurred in the late spring. The plots were under snow cover from late November through mid-March, and we never observed rust before this period. The earliest date at which we found rust at the plots was in the latter half of June, when wheat was in the boot stage (Table 2).

Spore trapping studies.–The average number of spores caught per trap per 24-hr exposure for each

TABLE 3. Spore trapping summary for northeastern Oregon

Month	Average number of spores caught in 24 hr/trap each month							
	1964			1965			1966	1967
	Columbia Basin	Union Co.	Wallowa Co.	Columbia Basin	Union Co.	Wallowa Co.	Columbia Basin	Columbia Basin
Jan.								
Feb.							1	14
Mar.				0	0		41	7
Apr.	5	0	0	4(1)[a]	0		34	1,081
May	92	1	1	31(1)	2	0	228	1,392
June	34	20	16	125(17)	117	5	1	82
July	23	1	210	23(20)	13	20	1	4
Aug.	1	0	349				1	
Sep.	1		4					
Oct.	2							0
Nov.	0							0
Dec.								0

[a] Number in parentheses excludes data from one severely rusted field in Gilliam County.

month was calculated for each year and wheat-growing area of northeastern Oregon (Table 3). Most spores were trapped from April through July in the Columbia Basin and Union County, which is the period of rapid disease development there. The wheat season is later in Wallowa County, which is reflected in the 1964 spore count data. The prevalence and severity of stripe rust varied considerably during the years 1964 through 1967 (12), and this was reflected in the number of spores trapped each year.

Spore traps were exposed from October through December in a Wasco County cherry orchard sown during August to a wheat cover crop. Rust was found in this wheat on 7 December 1967, but no spores were detected on the traps during the prior 3 months of exposure.

For all of the spore traps in northeastern Oregon, the percentage of spores impacting from the four cardinal directions for each of the years 1964 through 1967 were similar. Fifty percent of the spores came from the west, 11% from the east, 16% from the north, and 23% from the south. This pattern reflected the predominant spring and summer wind movements in the area.

TABLE 4. A comparison of the slopes of the regression lines of logit percent cumulative spore count/100 on time and the apparent infection rates for disease progress curves of fields in which spores were trapped

Field	Apparent infection rate	Regression line of cumulative spore count on time	
		Slope	Coefficient of correlation
A	0.163	0.093	0.978
B	0.175	0.095	0.992
C	0.187	0.099	0.938
D	0.074	0.109	0.936
E	0.193	0.129	0.965
F	0.217	0.130	0.928

In some wheat fields where traps were located, we estimated disease severity at regular intervals and calculated (12) apparent infection rates (14). A comparison of cumulative spore counts, converted to logits (10), indicated that spore counts reflected disease development (Table 4). Field D, whose spore count curve slope was disproportionately high, had very little rust, and the absolute numbers of spores trapped were much lower than the numbers of spores trapped in the other fields.

Field F was a planting of Baart spring wheat in the Willamette Valley. Some spores were caught on traps exposed between 20 April and 20 May, when rust was spreading rapidly on winter wheat, but the numbers were low. From 20 May until July, when the Baart matured, cumulative spore counts followed disease increase closely.

To study the movement of spores during winter, a plot of wheat in the Willamette Valley was inoculated on 27 September 1966 with stripe rust. By 13 October, the first uredia were producing spores. Light rust infection first appeared in a noninoculated plot 165 m east on 31 December 1966. Latent periods of that time of year were such that infections taking place in mid-November would be evident by the end of December (12). Rust development in the noninoculated plot remained confined to a few primary infection centers during the winter months. Spore traps exposed between the plots verified that little inoculum moved through the air until April. The highest spore count for a 24-hr period prior to April was three.

DISCUSSION.–Stripe rust of wheat in Oregon developed during the spring from overwintering infections within the crop (12). Volunteer wheat, which carries rust through the summer in some areas of the world (6, 15), is rare in Oregon because of the hot, dry summers. We investigated two other possible summer reservoirs of inoculum which are found in Oregon: (i) residual green wheat; and (ii) perennial grasses. Rust was found on residual green wheat (12) during the summer, although not in abundance. On grasses, rust appeared later in the spring and disappeared as early (or earlier) in the summer as the rust on wheat. Grasses at high elevations have been suggested as oversummering hosts for *P. striiformis* (3, 13); however, in northeastern Oregon, rust was found less frequently on grasses at high elevations than on grasses in the wheatland. Rust also appeared at high elevations later, and disappeared earlier each summer than it did in the wheatland. Therefore, we feel grasses in the mountains are of no importance in the epidemiology of the disease on wheat in contrast to the conclusions of others (3). Grasses in the wheatland may also be unimportant in the epidemiology of the disease on wheat. Had the grasses surrounding wheat fields been the source of primary inoculum in the fall, we would have expected to see the first infections near field borders. However, the initial infections were scattered throughout the fields.

Also, even though we demonstrated cross-infections of wheat and grass isolates of *P. striiformis*, Beaver (1) identified a race from *B. marginatus* and a race from *Elymus canadensis* L. as being different from 10 other wheat races he identified. If the stripe rust on residual green wheat and perennial grasses represent different populations, we would expect residual green wheat of commercially grown cultivars to be more important as an oversummering host than perennial grasses.

We found no evidence that primary fall infection was the result of long-distance spore dispersal, either from the late wheat areas (Wallowa County) or from distant sources such as California. Although urediospores were abundant in the air in Wallowa County in September, rust first appeared in the fall at the western end of the Columbia Basin, farthest from Wallowa County. If primary inoculum for the Columbia Basin came from Wallowa County, early infections should have occurred in Union County and the eastern end of the Columbia Basin, which they usually did not do (12). At the time of the first appearance of rust in the Columbia Basin, there were no large reservoirs of rust in adjacent states (3, 13), which could provide primary inoculum.

Early-seeded fields were the first to become infected (12), and they produced inoculum for subsequent infection of the winter wheat crop. These fields were often infected during the fall. Wet weather during late fall and winter did not favor aerial dispersal of urediospores, since spores were rarely caught on traps during these months even in the vicinity of rusted wheat. Rust seemed to spread mainly by leaf-to-leaf contact or by very limited aerial dispersal from primary infection centers during this period.

The most likely source of inoculum for early-seeded fields was the rust on residual green wheat. This inoculum, though scarce, was within the wheatland and therefore near the new wheat crop. The latest date at which we found rust on residual green wheat was early August. Some wheat sown in waterways or as a cover crop could be infected in early September. Thus, there was a 2- to 4-week period in which there may have been no infected living foliage in northeastern Oregon. Urediospores of *P. striiformis* have survived on dead leaves for 4 to 6 weeks (5, 8, 9, 11) and on air-dry soil for 1 month (11). Spores may survive the "wheat-free" period in northeastern Oregon in these ways. From a light infection of early-seeded wheat, infection centers could develop during fall which would provide the inoculum for an epidemic.

LITERATURE CITED

1. BEAVER, R. G. 1972. The influence of environment and pathogen variability on the infection of wheat by Puccinia striiformis West. Ph.D. Thesis, Oregon State Univ. 79 p.
2. BROMFIELD, K. R., J. F. UNDERWOOD, C. E. PEET, E. H. GRISSINGER, & C. H. KINGSOLVER. 1959. Epidemiology of stem rust of wheat. IV. The use of rods as spore collecting devices in a study on the dissemination of stem rust of wheat uredospores. Plant Dis. Reptr. 43:1160-1168.
3. HENDRIX, J. W., J. R. BURLEIGH, & J. TU. 1965. Oversummering of stripe rust at high altitudes in the Pacific Northwest. Plant Dis. Reptr. 49:275-278.
4. HUMPHREY, H. B., & A. G. JOHNSON. 1916. Observations on the occurrence of Puccinia glumarum in the United States. Phytopathology 6:96-97.
5. HUNGERFORD, C. W. 1923. Studies on the life history of stripe rust, Puccinia glumarum. J. Agr. Res. 24:607-620.
6. S'JACOB, J. C., & J. C. ZADOKS. 1957. Het overblijven van gele roest in Nederland. Tijdschr. Plantezieckten (Wageningen) 63:27-28 (Abstr.). (Abstr. Rev. Appl. Mycol. 36:580-581. 1957).
7. MANNERS, J. G. 1960. Puccinia striiformis Westend. var. dactylidis var. nov. Brit. Mycol. Soc. Trans. 43:65-68.
8. MEHTA, K. C. 1923. Observations and experiments on cereal rusts in the neighborhood of Cambridge, with special reference to their annual recurrence. Brit. Mycol. Soc. Trans. 8:142-176.
9. RAEDER, J. M., & W. M. BEVER. 1931. Spore germination of Puccinia glumarum with notes on related species. Phytopathology 21:767-789.
10. ROMIG, R. W., & V. A. DIRKS. 1966. Evaluation of generalized curves for number of cereal rust uredospores trapped on slides. Phytopathology 56:1376-1380.
11. SHANER, G. 1969. Epidemiology of stripe rust (Puccinia striiformis West.) of wheat in Oregon. Ph.D. Thesis, Oregon State Univ. 160 p.
12. SHANER, G., & R. L. POWELSON. 1971. Epidemiology of stripe rust of wheat, 1961-1968. Oreg. Agr. Exp. Sta. Tech. Bull. 117. 31 p.
13. TOLLENAAR, H., & B. R. HOUSTON. 1967. A study on the epidemiology of stripe rust, Puccinia striiformis West., in California. Can. J. Bot. 45:291-307.
14. VAN DER PLANK, J. E. 1963. Plant diseases: epidemics and control. New York, Academic Press. 349 p.
15. ZADOKS, J. C. 1961. Yellow rust on wheat. Studies in epidemiology and physiologic specialization. Tijdschr. Planteziekten (Wageningen) 67:69-256.