

AN ABSTRACT OF THE THESIS OF

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Title: THE INFLUENCE OF ENVIRONMENT AND PATHOGEN

VARIABILITY ON THE INFECTION OF WHEAT BY

PUCCINIA STRIIFORMIS WEST.

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Race identification of stripe rust (Puccinia striiformis West.) is influenced by environment, pathogen variability and host age. Isolates of stripe rust were collected in the Pacific Northwest and characterized on two sets of differential varieties; the "Oregon" and the United States. Six of the seven isolates tested on the seedling Oregon differentials were identified as separate races at the 2 C/18 C (night/day) temperature profile; however, seven races could be identified using mature plants.

Eight of the 16 Oregon differentials used as seedlings gave similar infection types as mature plants with all seven isolates tested. The remaining eight varieties changed from a susceptible seedling reaction to a more resistant reaction as a mature plant with specific host-pathogen combinations. This change can be used to separate the seven isolates into races. Only the variety Leda was consistently

more resistant as a mature plant than as a seedling. This "mature plant resistance" is contrasted to the "field resistance" of the variety Gaines which is conditioned by environment.

Five of the eight isolates tested on the United States differential varieties could be identified as separate races. With the aid of the eight supplemental varieties all eight isolates could be separated.

Six field races of stripe rust could be identified on wheat grown at 11 sites in Oregon using the Oregon field differential varieties. These varieties also indicated a shift in the make-up of the rust race populations during the last four years in the Willamette Valley. Similarities in field race characteristics at Pendleton, in eastern Oregon, and Aurora, in the Willamette Valley, were also noted.

Percentage of germination and penetration of uredospores of stripe rust differed on 15 Oregon differential varieties. An unidentified factor inhibited uredospore germination on certain varieties. Penetration of stomates was also delayed on some varieties but no consistent correlation could be made with inhibition of germination or host resistance to stripe rust.

Desiccation following short dew periods of three or four hours effectively reduced the amount of viable inoculum available during a 24-hour period. Inoculum removal by desiccation can be made more effective by the use of varieties that lengthen the interval from uredospore germination to penetration. Under field conditions,

inoculum removal can reduce final disease severity. For example, with an apparent infection rate of 0.0146 per unit per day for stripe rust, removal of inoculum from death of germinating spores for a five day period would reduce the final disease severity by 14.7 percent over a 40-day period.

Factors limiting fall spread of stripe rust in the Willamette Valley differ from those in eastern Oregon. In the Willamette Valley spore movement is by leaf to leaf contact during the wet winter months. In eastern Oregon little or no rust movement occurs until warm spring weather facilitates aerial spore movement. During most years sporulating leaves are killed by freezing winter weather and rust survival is limited to infected, non-sporulating green host tissue.

Competition for infection and sporulation sites between an albino race of stripe rust and four yellow races was noted. Some mechanism inherent to the albino race and presumably other races prevents invasion and/or sporulation within previously colonized host tissue. Competition between two races of stripe rust can reduce the potential number of sites for infection on a wheat leaf by 99 percent. In addition, competition can change the ratio of one race to another in the population from 1:1 to 3:1 in one generation.

Summer survival on grasses in mountain areas of Oregon is limited and does not appear to play an important role in overwintering of stripe rust in Oregon. Field race(s) of stripe rust found at the

Mountain Plots appears similar to race(s) in wheat growing areas.

Movement of inoculum from mountain areas to wheat fields in the fall of the year seems unlikely since rust on wheat and grasses inoculated in June could not be found the following September.

The Influence of Environment and Pathogen
Variability on the Infection of Wheat by
Puccinia striiformis West.

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THE INFLUENCE OF ENVIRONMENT AND PATHOGEN
VARIABILITY ON THE INFECTION OF WHEAT BY
Puccinia striiformis WEST.

I. GENERAL INTRODUCTION

Since the initial work on stripe rust (Puccinia striiformis West.) in the United States (Hungerford, 1923; Hungerford and Owens, 1923), the disease received little attention until severe epidemics occurred in 1960 and 1961 in the Pacific Northwest. During those intervening 50 years changes in wheat culture have taken place. These have a direct influence upon the severity of stripe rust epidemics. The wheat breeding program at that time was directed toward incorporation of smut resistance into new club wheat varieties. In the process of selecting for smut resistance, resistance to stripe rust was lost through the Vertifolia effect (van der Plank, 1968). Stripe rust resistant wheat varieties such as Rex, Golden and Turkey-Rio, that were developed prior to the time of the smut breeding program, remained resistant throughout the 1960-1961 stripe rust epidemic. Several of these old varieties have remained resistant to the present time. It has now become necessary to develop a thorough understanding of the stripe rust organism, its capability and its variability as a foliar pathogen of wheat in an attempt to better control stripe rust epidemics in the future.

Understanding disease development and its correlation with

meteorological data is dependent upon an understanding of the effects of environment on the rust fungus and its interactions with a host. Disease modeling, the development of mathematical models to simulate selected epidemic development, is entirely dependent upon this knowledge.

Infection type (IT), the visible signs and symptoms of disease on the host, is variable and strongly influenced by environment. Moisture, temperature, host as well as genetic variations in the pathogen can greatly influence infection type and are especially important during race identification. The objectives of this study were to determine what effects variations in the host, pathogen and environment have on the infection process, disease expression and spread of stripe rust in the Pacific Northwest.

Review of Literature

Stripe rust of wheat has been recognized in this country since 1915 (Humphrey and Johnson, 1916). The extent of stripe rust in this country prior to 1915 is not known because of its confusion with the related rust species Puccinia dispersa, P. graminis, and P. coronata.

Stripe rust is most commonly found in areas of the world having a humid marine or similar climate. A general discussion of the distribution of this disease and the favorable climatic conditions was given by Dickson (1956). The distribution of stripe rust in the United

States, however, is mainly limited to the western states of Washington, Oregon, Idaho, Montana and California.

The Stripe Rust Fungus

The name Puccinia glumarum has been in common usage since 1896, but in 1953 Hylander et al. (1953) invoked the Rules of Nomenclature to reinstate the name Puccinia striiformis, first used by Westendorp in 1854. A detailed discussion of the nomenclature of this fungus is given by Hassebrauk (1965). Since 1956, Puccinia striiformis has been used in the majority of the literature.

The life cycle of stripe rust is limited to the uredial stage. Telia are formed and are capable of germination but are functionless. Uredospores have been reported to survive for up to 51 days on dry foliage under summer field conditions in the Pacific Northwest (Shaner, 1969). The fungus commonly overwinters as mycelium in green cereal or grass foliage (Hungerford, 1923; Lloyd, 1969). Snow cover or mild winters which reduce loss of winter foliage favor survival of the fungus in infected leaves (Hungerford, 1923).

Host Range

Puccinia striiformis has been reported on a wide range of gramineous hosts throughout the world (Hassebrauk, 1965). The host range of this fungus in the Pacific Northwest has been reviewed by

several workers (Hungerford and Owens, 1923; Humphrey, Hungerford and Johnson, 1924; Sanford and Broadfort, 1932; Fisher et al., 1942; Shaner, 1969). Triticum aestivum, Elymus sp. and Bromus sp. comprise the principle hosts in the Pacific Northwest.

Physiologic Specialization

Until recently the extent of physiologic specialization of stripe rust in the Pacific Northwest has not been investigated. Sharp (1962), using the German set of standard differential host varieties, reported a race of stripe rust in Montana that differed from those previously reported from the United States and Europe. Purdy and Allen (1966) demonstrated the presence of two races of the rust in Washington and Tollenaar and Houston (1967) reported one race from California. Beaver (1969) has identified eight races from Washington, Oregon and Idaho. No comparisons of these reported races can be made, however, since the individual workers have employed different sets of differential wheat varieties.

European workers, employing a standard set of differential varieties used by Gassner and Straib (1932, 1934a, b), have identified many races of stripe rust from several countries (Manners, 1950; Fuchs, 1960; Zadoks, 1961). Rudolph (1929) concluded that the form of the German stripe rust differed from that in the United States based on a comparison of resistance of several wheat varieties evaluated in the United States and Germany.

Stripe rust from many grass genera has been shown to infect wheat (Hungerford and Owens, 1923; Zadoks, 1961; Hendrix et al., 1965; Tollenaar and Houston, 1967; Shaner, 1969). Whether the grass isolates were similar in pathogenicity to wheat isolates has not always been determined. Beaver (1969) showed that one isolate from Elymus canadensis was similar to three wheat isolates. Tollenaar and Houston (1967) reported grass and wheat isolates as similar in California.

Influence of Environment

Stripe rust uredospore germination and fungus-host interaction have been shown to vary with environmental factors (Zadoks, 1961; Shaw, 1963; Sharp, 1965). Disease expression is especially subject to control by light and temperature. Differentiation of infection structures produced by the fungus and outcome of host-parasite interactions that exert their effects after host invasion are directly affected by these parameters (Shaw, 1963).

Light. Stripe rust spore germination was influenced by light according to McCracken and Burleigh (1962). They reported significantly higher germination percentages under light than in the dark. Various colors of light were used, with white and blue light giving the highest percentages of germination. On the other hand, Tollenaar and Houston (1966) reported exposure to light during germination was

inhibitory at 6 C, but promoted germination at 11 C. If a pre-germination treatment at 15 C or a pre-germination exposure to light was used, germination at 6 C was enhanced.

Stubbs (1967) reported various influences of light on infection type of stripe rust on wheat. Decreasing light intensity caused an increase in IT of some varieties, a decrease in some, and still others showed no response. The post-inoculation light intensity was the most influential in changing IT.

Bever (1934) reported light intensity and day length have the same effect on uredospore development. Changing day length from 6 to 12 hours decreased incubation periods from 20 to 9 days at a mean temperature of 47.5 F. Days longer than 12 hours changed IT's from 4 to 0 on 'Pannier' barley.

An interaction of light and temperature was reported by Sharp (1965). Only dark-period temperatures during both pre- and post-inoculation phases were instrumental in determining infection type. Highly susceptible varieties showed no shift in infection type with temperatures as high as 32 C during the 15 hour photoperiod as long as temperatures during the dark phase did not exceed 15 C.

Stripe rust uredospores appear to be less sensitive to light during germination than uredospores of either stem rust, P. graminis tritici (Wiese and Daly, 1968) or leaf rust, P. recondita (Zadoks and Groenwegen, 1967). Penetration of leaves of "Little Club" by P.

graminis tritici was dependent upon the time of day, being maximum at 1:30 A.M. Penetration also varied with the amount of light or the time the light was applied after inoculation (Shipton et al, 1967).

Light was not required by P. graminis for penetration, but it enhanced penetration six-fold when CO₂-free air was used in the place of normal air (Yirgau and Caldwell, 1968). These workers reported that the light-mediated mechanism regulating penetration by P. graminis resided in the host.

Temperature. Straib (1940) noted that the temperature at which uredospores developed determined their germination potential. Spores produced at 20-25 C germinated sooner and over a wider range of temperatures than ones produced at 8-10 C. Optimum temperature for in vitro germination is usually considered to be 10-13 C (Newton and Johnson, 1936; Manners, 1950; Zadoks, 1961). McCracken and Burleigh (1962) reported that the highest germination occurred at 2-5 C for spores incubated in the dark.

Host-pathogen interaction is greatly influenced by pre- and post-inoculation temperatures (Manners, 1950; Zadoks, 1961; Sharp, 1962, 1965). Percentage of infection on host leaves was higher for plants at 15 C than at 24 C and both prevalence and severity of infection were higher at 2 C than at 13 C (Sharp, 1965). According to Sharp, wheat varieties can be separated into four groups on the basis of infection types after host preconditioning at 15 C and 24 C. He found some

varieties were susceptible at both temperatures, some were resistant at both, some susceptible at the lower and resistant at the higher temperature and some varieties exhibited the reverse effect.

Tollenaar and Houston (1966) list sporulation as occurring between 0.5 C and 24.5 C. Shaner (1969) showed that day temperatures of 31 C for ten hours with 10 C at night for more than five days would stop or prevent sporulation and presumably kill the fungus. Cold temperatures existing during winter months in Montana delayed sporulation for up to 159 days (Sharp and Hehn, 1963).

The persistence of stripe rust during winter months is influenced by the winter hardiness of the host foliage (Lloyd, 1969). Lloyd also reported that sporulating leaves were more susceptible to winter kill than leaves in the flecking stage.

Lewellen et al. (1967) reported the action of major genes for stripe rust resistance was not affected by different temperature profiles, but the minor genes gave better resistance at a higher temperature profile than at a lower temperature profile.

Using Puccinia graminis var. tritici, Wiese and Daly (1968) concluded that control of uredospore germination is dependent on factors such as temperature rather than self-inhibitors or water balance. They emphasize the necessity for care in providing and defining germination conditions in spore germination studies.

Rapilly et al. (1970) in France reported winter spread of stripe

rust was governed by temperature and depended on the autumn pattern of infection. In early spring the disease tended to become widespread when increasing temperature shortened incubation periods and sporulation cycles. Raeder and Bever (1931) reported freezing moist uredospores of stripe rust can revive lost germination ability.

Host. The growth stage of the host can play an important role in the development of stripe rust infection types. Seedling and mature plant resistance may or may not always be correlated. Zadoks (1961) observed that if a seedling is resistant to a given race of stripe rust, the mature plant almost always is resistant to that same race. Purdy and Allen (1962, 1963) reported both positive and negative correlations between seedling and mature plant reactions in Washington, although the tests on seedling plants were not carried out under the same conditions as were mature plant tests.

Differences in IT can occur between leaves of the same plant. Stubbs (1968) observed this phenomenon between the first and second leaves of F_2 seedlings. He suggested this difference may be related to the influence of the endosperm on the first leaf.

Beaver (1969) noted up to 88 percent reduction in prevalence on first leaves compared to second leaves of wheat seedlings grown at 2 C/18 C (night/day) temperature. No differences were noted, however, when the seedlings were grown at a constant 18 C and IT's were not different between the first and second leaves at either temperature.

Sharp (1965) suggests that inhibition of germination of stripe rust uredospores on wheat leaves at 24 C is due to secretions or emanations on the leaf surface, but he did not characterize them or their origin. Bacillus sp. were consistently isolated from leaves developed at 24 C and are presently being investigated for their effects on germination and penetration. Factors affecting spore germination may be derived from the host or from microflora colonizing the leaves. Morgan (1963) reported fungi and bacteria associated with uredospores inhibited their germination and penetration potential.

II. THE INFLUENCE OF VARIETY AND HOST AGE ON RACE IDENTIFICATION OF Puccinia striiformis

The persistence of stripe rust throughout the wheat growing regions of the Pacific Northwest since 1960 has presented problems in the breeding and maintaining of resistant varieties. New and adapted biotypes of stripe rust are continually being selected from the rust population by the introduction of new wheat varieties. Monitoring race characteristics within stripe rust populations is an essential prerequisite to the selection of proper breeding material.

Stripe rust race identification has been traditionally carried out on seedling wheat varieties. European workers have employed a standard set of differential wheat varieties (Gassner and Straib, 1932a, b; Manners, 1950; Fuchs, 1960), while race identification in the United States has been made on various sets of differential wheat varieties (Purdy and Allen, 1966; Tollenaar and Houston, 1967; Beaver and Powelson, 1969). Unfortunately, results from within the United States cannot be compared since a set of standard differential varieties was not employed by the various workers.

In 1970, Line, Sharp and Powelson published a list of wheat varieties to be used as a standard set of stripe rust differentials for the United States. These varieties were used in this study in conjunction with the Oregon differential varieties (Beaver, 1969) (Table 2) and the Oregon field differential varieties (Table 2). The present study

was undertaken to identify and compare races of stripe rust on seedling and mature plants of the Oregon differential varieties under controlled environmental conditions and to establish the identity of these races of stripe rust on a standard set of United States differential varieties. In addition, the Oregon field differential varieties were used to ascertain the distribution and variation of field races of stripe rust in Oregon.

Materials and Methods

Uredospores of Puccinia striiformis were collected from infected wheat from various locations in Oregon, Washington, Idaho and Montana (Table 1). Isolates were single spored by the method of Fleischmann et al. (1966) and increased on a mixture of Gaines and Omar seedlings. The spores were harvested and stored at 3 C and 50 percent relative humidity for up to six weeks prior to use. Liquid nitrogen was used for long term spore preservation.

Inoculated plants were given an 18-24 hour dew period at an air temperature of 12 C. A fine layer of moisture formed over the leaf surface within a half hour after being placed in the dew chamber. Following the dew period the plants were returned to the growth chamber programmed for a diurnal temperature profile of 2 C/18 C (night/day) with 1000 foot-candles of light for 12 hours for symptom development.

The three sets of differential varieties used in this study are

Table 1. Stripe rust isolates evaluated.

Isolate	Oregon race designation	U. S. race designation	Nearest town	Host	Date
W-54	OR 7-68		LaGrande, Oregon	Gaines wheat	June, 1968
SW-57-1	Moro race	2, 7, 5, 6/1, 3, 4	Bonnors Ferry, Idaho	Moro wheat	July, 1968
SW-63s-2	OR 8-69	4, 5, 7, 2, 6/1, 3	Pendleton, Oregon	winter wheat	March, 1969
SW-75s-2	OR 8-69	4, 5, 6, 2, 7/3, 1	Corvallis, Oregon	winter wheat	April, 1969
SW-82-1	OR 9-69	2, 4, 5, 7/6, 1, 3	Pendleton, Oregon	Suwon x Burt wheat	June, 1969
SW-89-1	OR 10-70	4, 5, 7/3, 6, 2, 1	Pendleton, Oregon	Wanser wheat	February, 1970
SW-93-1	Yamhill race	4, 5, 7, 2, 6/1, 3	Aurora, Oregon	Yamhill wheat	June, 1970
SW-95-1	Druchamp race	2, 5, 4, 7/3, 6, 1	Aurora, Oregon	Druchamp wheat	July, 1970
SW-92-1	Albino race	3, 7, 4, 5, 6/1, 2	Bozeman, Montana	unknown wheat ^a	unknown ^a

^aIsolate supplied by E. L. Sharp, Bozeman, Montana. Host and date of collection were not known.

Table 2. Differential wheat varieties used to identify races of stripe rust.

Variety no. in differential set	Differential variety	PI or CI no.	Variety no. in differential set	Differential variety	PI or CI no.
<u>Oregon</u>					
1	Cappelle Desprez	262223	9	Ibis	-
2	Chinese 166	11765	10	Leda	-
3	Dippes Triumph	-	11	Michigan Amber	11371
4	Druchamp	13723	12	Moro	13740
5	Etoile de Choisy	262231	13	Omar	13072
6	Flamingo	260899	14	Rubis	-
7	Gaines	13448	15	Suwon 92 x Omar ⁴	13749
8	Golden	10063	16	Yamhill	14563
<u>U. S.</u>					
1	Lemhi	11415	8 ^a	Lee	12488
2	Chinese 166	11765	9	Heines Kolben	180619
3	Heines VII	201195	10	President Riverain	174687
4	Moro	13740	11	PI 178383	PI 178383
5	Suwon 92 x Omar ⁴	13749	12	Medeah	-
6	Druchamp	13723	13	Golden	10063
7	Riebesel	295999	14	Alba	13256
			15	Vilmorin 23	-
<u>Oregon Field</u>					
1	173438 x Elgin	-	7	Hymar x Orfed	-
2	Cappelle Desprez	262223	8	Moro	13740
3	Chinese 166	11765	9	Nugaines	13968
4	Druchamp	13723	10	Omar	13072
5	Golden	10063	11	Riebesel	295999
6	Heines VII	201195	12	Suwon 92 x Omar ⁴	13749

^aVarieties 8 through 15 are supplemental varieties to U. S. differentials.

listed in Table 2. The Oregon differential and Oregon field differential varieties were selected from commercially grown wheat varieties of the Pacific Northwest and the European set of stripe rust differentials. The U.S. differential varieties were assembled from selected varieties of wheat supplied by stripe rust workers from the United States and Europe (Line et al., 1970). The seedling plants were grown in vermiculite in four inch plastic pots and sub-irrigated with Hoagland's solution. Mature Oregon differentials were grown from vernalized seedlings to a growth stage just prior to flag leaf emergence in the greenhouse and then transferred to a growth chamber at the 2 C/18 C temperature profile along with a freshly planted set of the Oregon and U.S. seedling differentials. The seedling and mature differentials were inoculated simultaneously when the seedling plants were in the two leaf stage and the flag leaf was emerging on the mature plants. The seedling and mature differentials were grown together until symptoms had fully developed.

Differences in pathogenicity of the various isolates were based on infection types (IT's) on the differential varieties. When the replicated results varied more than one IT unit, the range was recorded; otherwise, the highest IT was used. The IT's were recorded using a modified scale of Gassner and Straib (1932) (Table 3). Host IT's varying more than two IT units were not used for race identification, but were included as additional information.

Table 3. Infection types used for race identification.

oo	- no pustules, only minute chlorotic flecks
00	- no pustules, only small angular chlorotic or necrotic patches
0	- no pustules, only general chlorosis or necrosis
1	- some separated, very small pustules accompanied by chlorosis or necrosis
2	- a few pustules, also chlorosis, perhaps necrosis
3	- normal pustule formation, also chlorosis
4	- normal pustule formation without chlorosis
i	- no symptoms observed

Results

Oregon Seedling Differentials

Six races were identified based on their IT's (Table 4). Varieties Suwon 92 x Omar⁴ and Ibis were resistant to all seven isolates tested. Chinese 166, Moro and Yamhill were resistant to all but one isolate each. These varieties alone identify SW-82-1 (OR 9-69), SW-57-1 (Moro race), and SW-93-1 (Yamhill race), respectively as separate races since the resistance of each variety is distinct.

Rubis, Omar, Michigan Amber, Leda and Gaines were highly susceptible to all isolates tested, each giving an IT of three or four. The remaining five varieties were differentially susceptible. Flamingo's resistance to both SW-75s-2 and SW-63s-2 separates them from the remaining isolates; therefore, these two isolates are

Table 4. Infection types of seven isolates of stripe rust on the Oregon differential varieties^a of winter wheat in the seedling and mature plant growth stages.^b

Variety	SW-57-1		SW-63s-2		SW-75s-2		SW-82-1	
	seedling	mature plant	seedling	mature plant	seedling	mature plant	seedling	mature plant
Cappelle Desprez	00	oo	00	i	00	oo	0	00
Chinese 166	oo	oo	oo	i	0	0	3	i
Dippes Triumph	2	1	3	3	3	2	3	3
Druchamp	00	oo	00	i	00	i	2	oo
Etoile de Choisy	3	00	3	3	2-4	i	3	3
Flamingo	3	oo	00	i	00-2	oo	3	oo
Gaines	4	3	3	3	3	3	3	3
Golden	3	3	3	2	3	i	4	3
Ibis	oo	00	00-2	3	00	i	00	oo
Leda	3	00	3	i	3	i	4	i
Michigan Amber	3	4	3	3	3	4	3	4
Moro	3	4	oo	i	oo	i	oo	i
Omar	3	3	3	3	3	3	3	3
Rubis	4	3	3	4	3	3	4	4
Suwon 92 x Omar ⁴	00	oo	00	i	00	i	0	00
Yamhill	00	00	-	-	-	-	00	00

(Continued on next page)

Table 4. (Continued)

Variety	SW-93-1		SW-95-1		SW-92-1	
	seedling	mature plant	seedling	mature plant	seedling	mature plant
Cappelle Desprez	2	00	3	2	0	i
Chinese 166	00	i	00	00	00	i
Dippes Triumph	4	3	4	i	3	3
Druchamp	3	0	3	3	00	i
Etoile de Choisy	3	3	3	3	3	i
Flamingo	3	2	3	i	3	i
Gaines	3	4	3	3	3	3
Golden	3	3	3	3	3	3
Ibis	i	i	00	i	00	i
Leda	3	2	3	i	3	i
Michigan Amber	3	4	3	3	3	4
Moro	i	i	00	i	00	i
Omar	3	3	3	4	3	3
Rubis	3	3	2	3	4	4
Suwon 92 x Omar ⁴	0	00	00	i	00	i
Yamhill	3	3	00	i	00	i

^a Yamhill was added to the Oregon differentials to characterize SW-93-1.

^b Average of three or more different replicated tests at the 2 C/18 C temperature profile.

identified as one race (OR 8-69) on the Oregon seedling differentials. Cappelle Desprez was used to separate SW-95-1 (Druchamp race) and SW-92-1 (albino race) as distinct races. SW-92-1 is an albino isolate from Montana originally isolated by Dr. E. L. Sharp at Bozeman. This isolate is identical in virulence to the yellow isolate from which it mutated based on IT's of more than 50 varieties (Brown and Sharp, 1970). On the Oregon commercial varieties Druchamp, Gaines, Golden, Moro and Omar, the albino race displays the same IT's as OR 8-69. Host IT rather than spore color was used to separate the albino race from other isolates.

Mature Oregon Differential Varieties

Seven races were identified on the mature differential varieties based on their IT at the 2 C/18 C temperature profile (Table 4). Suwon 92 x Omar⁴ and Chinese 166 remained resistant to all isolates. Ibis was susceptible to SW-63s-2, separating it from all other isolates. The susceptibility of Ibis to SW-63s-2 was indicated in the seedling tests, but was not sufficiently consistent to identify it as a separate race from SW-75s-2 on the seedling plants. Moro, Yamhill, and Druchamp separate the Moro race, the Yamhill race and the Druchamp race respectively. Golden was resistant to SW-75s-2, separating it from OR 9-69 and the albino race. The latter two isolates were separated by Etoile de Choisey's resistance to the albino race.

Eight of the 16 varieties tested as seedlings gave similar IT's as mature plants with all seven isolates (Table 4). The remaining eight varieties changed from a susceptible seedling reaction to a resistant reaction as a mature plant. The change to a more resistant nature on the mature plants was characteristic of individual host-pathogen combinations. Only Leda consistently gave a more resistant reaction for all isolates on the mature hosts. Thus, Leda is the only variety of the Oregon differential set whose resistance to all isolates tested increased as a result of the change from the seedling to the mature plant growth stage.

The commercial variety Gaines, on the other hand, showed no change in IT at the 2 C/18 C temperature profile, but under field conditions changed from susceptible (IT = 3-4) as a seedling to moderately resistant (IT = 1-2) as a mature plant. This implies that the so called "mature plant resistance" of Gaines is a product of the warmer temperatures that prevail during the time the plant is maturing and not due to direct genetic resistance of the host. The type of resistance exhibited by Gaines would best be termed "field resistance" while the type exhibited by Leda should be termed "mature plant resistance." A variety such as Gaines that has "field resistance" instead of "mature plant resistance" might become completely susceptible under unseasonably cool weather conditions.

The increase in resistance from the seedling to the mature plant

growth stage can also be used to separate the seven isolates into races (Table 4). The change in resistance of Cappelle Desprez, Chinese 166, Dippes Triumph, Etoile de Choisy, Golden and Leda separate the Yamhill race, OR 9-69, the Druchamp race, the Moro race, SW-75s-2 and SW-63s-2 respectively. Dippes Triumph and Etoile de Choisy are required to separate the albino race from the other isolates.

Evaluation of varietal resistance to stripe rust may be made on seedling plants as well as mature plants since the tendency is toward more resistance in the mature plant.

United States Differential Varieties

The U.S. differentials consist of two parts, the standard set of seven varieties of wheat (Line et al., 1970) and a supplemental set of eight additional varieties not cited in Line's paper (Table 2). Five races can be identified with the standard set (Table 5). Lemhi is the universal suscept. Riebesel and Suwon 92 x Omar⁴ are resistant to all isolates tested. The variety Moro identifies the Moro race while OR 8-69 and the Yamhill race cannot be separated on the standard set. The resistance of Heines VII to the albino race separates it from the remaining isolates. Chinese 166 is resistant to OR 9-69 and susceptible to OR 10-70, separating them as distinct races, but OR 9-69 and the Druchamp race appear to be similar on the standard set.

Table 5. Infection types of eight isolates of stripe rust on the U. S. differential wheat varieties incubated at the 2 C/18 C profile.

U. S. varieties	Variety number	SW-57-1	SW-63s-2	SW-75s-2	SW-82-1	SW-89-1	SW-93-1	SW-95-1	SW-92-1	
Lemhi	1	3	3	4	3	4	4	4	3	
Chinese 166	2	oo	00	0	00	3	0	i	3	
Heines VII	3	3	3	3	3	2	4	2	oo	
Moro	4	3	i	oo	00	00	i	oo	00	
Suwon 92 x Omar ⁴	5	00	i	00	00	00	00	i	00	
Druchamp	6	00	00	00	2	2	00	3	00	
Riebesel	7	oo	i	0	00	00	00	00	oo	
<u>Supplemental Varieties</u>										
Lee	8	00	0-3	0	0	2	00	i	00	
Heines Kolben	9	00	2	3	00	1	3	i	00	
President Riverain	10	2	3	3	3	3	3	oo	oo	
PI 178383	11	2	i	oo	oo	oo	i	i	oo	
Medeah	12	00	2	2	00	2	3	3	-	
Golden	13	3	2	3	4	4	3	3	2	
Alba	14	2	2	3	3	3	3	3	-	
Vilmorin 23	15	00	2	1	3	3	3	3	-	
<u>U. S. Race designation</u>										
		2, 7, 5, 6/1, 3, 4	4, 5, 7, 2, 6/3, 1	4, 5, 6, 2, 7/3, 1	2, 4, 5, 7/6, 1, 3	4, 5, 7/3, 6, 2, 1	4, 5, 7, 2, 6/1, 3	2, 5, 4, 7/3, 6, 1	3, 7, 4, 5, 6/1, 2	

With the exception of PI 178383 all the supplemental varieties respond differentially to the isolates tested. PI 178383 contains the same major gene as Moro but also has additional minor genes (Sharp and Hehn, 1967). Thus it gives a type one to two reaction compared to a type three for Moro when inoculated with the Moro race. With the supplemental varieties, OR 8-69 and the Yamhill race can be separated using Vilmorin 23. The latter could be identified on Yamhill alone if the variety were included in the U.S. set of differential varieties. Additionally, OR 9-69 and the Druchamp race can be separated with the aid of President Riverain.

The supplemental varieties offer additional evidence for the race identification made on the standard set, and divide the isolates used into additional races.

Oregon Field Differential Varieties

Because of the variability in IT and possible escape from infection under field conditions, field race identification was not possible of all locations. The IT's for the 12 field differentials at 11 locations are given in Table 6. Data for four sites were sufficiently sparse to prevent any race analysis. Either rust failed to develop at all (Klamath Falls) or percentage of attack was sufficiently low to suggest several susceptible varieties may have failed to become infected (Ontario, Moro, Madras).

Table 6. Infection types of 12 Oregon field differential wheat varieties at 11 field locations from 1968 through 1971.

Variety	Hyslop				Aurora				Astoria				Medford				Klamath Falls				Madras				
	68	69	70	71	68	69	70	71	68	69	70	71	68	69	70	71	68	69	70	71	68	69	70	71	
173438 x Elgin	3	3	2	3	4	3	2	2	4		2		2										3	i	-
Cappelle Desprez	i	2	i	i	i	2	2	2	i		i		i										i	i	-
Chinese 166	-	-	2	i	-	-	3	3	-		i		-										-	i	-
Druchamp	i	i	i	i	i	i	1	1	i		i		i										i	i	-
Golden	3	3	3	4	4	3	3	3	4		3		3										i	2	-
Heines VII	2	2	2	3	2	2	2	3	i	No Rust	2	No Rust	3	No Rust	No Rust	No Rust	No Rust	No Rust	No Rust	No Rust	No Rust		i	i	-
Hymar x Orfed	3	3	4	4	4	3	4	4	3	No Rust	3	No Rust	i	No Rust	No Rust	No Rust	No Rust	No Rust	No Rust	No Rust	No Rust		3	3	-
Moro	i	i	i	2	i	i	i	i	i		i		i										i	i	-
Nugaines	2	2	2	2	i	2	2	3	i		2		i										i	2	-
Omar	3	3	3	3	3	3	3	3	3		3		3										i	2	-
Riebesel	-	i	i	i	-	i	i	i	-		i		i										i	i	-
Suwon 92 x Omar ⁴	i	i	i	i	i	i	i	i	i		i		2										i	i	-

(Continued on next page)

Table 6. (Continued)

Variety	Pendleton				Moro				LaGrande				Ontario				Roseburg			
	68	69	70	71	68	69	70	71	68	69	70	71	68	69	70	71	68	69	70	71
173438 x Elgin		3	3	3		i			-	-	2	i	i	i	-	-	-	2	-	
Cappelle Desprez		2	i	-		i			-	-	i	i	i	i	-	-	-	i	-	
Chinese 166		-	3	-		i			-	-	3	i	i	i	-	-	-	2	-	
Druchamp		i	i	i		i			-	-	2	i	i	i	-	-	-	i	-	
Golden	No Rust	3	3	3	No Rust	2	No Stand	No Stand	-	-	3	4	i	i	No Rust	-	-	-	3	-
Heines VII	No Rust	3	2	2	No Rust	i	No Stand	No Stand	-	-	2	i	i	i	No Rust	-	-	-	i	-
Hymar x Orfed		3	3	3		i			-	-	3	3	2	i	-	-	-	3	-	
Moro		i	i	2		i			-	-	i	i	i	i	-	-	-	i	-	
Nugaines		2	1	2		i			-	-	i	2	i	i	-	-	-	1	-	
Omar		3	3	3		2			-	-	3	4	i	2	-	-	-	3	-	
Riebesel		i	i	i		i			-	-	i	i	-	i	-	-	-	i	-	
Suwon 92 x Omar ⁴		2	i	i		i			-	-	i	i	-	i	-	-	-	i	-	

Field races at Hyslop site appear to be different than at the Aurora site. The differences are based on the general resistance of Cappelle Desprez and Chinese 166 at Hyslop compared to a more susceptible reaction at Aurora.

A tendency toward a more susceptible reaction on Cappelle Desprez, Druchamp, Heines VII and Nugaines over a four year period at Aurora suggests a race shift in the rust population at that location. Although Omar has given a type three reaction over the same period of time, an increasing amount of chlorosis has been noted, suggesting a more resistant nature of the variety to the prevailing field races.

Field races at Pendleton appear to be similar to those present at Aurora. Cappelle Desprez and Chinese 166 were infected at both sites as were the more susceptible varieties Omar, Nugaines, Heines VII, Hymar x Orfed, Golden and 173438 x Elgin. Suwon 92 x Omar⁴, Riebesel, Druchamp and Moro remained resistant for the four years noted at Hyslop and Pendleton with the exception of Moro at both sites in 1971.

Except for the questionable resistance of Hymar x Orfed and Nugaines at Medford, field races at Astoria and Medford were similar. Field races at Roseburg and LaGrande differ from each other and from Medford and Astoria based on their resistance to Druchamp and Heines VII respectively.

At the Pendleton and Hyslop sites a new race pathogenic on Moro

was noted in 1971. This race is believed to have derived from OR 7-68 used in field inoculations at both sites. OR 7-68 is a bulk isolate from LaGrande, Oregon, and may contain several biotypes of unknown pathogenicity. Since its collection, the isolate has been increased in limited quantity in the growth chamber on Gaines and Omar seedlings. OR 7-68 was screened on the variety Moro only during race identification studies, exposing it to relatively few Moro plants. It is possible that the Moro biotype failed to appear under these conditions due to its low frequency in the population, but when increased under field conditions, was screened from the population on the variety Moro. The possibility that the new Moro race arose from OR 7-68 as a mutation under growth chamber conditions seems unlikely, but should not be discounted.

Discussion

Six races of stripe rust were identified on seedlings of the Oregon set of stripe rust differential varieties. Using these same varieties, seven races were identified on the mature plants. The differential action of Golden as a mature plant separates SW-75s-2 from SW-63s-2. Golden is susceptible to SW-75s-2 as a seedling, but is resistant as a mature plant. This change in resistance is exhibited by other variety-isolate combinations and permits differential separation of the seven isolates. Changes in resistance of seedling

differentials grown at the 2 C/18 C temperature profile compared to 18 C constant temperature were used by Beaver (1969) to identify races of stripe rust. Changes in host-pathogen interaction due to controlled variations in the environment appear to be as reliable for race identification as the standard technique where environmental factors are not varied. These two techniques provide a dual system for race identification with a resultant check on the accuracy of race separation.

In comparing the seedling and mature plant reactions of the Oregon differentials, the change in IT was always toward the more resistant reaction on the mature plant and appears to be under host control. Only specific host-pathogen combinations such as the Moro race on Flamingo trigger this event with the exception of the variety Leda. In this case a shift toward a more resistant infection type took place with all isolates, suggesting that the direction and triggering of the shift are controlled by the variety alone. This response on Leda is true mature plant resistance, since it is a character of the host alone and not influenced by variations in the pathogen or environment.

Varieties such as Gaines and Nugaines are highly susceptible as seedlings, but are moderately resistant as mature plants under field conditions. In the growth chamber at the 2 C/18 C temperature profile the mature plants were as susceptible as the seedlings. The resistance of these varieties is brought on by an increase in seasonal

temperature as the crop matures. This type of resistance, sometimes called "mature plant resistance," would be better called "field resistance" and distinguished from "mature plant resistance" of the kind described for Leda.

Care should be exercised in reliance upon "field resistance" for protection from stripe rust epidemics, especially in areas where periodic cool weather is possible late in the growing season.

The standard set of U. S. differentials is not as definitive as the Oregon differential varieties in separating races of stripe rust, but with the addition of the eight supplemental varieties all eight isolates can be separated as distinct races. The standard set of U. S. differentials is capable of identifying new races virulent on present sources of stripe rust resistance in the breeding program and to this end it is satisfactory. However, for use in identifying and describing race distribution and variation, additional differential varieties would be desirable.

The extent of physiologic specialization of stripe rust in the Pacific Northwest appears to be extensive. In conjunction with other recent work (Beaver, 1969), 12 races of stripe rust have been identified from 14 isolates selected to maximize race variation, most of them from areas of Oregon (Table 7). The Oregon field differentials further substantiate the extensive race variation in Oregon since different field races could be identified at six of the 11 sites.

Table 7. Identification of 12 races of stripe rust from 14 selected isolates on the Oregon differentials at the 2 C/18 C temperature profile.

Variety	SE-2-1	SB-40-1	W-7	SW-7-1	SW-47-1	SW-2-1	SW-57-1	W-54	SW-75s-2	SW-63s-2	SW-95-1	SW-82-1	SW-92-1	SW-93-1
Cappelle Desprez	R ^a	R	R	R	R	R	R	R	R	R	S	R	R	MR
Chinese 166	R	R	S	R	S	R	R	R	R	R	R	S	R	R
Dippes Triumph	S	S	S	R	S	R	MR	MR	S	S	S	S	MR	S
Druchamp	R	MR	R	R	R	R	R	R	R	R	S	MR	R	S
Etoile de Choisy	S	S	S	S	R	R	S	S	S	S	S	S	MR	S
Flamingo	R	MR	S	R	R	MR	S	R	R	R	S	S	S	S
Gaines	S	S	S	S	R	MR	S	S	S	S	S	S	S	S
Golden	S	R	R	S	R	R	S	S	S	S	S	S	MR	S
Ibis	R	R/S	R	R	R	S	R	R	R	R	R	R	R	R
Leda	R/S	R	S	MR	R	S	S	S	S	S	S	S	S	S
Michigan Amber	S	S	S	S	R	S	S	S	S	S	S	S	S	S
Moro	R	R	R	R	R	R	S	R	R	R	R	R	R	R
Omar	R	S	S	S	R	R	S	S	S	S	S	S	S	S
Rubis	S	S	S	S	S	S	S	S	S	S	MR	S	S	S
Suwon x Omar ⁴	R	R/S	R	R	R	R	R	R	R	R	R	R	R	R
Yamhill	R	R	R	R	R	R	R	R	R	R	R	R	R	S
	<u>Oregon race designation</u>													
	OR 3-65	OR 4-67	OR 1-64	OR 2-64	OR 5-67	OR 6-67	Moro	OR 7-68	OR 8-69	OR 8-69	Druchamp	OR 9-69	Albino	Yamhill

^aR = Resistant, S = Susceptible, MR = Moderately Resistant, R/S = Variable

The presence of stripe rust at all 11 sites indicates that the fungus is ubiquitous in Oregon although its presence may vary from year to year. A further study of physiologic specialization from wheat growing areas in Washington, Idaho and Montana will undoubtedly reveal a population of races of stripe rust as varied as found in Oregon.

III. INFLUENCE OF WHEAT VARIETY AND DEW PERIOD ON GERMINATION, PENETRATION AND INFECTION BY STRIPE RUST

The infection process of Puccinia striiformis West. is more sensitive to environment than other cereal rusts. Consequently rigid environmental controls must be used to obtain reproducible results. Straib (1940) noted that the temperature at which uredospores develop determines their germination potential. Spores produced at 20-25 C germinated sooner and over a wider range of temperatures than spores produced at 8-10 C. Straib also noted that light frosting during fructification enhanced germination rates at temperatures just above freezing. Sharp (1965) reported up to 44 percent reduction in germination of stripe rust on wheat leaves grown at 24 C compared to leaves grown at 15 C. He suggested that this inhibition was due to secretions or emanations on the leaf surface, but gave no supporting data. A minimum dew period of two to three hours is required for infection (Shaner, 1969); however, little is known of the effects of different wheat varieties or variations in the dew period on the infection process.

Materials and Methods

Seedlings of the 15 Oregon differential varieties (Table 2) and the variety Lemhi were grown in 17 x 95 mm plastic disposable test

tubes in an environment chamber programmed for 2 C/18 C (night/day) temperature with 1000 foot candles of light for 12 hours. The seedlings were inoculated with single spore isolates of stripe rust previously increased on the variety Omar and stored at 3 C and 50 percent relative humidity. Inoculations were made by atomizing a freon-113 suspension of uredospores over the wheat leaves from a distance of 8-12 inches (Miller, 1965). After inoculation the plants were placed in a dew chamber with 12 C air temperature for up to 24 hours and then examined or returned to the growth chamber for symptom development.

All observations were made directly on the leaf surface with a microscope and an epi-illumination attachment. Results were based on examination of 100-200 spores per leaf. Any spore with a germ tube longer than the spore diameter was considered germinated. Any germ tube that stopped and turned down at a stomate was considered as a penetration. Infections per leaf were determined by counting the small flecks that developed on the leaf six to eight days after inoculation.

Results

Inhibition of Germination

Seedlings of the 15 Oregon stripe rust differential varieties

were inoculated with race OR 8-69 of stripe rust and placed in a dew chamber. Four plants of each variety were removed and examined every two hours over an eight hour period. The number of uredospores on the leaf surface that had germinated or penetrated were counted. After examination, the plants were placed in a growth chamber at the 2 C/18 C temperature profile for symptom development.

Inhibition of germination compared to the water-agar control occurred in five varieties between two and four hours (Figure 1). After six hours of dew, germination increased on the same five varieties and then dropped below the 30 percent level after eight hours. On those varieties where germination was not inhibited, it exceeded the 62 percent germination on the water-agar control, indicating that some wheat leaves are a better substrate for germination than water-agar. Varieties selected could be grouped statistically on the basis of uredospore germination at all three time intervals. Grouping of varieties suggests that an inhibiting factor is functioning at nearly the same level on all varieties in one group. It is unknown whether this factor is mechanical or chemical in nature.

Germ tube penetration generally increased over the three time periods (Figure 2). Penetration of several varieties was significantly greater over other varieties at each time period. Stimulation of penetration appears to act through more rapid germ tube elongation.

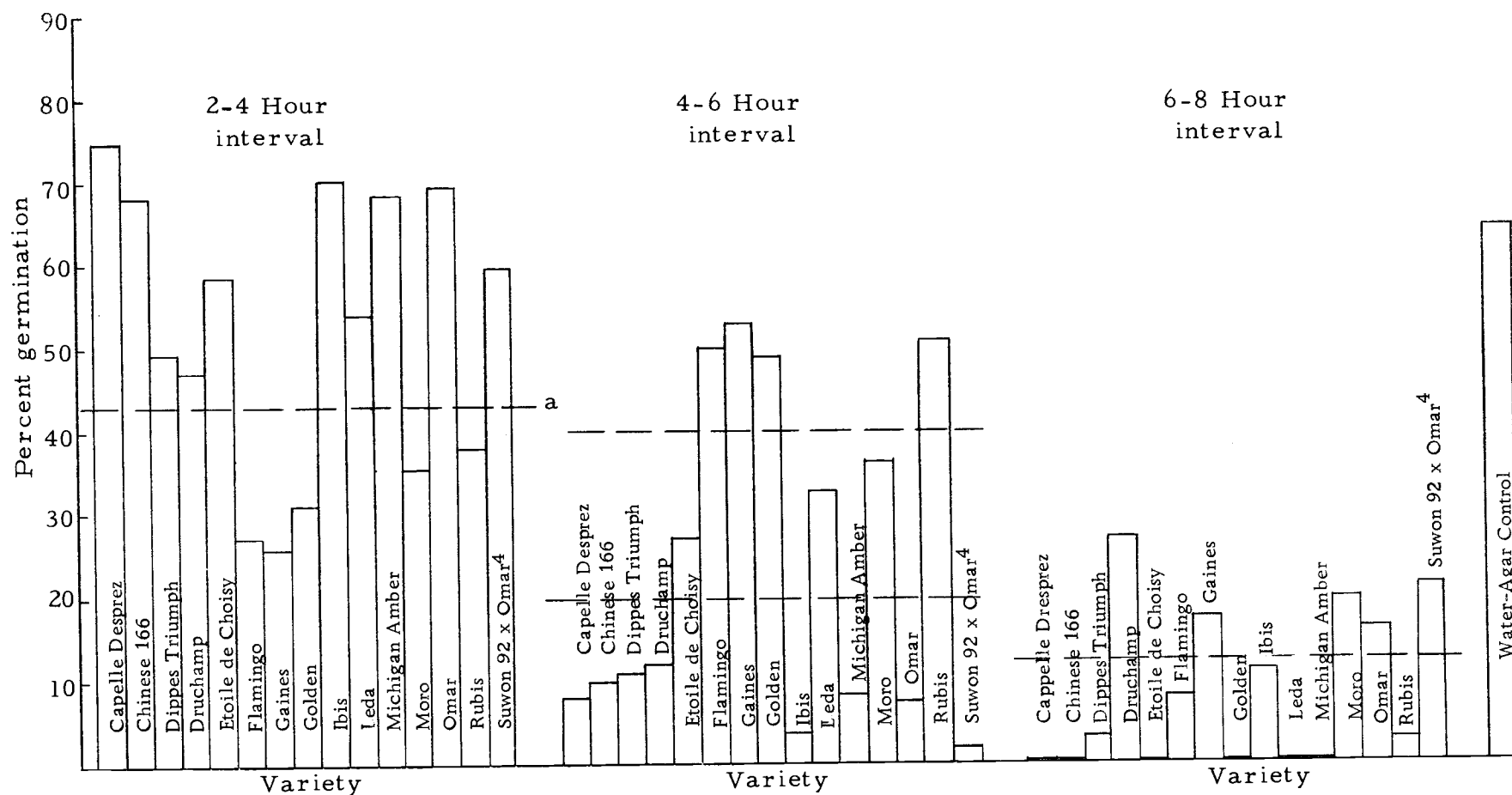


Figure 1. Stripe rust uredospore germination on leaves of 15 Oregon differential varieties at two-hour incubation intervals.

^aVarieties above line significantly different from those below line ($P = .01$).

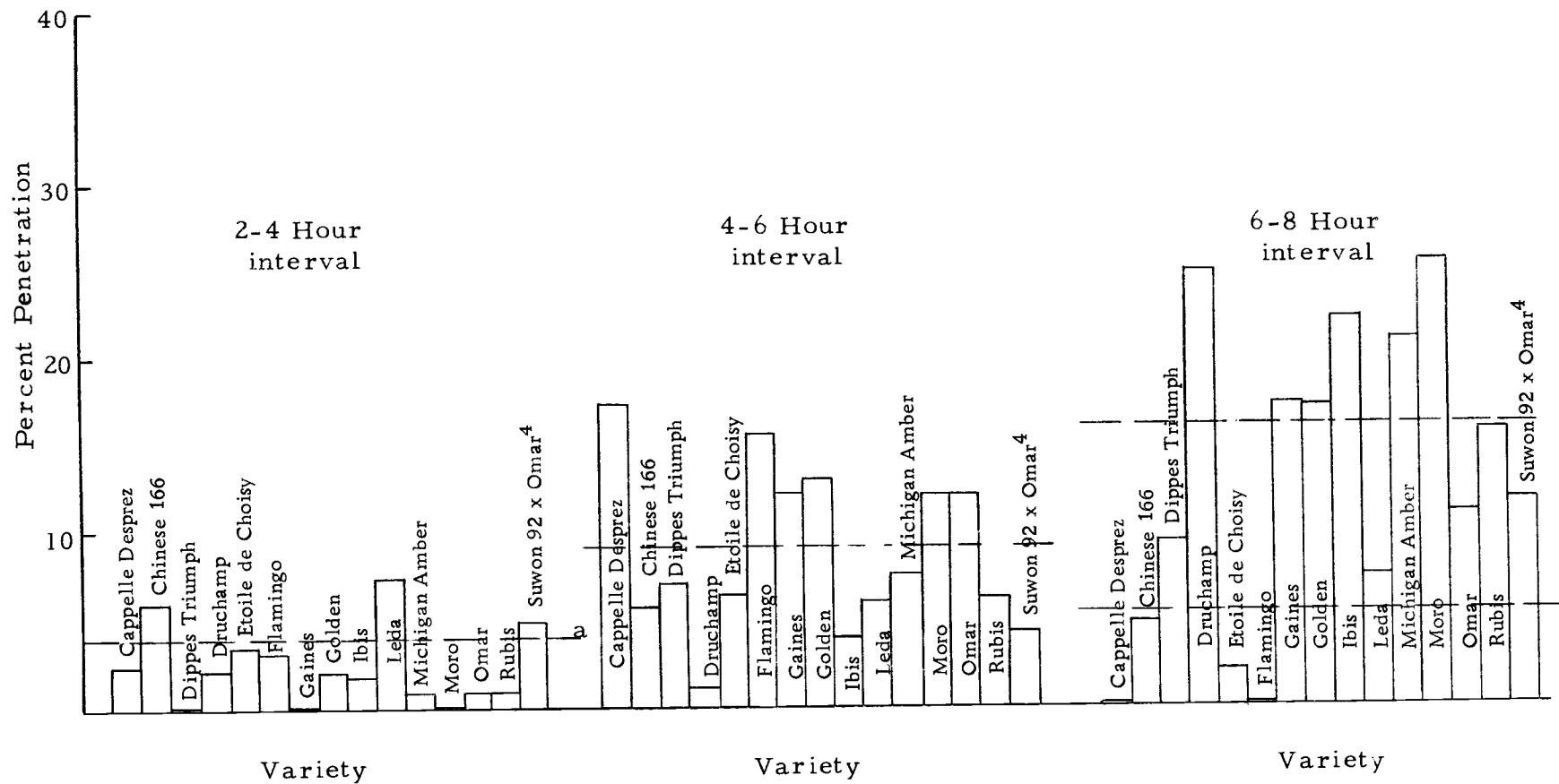


Figure 2. Germ tube penetration of wheat leaves of 15 Oregon differential varieties at two-hour incubation intervals.

^aVarieties above line significantly different from those below line (P = .01).

Germ tube elongation was not measured directly but was based on differences in times from germination to penetration. Exudates or other stimuli on the leaf surface or emitted from stomatal openings may speed germ tube elongation and/or stomatal entry. As with germination, varieties could be grouped statistically on the basis of germ tube penetration. No varietal correlations could be made between inhibition of germination and penetration. With varieties 4, 9, 11 and 12 the greatest percentage of spore germination took place in the first time period (two to four hours) while the major portion of penetration took place during the third time period (six to eight hours). The time between spore germination and penetration may be as long as six hours on these varieties, leaving the growing germ tubes subject to drying and death over a relatively long period of time. This response does not appear to correlate with resistance (Table 8).

Infection, based on leaf flecking six to eight days after inoculation, was calculated as a percent of germ tube penetration (Figure 3). Again varieties could be statistically grouped, but percentage of infection and varietal resistance were not related. This does suggest, however, that prudent selection for a susceptible variety for single sporing could improve percentage of success. Variety 14, Rubis, appears to be a universal suscept and gave the highest percentage of infection in this study. A comparison of the mean percent infection for the 15 varieties with the mean percent success for single sporing

Table 8. Mean germination, penetration and infection percentages for stripe rust uredospores on 15 Oregon differential wheat varieties.

Varieties ^a	Variety no.	Germination (%) ^b			Penetration (%) ^b			Infection ^b (%)
		Time interval			Time interval			
		2-4	4-6	6-8	2-4	4-6	6-8	
Suwon 92 x Omar ⁴	15	59.3	2.0	21.0	4.6	4.0	11.6	2.7
Moro	12	35.3	36.7	19.3	0.7	12.0	25.3	3.3
Ibis	9	70.0	3.7	10.7	1.7	3.7	22.3	3.0
Druchamp	4	47.3	12.0	26.7	2.7	1.0	25.0	3.0
Cappelle Desprez	1	74.7	8.0	0.0	2.3	17.3	0.0	2.3
Flamingo	6	27.0	50.0	8.3	3.0	15.7	0.0	6.3
Chinese 166	2	68.0	10.0	0.0	6.0	5.7	4.7	2.7
Leda	10	54.0	33.0	0.0	7.3	5.7	7.7	7.0
Dippes Triumph	3	49.0	11.0	3.0	0.7	7.0	9.3	2.3
Etoile de Choisy	5	58.7	27.0	0.0	3.3	6.3	2.0	5.7
Gaines	7	25.7	53.3	17.0	0.7	12.0	17.3	2.7
Golden	8	31.0	49.0	0.0	2.0	13.0	17.0	1.7
Omar	13	69.3	7.7	16.0	1.0	12.0	11.0	6.7
Michigan Amber	11	68.0	8.3	0.0	1.0	7.3	21.0	5.7
Rubis	14	38.0	51.0	2.7	1.0	6.0	15.7	9.3

^a Ranked in order from most resistant to most susceptible.

^b Mean of three replications.

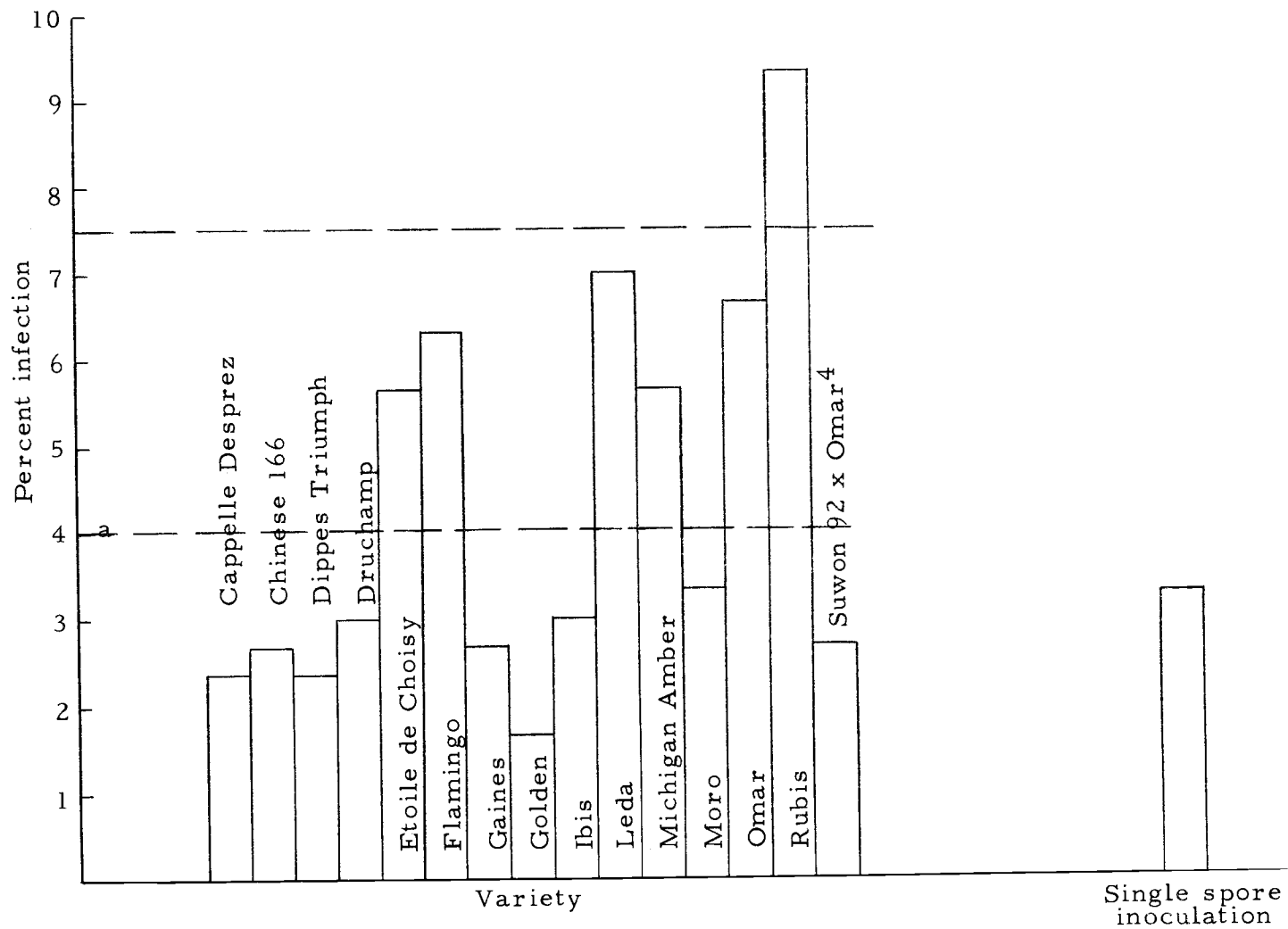


Figure 3. Infection of wheat leaves of 15 Oregon differential varieties incubated at 2 C / 18 C temperature profile.
^aVarieties above line significantly different from those below line (P = .01).

(3.16 and 3.33 percent respectively) suggests that the observed infection rate is a realistic figure.

Dew Period

Drying of foliage for less than ten minutes at intervals of one, two or four hours after dew formation reduced or prevented leaf infection even after 12 hours of dew. Figures 4 and 5 show the percentage of leaves infected with OR 8-69, the Druchamp race and OR 9-69 on two varieties of wheat.

The first four hours of dew render the uredospores most sensitive to drying. The first hour is, however, not as critical as the succeeding three. A "J" shaped curve is generated in all six cases, but is more pronounced with the spring wheat Lemhi. Under drying conditions, a visible inspection of the leaf surface revealed all germinating spores and germ tubes were collapsed and no longer viable.

Discussion

Germination and penetration of wheat leaves by uredospores of Puccinia striiformis differs on the 15 Oregon differentials. The factors controlling responses appear to be distinct, since relationships between germination and penetration were not consistent for a given variety (Table 8).

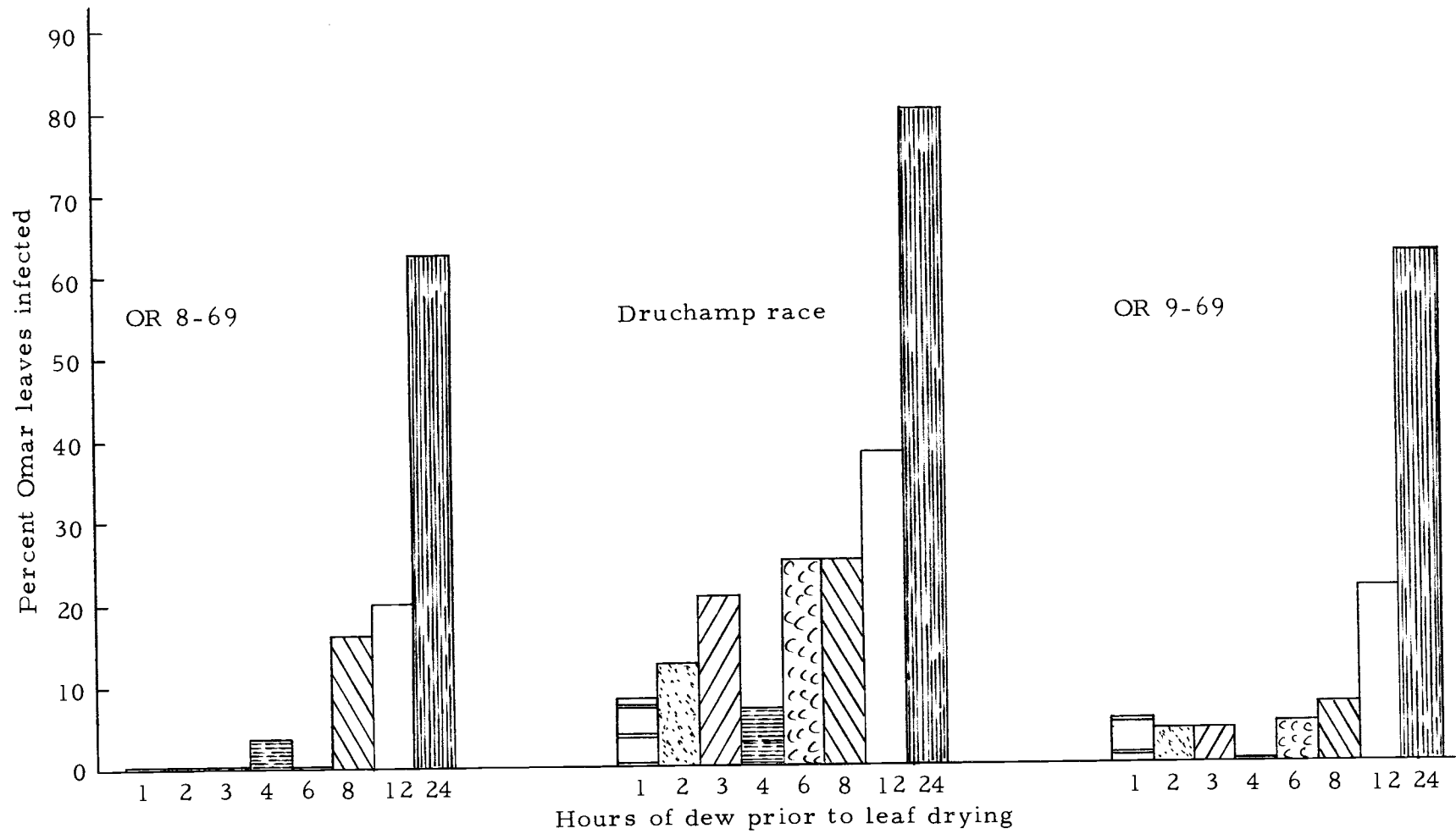


Figure 4. Effect of drying during the dew period on infection of Omar leaves by three isolates of stripe rust.

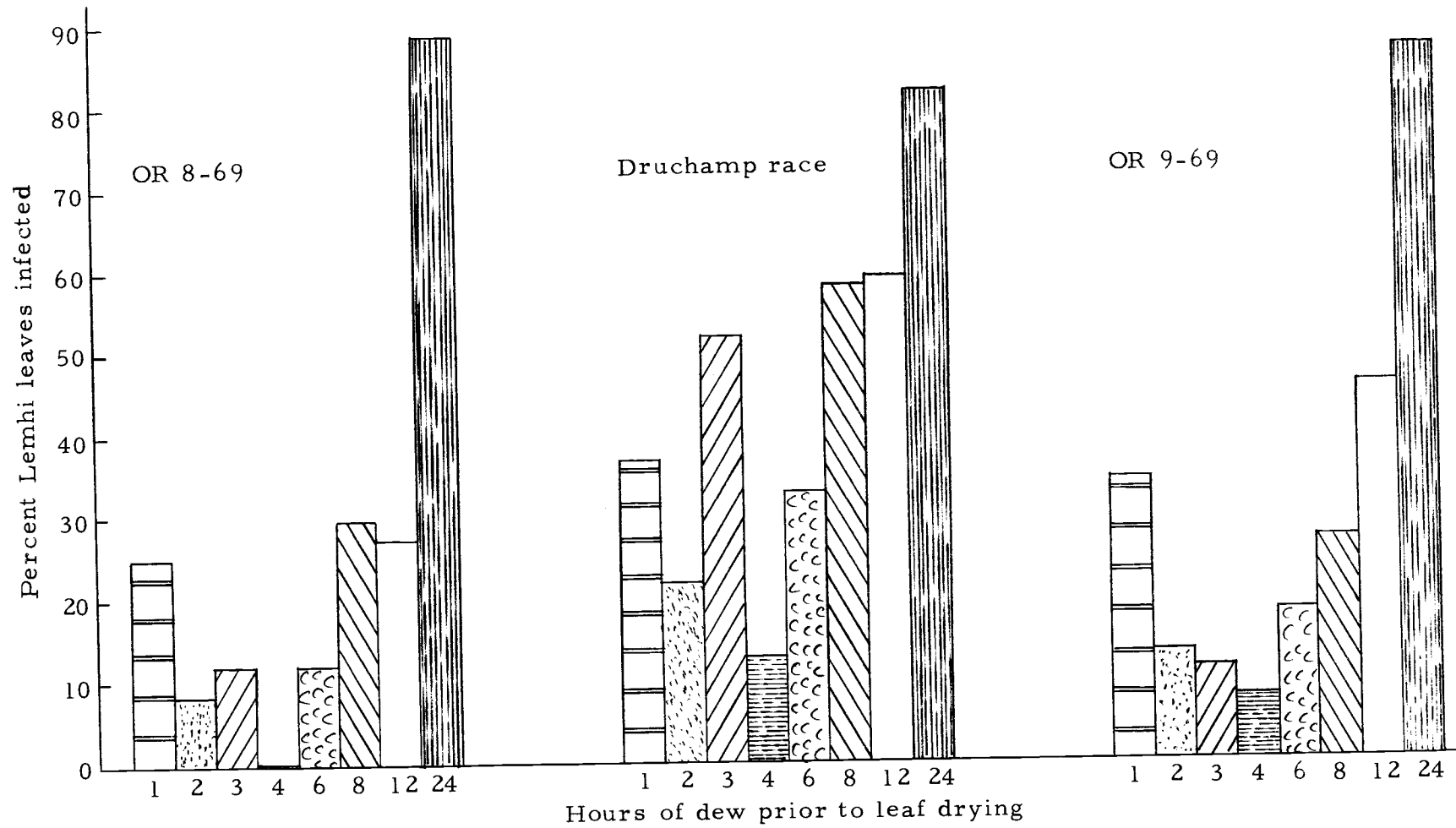


Figure 5. Effect of drying during the dew period on infection of Lemhi leaves by three isolates of stripe rust.

Factors retarding spore germination on wheat leaves were noted by Morgan (1963) and Sharp (1965). These may be derived from the host or from the microflora colonizing the host leaf surface. In either case the response appears to be characteristic of certain varieties (Figures 1 and 2). Grouping of varieties at each of the two-hour intervals reflects similar varietal influences on germination at each group.

Spore germination tests carried out on polyethylene sheets revealed that only spores in contact with water droplets germinated. Burrage (1969) noted similar effects with Puccinia graminis. He also noted that the growth of germ tubes was restricted to areas of the leaf not covered by water droplets. Germ tubes of stripe rust, however, grow randomly over the surface of the polyethylene sheet and exhibit no hydrophobic response.

Variations in leaf surfaces which affect the size or locations of dew droplet formation and prevent spore-droplet contact could retard or prevent spore germination. No visible differences in dew formation on the 15 varieties used in this study were noted; however, close observations were not carried out. Burrage (1969) suggests that chemotropic or hydrotropic responses aid in penetration of germ tubes. This attraction would be preferential for open stomates. Varietal differences such as number of stomates per leaf and time and duration of stomatal opening could influence germ tube attraction and

stomatal penetration. Any delay, therefore, in the infection process is of value in delaying epidemic development of stripe rust.

Drying after short dew periods of three or four hours effectively reduces the amount of viable inoculum available for infection during a 24 hour period. The longer the time period between germination and penetration, the more effective are short dew periods. The effects of inoculum removal on the final disease severity is best explained by the following example:

A useful way to examine the increase in disease severity is to plot the severity of disease against time. Using the logit transformation of van der Plank (1963), the apparent infection rate r characterizes the rate of disease increase. For stripe rust, $r = 0.146$ per unit per day is a realistic apparent infection rate. Using this value for r , the effects of periodic inoculum removals can be demonstrated (Figure 6). For the purpose of illustration, the following assumptions are made:

1. $r = 0.146$ per unit per day before and after inoculum removal
2. 100 percent inoculum removal for five days during a 40 day period
3. initial disease severity = 1 percent
4. time period = 40 days
5. all other influencing factors are constant

Referring to Figure 6, the distance between points A and B

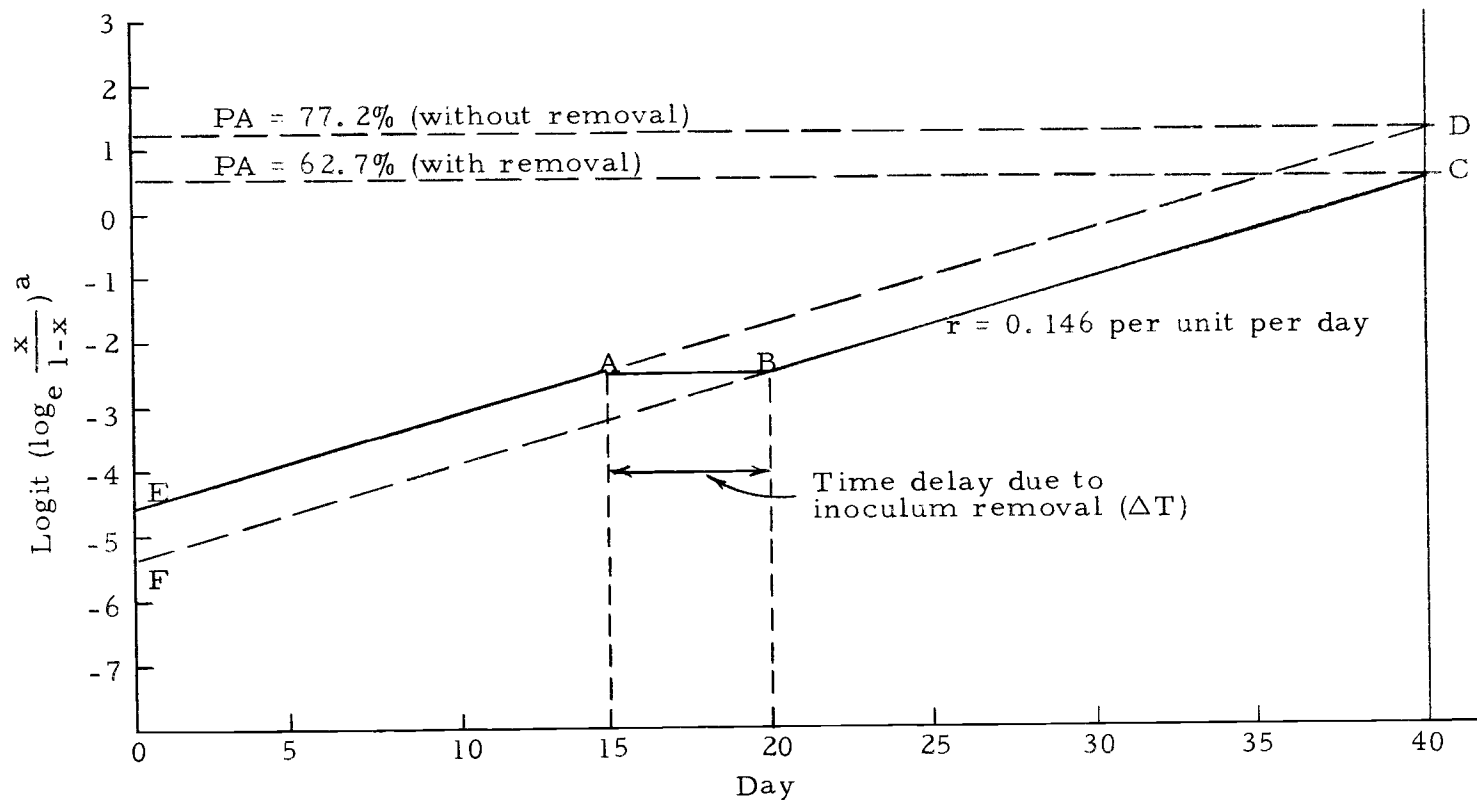


Figure 6. Effect of inoculum removal on final disease development over a 40 day period.

^avan der Plank, 1963

represents the time delay (ΔT) in the disease buildup due to inoculum removal. The distance between points C and D represents a reduction of 14.7 percent in disease severity resulting from inoculum removal for a period of five days. Removal, in this case, has the same effect as reducing the initial inoculum from one percent to 0.5 percent shown at points E and F respectively. Thus, within the 40 day period, the final disease severity would be 77.2 percent compared to 62.7 percent with inoculum removal.

Inoculum removal caused by uredospore death from drying during the dew period effectively reduces final disease severity. This feature undoubtedly functions under field conditions, but has gone unnoticed since it is not reflected in epidemic analysis. Inoculum removal could be exploited by the use of wheat varieties which delay the infection process of stripe rust, rendering the germinating spores more subject to removal from the inoculum supply through drying under short dew periods.

IV. FACTORS INFLUENCING THE SPREAD AND SURVIVAL OF STRIPE RUST UNDER FIELD CONDITIONS

Summer survival of Puccinia striiformis in the Pacific Northwest is a critical stage in its life cycle. The means of overwintering are not well understood and reservoirs of overwintering inoculum have not been clearly defined. In California, grasses in the high mountain areas above 6000 feet have been reported to carry the stripe rust fungus through the summer (Tollenaar and Houston, 1967). Stripe rust has been found on grasses in the high mountains of the Pacific Northwest, but only rarely (Hendrix et al., 1965; Shaner, 1969).

Low levels of overwintering inoculum can place survival pressures on the rust population. Differences in survival ability between biotypes can create shifts in the overwintering rust population. These shifts can be reflected in the rust population the following year. Survival of biotypes depends upon their ability to compete for infection and sporulation sites on a host. Brown and Sharp (1970), however, noted that when collections of an albino isolate and an isolate from the variety Moro were inoculated onto the wheat variety President Riverain, the Moro isolate gave an IT of three while the albino isolate gave an IT of 0. When seedlings were inoculated with a mixture of the two pathogenic types, both produced type three IT's. These workers suggest this phenomenon may explain the persistence of some races of stripe rust for long periods in the absence of

susceptible cultivars.

Spread of stripe rust from small foci in the spring has been difficult to follow because of confusion with outside sources of inoculum. Differences in precipitation and temperature during the winter and spring months can vary the time spore movement begins in the spring as well as the rate at which it moves. The use of an albino isolate of stripe rust eliminates the problem of identification under field conditions and permits a more critical study of the effects of environment on winter and spring spore movement.

September field inoculations with the albino and two yellow isolates were made to evaluate the ability of stripe rust isolates to survive in mixed populations, infect and spread. Mountain plots were also established to evaluate the spread and survival of stripe rust on wheat and native grasses.

Materials and Methods

Omar and Nugaines wheat (1969) and Omar wheat (1970) were planted on 50 x 50 foot pre-irrigated plots in early August. The plots were located at Dufur, Pendleton and LaGrande, Oregon, in 1969 and at Aurora, Moro and Pendleton, Oregon, in 1970.

Plots were also established at two locations in the mountains adjacent to wheat growing regions of Oregon (Table 9). Twelve varieties of wheat differing in their susceptibility to stripe rust were

Table 9. The locations of the mountain plots.

Plot	County	Legal description	Elevation (feet)
Fox Prairie	Umatilla	Sec. 36, T1S, R36E	4000
Tupper	Morrow	Sec. 9, T6S, R27E	4300

grown at each site (Table 13). In addition to the wheat varieties, 12 species of grasses were used during a two year period (Table 14). The plots were 6 x 12 feet and oriented at right angles to one another. Each was surrounded by a wire enclosure to prevent damage from grazing animals. Inoculations were made by spraying a freon-113 suspension of uredospores over the host plants or by transferring infected seedling wheat plants into the plots.

Results

1969 Plots

Field plots were established at Pendleton, LaGrande, and Dufur, Oregon, in August, 1969. A one foot square at the center of each site was inoculated on September 8, 1969, with uredospores of race OR 7-68. The plants were in the three to four leaf stage of growth. One-half the inoculated area was covered with plastic to facilitate dew formation.

Initial infection occurred only on plants covered with plastic at

the Dufur and LaGrande sites. At Pendleton, infection also occurred on plants not covered. The spread of stripe rust from the inoculation center was observed over a 75-day period (Table 10). Final readings were made on November 18-19.

Table 10. Disease gradients in late summer inoculated wheat plots, 1969.

Location	Days after inoculation ^a	Percentage of attack					
		Feet from inoculation point					
		0	5	10	15	20	25
Dufur	18	1	0	0	0	0	0
Dufur	35	10	1	0.01	0	0	0
Dufur	75	50	5	0.01	0	0	0
Pendleton	18	5	0	0	0	0	0
Pendleton	35	25	10	1	0.1	0	0
Pendleton	75	75	75	50	10	1	0.1
LaGrande	18	0	0	0	0	0	0
LaGrande	35	0.01	0	0	0	0	0
LaGrande	75	5	0	0	0	0	0

^aInoculated September 8, 1969.

At La Grande there was no sporulation from secondary infection at the time of the final reading. At Pendleton there had been three infection and sporulation cycles with a sharp gradient of attack toward the perimeter of the plot 25 feet away. The percentage of attack (PA) at the inoculation site was 75 and at the perimeter only about 0.1 percent. At the Dufur location secondary sporulation was found no greater than ten feet from the site of inoculation.

1970 Plots

In August, 1970, field plots were established at Pendleton and Moro in eastern Oregon, and at Aurora, Oregon, in the Willamette Valley. Three pots containing four to five inoculated non-sporulating wheat seedlings in the three to four leaf growth stage were transplanted 15 feet apart in a line across the center of each of three field plots on September 15, 1970, at all three locations. Each pot contained plants inoculated with one of three isolates, the albino race, OR 8-69 or OR 9-69. The spread of stripe rust from the three pots of inoculated wheat was followed through the entire growing season (September through July) (Table 11).

At the Pendleton site, initial sporulation occurred about September 30, 1970, followed by one infection and sporulation cycle. By December 24, no sporulating rust could be found in the plot. Rust was not visible again until March 23 when one of the yellow isolates appeared near the North edge of the plot. On April 19 the albino isolate was also found sporulating along the south edge of the plot. On May 18 the albino isolate was located a distance of 30 yards outside the plot area and on June 9 was located at a point 150 yards from the plot.

The general pattern of spread and infection at the Moro location paralleled that of the Pendleton location except that its disappearance

Table 11. Disease gradients and spread from late summer inoculated wheat plots at Aurora, Moro, and Pendleton, Oregon, 1970.

Days after inoculation ^a	Percentage of attack						Distance albino found from plot		
	Feet from inoculation point						100	500	1000
	0	5	10	15	20	25			
<u>Aurora</u>									
15	10	0	0	0	0	0			
41	10	1	tr	0	0	0			
48	25	25	5	1	tr	0			
89	25	5	5	5	1	1			
143	50	25	10	5	5	5			
176	75	50	50	25	10	10			
205	75	75	75	50	50	25	X	X	
226	100	100	100	75	75	75	X	X	
247	100	100	100	100	100	100	X	X	X
<u>Moro</u>									
15	5	0	0	0	0	0			
41	5	tr	0	0	0	0			
89	1	tr	tr	0	0	0			
143	0	0	0	0	0	0			
176	tr	tr	0	0	0	0			
203	0	0	0	0	10	5			
254	1	1	1	5	10	25	X		

(Continued on next page)

Table 11. (Continued)

Days after inoculation ^a	Percentage of attack						Distance albino found from plot		
	Feet from inoculation point						100	500	1000
	0	5	10	15	20	25			
	<u>Pendleton</u>								
15	5	0	0	0	0	0			
41	5	1	0	0	0	0			
90	0	0	0	0	0	0			
143	0	0	0	0	0	0			
176	0	0	0	0	0	5			
203	0	0	0	0	5	10			
232	tr	tr	tr	1	10	25	X		
254	1	1	1	1	25	50	X	X	

^aInoculated September 15, 1970.

and reappearance were approximately one month later.

At the Aurora location in the Willamette Valley sporulation and spread continued steadily through the winter. The apparent infection rate (r) (van der Plank, 1963) at the inoculation site was 0.0255 per unit per day from day 15 through day 247. At the edge of the plot 25 feet from the site of inoculation, r equaled 0.0516 from day 89 through day 247. The difference in time of rust appearance at the inoculation site (day 15) and the edge of the plot (day 89) is reflected in the difference between the two r values, since final disease severity was reached simultaneously at the two locations (day 247). Thus, r is greater at the edge of the plot since fewer days were required for rust development to reach 100 percent.

On October 26, 1970 (day 41), foci around the inoculation site were obvious. Their shapes were elliptical and elongate toward the southwest (Figure 7). The prevailing winds in the valley are from the west; however, these winds are moist. At times, dry winds from the northwest prevail for short periods, and it is these dry winds that facilitate spore movement as witnessed by the shapes of the foci within the plots. The foci surrounding the albino inoculation site were initially larger than the other two. This may indicate a larger production of inoculum by this isolate in the fall. By May 12 the foliage in the entire plot was 100 percent infected by the albino and yellow isolates. On April 21 the albino isolate was found in adjacent wheat 200

yards from the plot and by June 2 could be located at the edges of the experiment station 1/4 mile from the inoculation site. On April 21 it became apparent that a gradient of white and yellow isolates existed across the plot (Figure 7). There appears to be a mutual exclusion between the albino and yellow isolates when infection of the same leaf occurs.

Race Compatibility

To further study the relationship seen in the field between the albino isolate and other stripe rust isolates, a study was undertaken in the growth chamber where closer control could be kept over mixing of the various isolates.

The Moro race, the Druchamp race, OR 2-69 and OR 1-69 were inoculated individually or mixed with equal amounts of the albino race and inoculated onto the wheat varieties Omar, Druchamp, Lemhi, President Riverain and Moro. After inoculation the plants were given a 24 hour dew period and placed in a growth chamber at the 2 C/18 C temperature profile for symptom development.

The results are given in Table 12. The varieties Omar and Lemhi gave an IT of three to four with all five isolates when inoculated separately or in paired inoculations with the albino race. Druchamp, President Riverain and Moro were resistant to the albino race in both the individual and paired tests. Druchamp and Moro gave an IT of

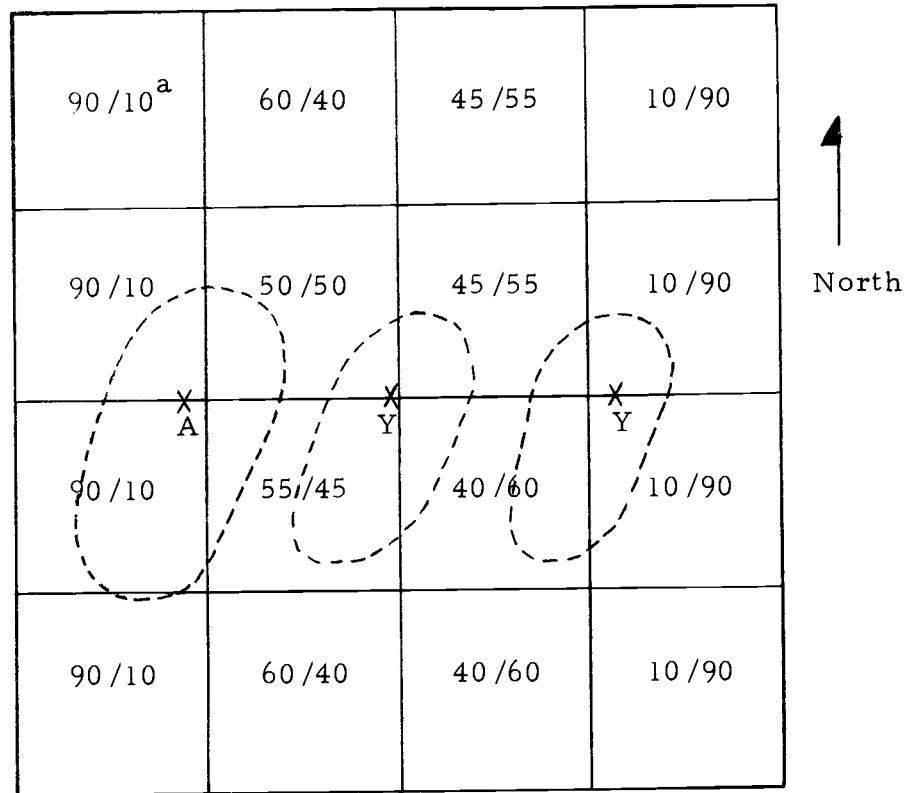


Figure 7. Foci development and proportion of albino to yellow isolates in late summer inoculated wheat plot at Aurora, Oregon, 1970.

^aProportion of albino/yellow isolates in each grid on May 13, 1971

X = Site of inoculations (one 4-inch pot of infected seedlings)

A = albino race; Y = yellow race

--- = Foci present on October 26, 1970

Table 12. Infection types produced on five wheat varieties inoculated with the albino race and four yellow isolates (Moro race, Druchamp race, OR 8-69, OR 9-69) of stripe rust individually and paired when incubated at the 2 C/18 C temperature profile.

Variety	Inoculated individually					Inoculated in pairs							
	SW-57-1	SW-95-1	SW-82-1	SW-75s-2	SW-92-1	SW-57-1	SW-92-1	SW-95-1	SW-92-1	SW-82-1	SW-92-1	SW-75s-2	SW-92-1
Omar	4	3	3	3	3	3	3	3	3	3	3	3	3
Druchamp	00	3	00	00	00	00	00	3	i ^a	00	00	00	00
Lemhi	4	4	4	4	4	4	4	4	4	4	4	4	4
President Riverain	3	00	3	3	00	3	i	00	00	3	i	3	i
Moro	3	00	00	00	00	3	i	00	00	00	00	00	00

^aNo sporulation of albino isolate; other symptoms masked by sporulation of yellow isolate.

three to the Druchamp race and the Moro race respectively in both tests. The resistance of President Riverain, Moro and Druchamp to the albino race was not changed when each variety was simultaneously inoculated with a virulent race in the paired test.

Whenever the albino and another isolate sporulated on the same leaf, there was no mixing of sori. A distinct border divided sporulation zones of the two isolates, giving an appearance of bands or islands of white or yellow sori in a field of opposite color (Figure 8). Microscopic examination of the sporulating zones confirmed the exclusion of one isolate from the other. No sorus was found which contained spores of both colors. This same observation was made in the field under natural conditions and the same results were noted.

Mountain Plots

Stripe rust was found on wheat planted in 1969 and 1970 at the Fox Prairie site and in 1967 at the Tupper site. No rust appeared on wheat or grass in 1968 and in 1971 snow mold destroyed the stand at both sites and no evaluations could be made. Only varieties that normally rusted in the wheat growing areas rusted at either location indicating race(s) of stripe rust present in the mountain plots were similar to race(s) in the wheat growing areas (Table 13).

Rust, if present, could generally be found from June through August, but by September when the plots were reseeded for the

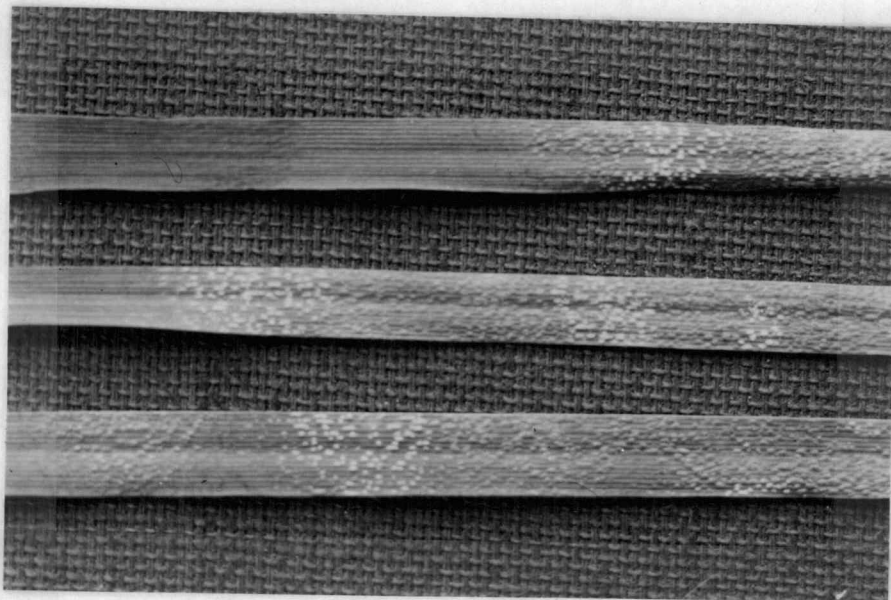


Figure 8. Sporulation zones on wheat leaves inoculated with a yellow isolate (OR 8-69) and the albino race of stripe rust.

Table 13. Infection types produced on the wheat grown at the mountain plots.

Variety	Infection Types (IT)									
	Fox Prairie					Tupper				
	1967	1968	1969	1970	1971	1967	1968	1969	1970	1971
Cappelle Desprez			i	i		i				
Chinese 166			3	3		-				
Druchamp			i	i		i				
Golden	No Rust	No Rust	4	3	No Stand	3	No Rust	No Rust	No Rust	No Stand
Hymar x Orfed			3	3		4				
Moro	No Rust	No Rust	i	i	No Stand	i				
Nugaines			2	i		3				
Omar			4	i		3				
Suwon 92 x Omar ⁴			i	i		i				
173438 x Elgin			3	3		3				

following year, no sporulating rust could be found on late green tillers or native grasses.

The 12 grass species planted in September, 1968, were inoculated on June 6, 1969, to determine the ability of susceptible grass species to become infected under natural conditions in the mountain area (Table 14). In addition several native grasses adjacent to the plots were inoculated at the same time. At the time of inoculation Elymus canadensis was already infected and sporulating with stripe rust from natural infection. On August 16, 1969, Hordeum jubatum, Elymus glaucus, and E. canadensis at the Fox Prairie site and Elymus glaucus and E. canadensis at the Tupper site were rusted. By late September the grasses had dried and no sporulating rust could be found in or out of the plots.

An examination of the grasses the following year revealed no evidence that the rust had overwintered in the mountain plots. Several of the grass species had winter-killed and no rust was found on the remaining plants during the summer of 1970.

Discussion

Factors limiting fall and winter spread of stripe rust in the Willamette Valley differ from those in eastern Oregon. Temperatures in the Willamette Valley generally remain above freezing during most of the winter months and rainfall for the period from October

Table 14. Infection types produced on the grass species grown at the Mountain Plots.^a

Variety	Infection types (IT)					
	Fox Prairie			Tupper		
	6-5-69	7-9-69	6-16-70	6-4-69	8-16-69	7-7-70
<u>Bromus marginatus</u>	i	i			i	
<u>Hordeum jubatum</u>	i	4			i	
<u>Brachypodium sylvaticum</u>	i	i			i	
<u>Festuca pratensis</u>	i	i	No Rust	No Rust	i	No Rust
<u>Elymus glaucus</u>	i	4	No Rust	No Rust	3	No Rust
<u>E. canadensis</u>	3	3	No Rust	No Rust	2	No Rust
<u>E. arenarius</u>	i	i			i	
<u>Calamagrostis epigeios</u>	i	i			i	
<u>Agropyron repens</u>	i	i			i	
<u>A. smithii</u>	i	i			i	
<u>A. tererum</u>	i	i			i	
<u>Poa pratensis</u>	i	i			i	

^a Planted September 24, 1968

through March averages 25-30 inches. Heavy rainfall washes spores from pustules and leaves. Pustules thus emptied take up to five hours to liberate new spores as compared to one hour for wind emptied pustules (Rapilly et al., 1970). These workers also noted that rain washing and cool temperatures reduce the total production of inoculum and rate of winter spread. Spore movement taking place in the winter is by leaf to leaf contact, permitting a slow, steady increase in size of foci.

In eastern Oregon, late fall and winter spread is severely limited by freezing temperatures and snow cover. Actively sporulating leaves could be found under the snow at Moro, but the cover prevented any spore movement. Lack of snow cover at Pendleton subjected the sporulating leaves to freezing and death. Lloyd (1969) found non-sporulating infected wheat leaves to be more winterhardy than sporulating leaves. Prior to warming spring temperatures, all sporulating leaves in the plots had been eliminated by freezing. At the Moro and Pendleton plots the rust survived as mycelium within green wheat leaf tissue as evidenced by new sporulation in March and April.

In the spring of 1971 appreciable spore movement at all three sites was confined until dry air movement allowed for more efficient separation of spore masses as suggested by Rapilly et al. (1970). This took place about April 1 when infections of the albino isolate were found in adjacent wheat plots. Spore movement (Table 11) progressed

100-200 yards per sporulation cycle throughout the spring and early summer. Spore movement exceeding 200 yards within a period of 10-14 days was not noted although observations in future years may substantiate movements of greater distance for the albino race.

Spread of infection from a point source or foci is along a gradient (van der Plank, 1963). Under wet winter conditions the gradient may be very steep because of poor conditions for dispersal. As warm drier weather begins, rust spread increases and gradients become less steep. In the Aurora plot, foci with steep gradients were seen in October (Figure 7). As the season progressed and the foci coalesced, a gradient between the yellow and albino isolates became apparent and remained until all green foliage was infected by the rust. Presumably, some mechanism of competition prevented an equal buildup of both isolates within an area on either side of the plot. By competition it is meant that one race will be unable to occupy host tissue already occupied by another race. The gradient of albino and yellow isolates across the plot appears to be characteristic of increase from a point source, but not from general spore showers. Spring wheat (Lemhi) 300 yards from the inoculated plot became infected with both the albino and an unknown yellow isolate. The distribution within this plot was uniform with an equal mixture of yellow and white on the leaves. Competition was still visible, however, on individual leaves since zones of yellow and white pustules were common.

Competition between isolates was also exhibited under growth chamber conditions at the 2 C/18 C temperature profile. No mixing of white and yellow pustules was noted on the same leaf. This does not appear to be characteristic of a particular host since the phenomenon occurred on all varieties susceptible to the albino isolate. Some mechanism inherent in the albino isolate and presumably other isolates prevents invasion and/or sporulation within previously colonized host tissue. Zones smaller in area than 1 mm^2 are not formed, suggesting a sphere of influence is established around the site of infection. Hassebrauk and Schroeder (1964) have shown that one biotype of stripe rust is capable of inhibiting spore germination of another biotype. Such an influence can essentially reduce the number of available infection sites per leaf. Thus on a wheat seedling with an average leaf area of 420 mm^2 , there would be a maximum of 420 sites for infection assuming the inoculum contained a mixture of two or more biotypes. Using one percent for efficiency of infection of stripe rust based on the findings of Peterson (1959) for Puccinia graminis and Knutson and Eide (1961) for Phytophthora infestans, 42,000 spores would be required for utilization of all sites for infection on a seedling leaf.

Omar seedling second leaves have an average of 35,000 to 40,000 stomates, each a potential site for infection. With the introduction of competition between races, sites for infection are reduced

99 percent. Assuming a probability (P) of one for infection with a single race, P for two races would be 0.5. Under conditions of short dew periods (two to four hours) and with infection time twice as long for one race as for the other, P for infection would equal 0.25 or less for the slower race depending upon environmental factors. The ratio of one race to the other in the population would be changed from 1:1 to 3:1 in one generation and this trend would continue with ensuing generations until the slower infecting race was reduced to near zero in the population. A change in competitive nature of the two races could reverse this effect--as could a change in host resistance.

Summer survival of stripe rust is dependent on availability of a susceptible host and proper conditions for infection. Residual green wheat is not common in either northeastern Oregon or the Willamette Valley during the summer. The dry summers prevent emergence of volunteer wheat until about the time the fall-sown crop emerges. Rust is then limited to post harvest late tillers and green grasses (Shaner, 1969). There is a period from August until emergence of the fall-sown crop that rust cannot be found. Summer inoculations of wheat and grasses at the mountain plots (Table 13-14) demonstrate that conditions for infection are suitable. Rust could be found from June until early August, but was not found on green wheat tillers or grasses in September. Overwintering rust was not found the following spring. Stripe rust in the mountain areas represents residual

infections initiated from inoculum from wheat growing areas. Movement of stripe rust inoculum appears to be in one direction--from wheat fields to the mountain areas.

Rust carryover from one year to the next is in small isolated foci in or adjacent to the wheat growing areas. The rust slowly builds in these foci in the spring, as indicated by test plots, until warm dry air movement allows for more efficient separation of spore masses and dispersal to adjacent fields during early to mid April.

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