

AN ABSTRACT OF THE THESIS OF

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WEST.) OF WHEAT IN OREGON.

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Stripe rust of wheat (Puccinia striiformis West.) has become a serious disease of wheat in Oregon. The means of overwintering, the nature of inoculum dispersal and the development of disease were studied to learn more of the factors responsible for epidemics.

During the summer little active stripe rust can be found on green hosts, either in the wheat area or in the mountains. Although a number of grass species common to the wheat area and to the mountains could be infected in the greenhouse most were never found to be infected in the field. By growing wheat in certain of these mountainous areas it was demonstrated that inoculum was present and that conditions for infection and incubation on wheat were favorable. Stripe rust infections were seen in the field on two grass species on several occasions. These were Bromus marginatus and Elymus cinereus. However, most specimens of these grasses which were examined were evidently not infected.

Uredospores can survive during the summer on dry stubble for at least 51 days and on dry soil for up to one month when mean maximum temperatures are in the range of 25 to 30 C. The length of time between the disappearance of stripe rust on residual green wheat and grasses (early August) and the emergence of early-sown wheat (early September) might therefore be survived by uredospores on stubble or soil. One large planting of early-sown, stripe rust-susceptible wheat is the orchard cover crops of Wasco County. During two years when fall infection by stripe rust could not be found in commercial wheat fields, infected wheat was found in the orchards in December.

Spore trapping records show that most spores move in a west-to-east trajectory which further suggests the importance of early infection and spore production in the western Columbia Basin (Wasco and Sherman Counties). Spore trapping records also showed that few if any spores were caught before disease was well established on the crop in the area of the trap. Thus the primary inoculum is not a heavy spore shower from some outside source, but consists of a relatively few spores probably produced near the site of infection.

During the spring the frequency of periods of sufficient moisture limits infection more than does temperature. Three hours is the minimum period of free moisture required for infection, but for a high incidence of infection, seven or

more hours are needed. Even when conditions are not favorable for infection, disease severity can increase because of systemic growth of mycelium within leaves. Lesion length may increase at the rate of 5 mm/day following single spore infections. Unusually cold weather in the spring can retard disease development by lengthening a temperature sensitive latent period. As mean temperatures fall below 9 C the latent period lengthens rapidly and can be as long as 45 days at temperatures below 5 C. Spores can survive as effective inoculum for up to 16 days on green foliage so that conditions need not be favorable for infection on the day that a spore lands on the foliage.

The quantitative examination of epidemics, using van der Plank's analysis, has shown that stripe rust in Oregon has a moderately high apparent infection rate (0.1 to 0.2 per unit per day). Because the apparent infection rate remains nearly constant throughout most of an epidemic and the latent period continually decreases throughout the same period, the basic infection rate decreases considerably during the epidemic. This indicates that in Oregon conditions become less favorable for disease development as the season progresses and the crop matures.

The moderately high apparent infection rate for stripe rust, the long period of disease development and the systemic nature of mycelium within the leaf combine to permit epidemics to develop

from exceedingly small levels of inoculum. The quantitative examination of epidemics in northeastern Oregon demonstrated that a prevalence of one infected leaf in five acres of wheat in mid-February is sufficient for the development of a severe epidemic in the spring when climate is favorable.

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EPIDEMIOLOGY OF STRIPE RUST (Puccinia striiformis WEST.) OF WHEAT IN OREGON

INTRODUCTION

Stripe rust (Puccinia striiformis West.) is a serious foliar parasite of wheat in the Pacific Northwest. Losses in individual fields can be from 20 to 75 percent in epidemic years. The loss to Oregon wheat growers because of stripe rust was estimated to be 15 million dollars in 1961.

The development and final severity of the disease vary from year to year. For two decades prior to 1960 stripe rust drew little attention in the Pacific Northwest. The severe stripe rust epidemic of 1961 in Oregon and Washington stimulated interest in the disease again. Since that time studies have been conducted in Washington, California, and Oregon on the epidemiology of stripe rust.

The Pacific Northwest produces about ten percent of the nation's wheat of which Oregon contributes 2.3 percent. Altogether about 1.7 million acres in the state are devoted to wheat production. In any given year wheat is grown on approximately one million acres with the other acres in summer fallow. Average yields in Oregon (33.6 bushels per acre) are high compared to many other parts of the country.

Wheat was first grown in the Pacific Northwest in the area around Vancouver, Washington in about 1825 (Hollands, 1956). Not

until the 1880's did the area east of the Cascades become the chief wheat producing area of the region.

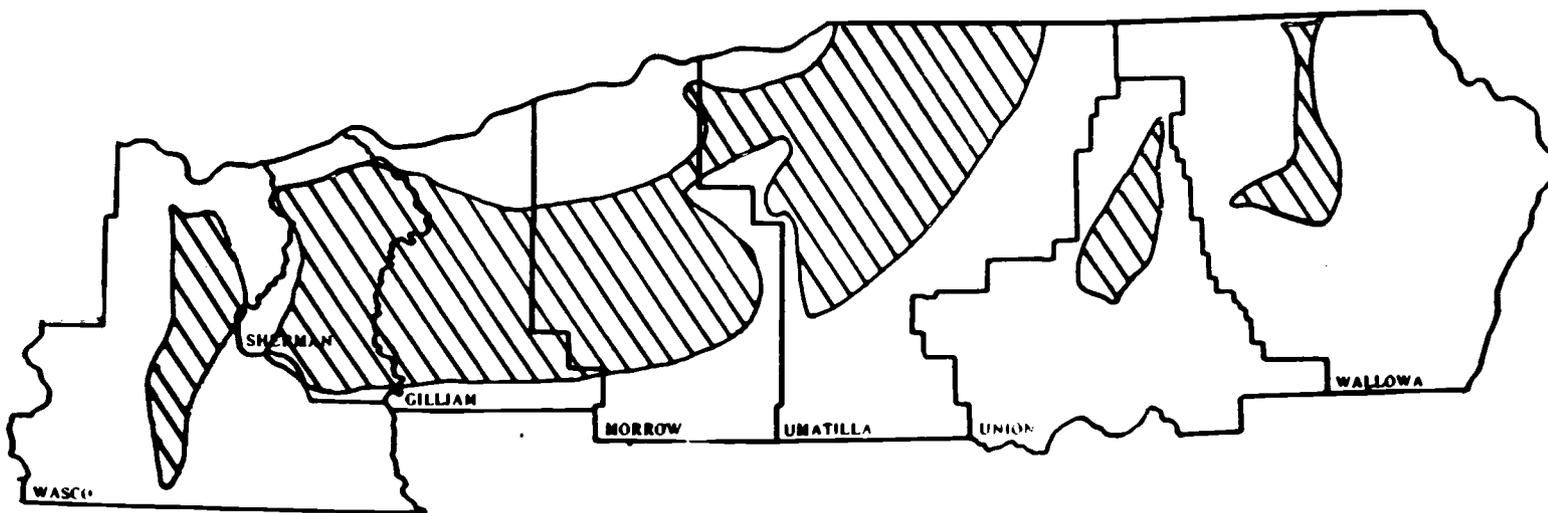
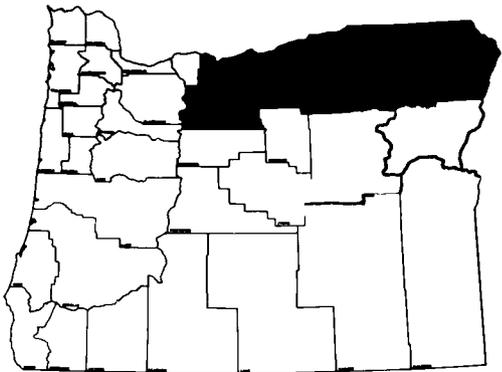
Today most of the wheat in Oregon is grown along the northern edge of the state from Wasco County in the west to Wallowa County in the east (Fig. 1). The combined counties of Wasco, Sherman, Gilliam, Morrow, and Umatilla comprise the Columbia Basin of Oregon. One-third of Oregon's cropland is in this area, most of which is devoted to wheat (Stippler and Castle, 1961). The western border of this area is the Cascades; the eastern border is the Blue Mountains. The wheatland slopes upward to the south and finally gives way to forest. Except for a part of Umatilla County the Columbia Basin is bordered on the north by the Columbia River.

The wheatland is an area of rolling hills with many shallow valleys. Wheat is grown mostly on the plateaus which are at elevations of 1500 to 2000 feet.

Precipitation on the wheatland of the Columbia Basin is from 10 to 20 inches annually. Approximately 60 percent of the precipitation falls from November through March. The months June through August are dry, receiving only 12 percent of the annual precipitation. In most of the wheat growing area only 10 to 15 percent of the precipitation is in the form of snow. Winds in the Columbia Basin are usually southwesterly during the day and easterly at night.

Wheat in Union County is grown in the Grande Ronde Valley

Figure 1. The wheat-producing counties of north-eastern Oregon. Their location on the state map (upper left) is shown by shading. The cross-hatched areas indicate where wheat is grown.



which lies between the Blue Mountains and the Wallowa Mountains (Fig. 1). The valley is rather flat, but wheat is also grown in the foothills at the edges of the valley. The annual precipitation in the Grande Ronde Valley is 21 inches.

Wheat is grown in Wallowa County along the Wallowa River. This area is at a higher elevation than the Columbia Basin and the Grande Ronde Valley. The annual precipitation is 14 inches. Wheat matures later in this valley than it does in Union County and in the Columbia Basin.

Because of the low annual rainfall in most of the Columbia Basin, wheat is grown on a summer fallow rotation program. A particular field will be fallow from the time of harvest in one year (summer) until the late fall of the following year when the new crop is seeded. Land is not summer fallowed in eastern Umatilla County, but wheat is commonly rotated with peas. Wheat can be cropped annually in the Grande Ronde Valley. It is often fallow-rotated in Wallowa County.

Where summer fallowing is practiced, the stubble is left standing on a field until the following spring as a wind- and water erosion control measure. Wheat is sown from late August through November depending on soil moisture conditions.

Wheat is also produced in the Willamette Valley of Oregon. This valley runs north and south and is situated between the coast mountain range and the Cascades. Average annual rainfall in the

Willamette Valley is around 38 inches. The summers are quite dry, even drier than the summers east of the Cascades. Wheat fields are more scattered in the Valley than in the Columbia Basin. In both western and eastern Oregon nearly all of the wheat is of the soft white winter type.

Since the time of some initial studies on stripe rust in Oregon in the first quarter of this century (Hungerford, 1923; Hungerford and Owens, 1923), the disease has received little attention. In the intervening 50 years many changes in the wheat culture have taken place which could have a direct bearing on the epidemiology of stripe rust. Therefore a general study of the epidemiology of the disease with these objectives was needed:

1. To determine the source and distribution of inoculum.
2. To determine the mode of winter and summer survival of the pathogen.
3. To gather data on disease development for correlation with meteorological data.

REVIEW OF LITERATURE

Stripe rust of wheat has been recognized as such in this country since 1915 when the visiting Danish plant pathologist F. Kølpin Ravn identified it (Humphry and Johnson, 1916). Prior to the recognition of stripe rust in this country, people considered the disease to be the same as that caused by Puccinia recondita, referred to as leaf rust. Therefore, it is difficult to determine the extent of stripe rust on wheat in this country before 1915.

The disease is widely distributed throughout the world, being found on all continents where wheat is grown save Australia (Zadoks, 1961). In the United States the disease is confined mostly to the Pacific Northwest and California.

The Stripe Rust Fungus

The uredial stage of Puccinia striiformis was first described by Schmidt in 1818 as Uredo glumarum. In 1854 Westendorp placed the fungus in the genus Puccinia after observing the telial stage. He named it Puccinia straeiformis. Eriksson and Henning, referring back to Schmidt's specific epithet, applied the name Puccinia glumarum to the fungus in 1896. It went by this name until 1953 when Hylander et al. (1953) argued that Westendorp's name was the valid one in accordance with the Rules of Nomenclature. Cummins and

Stevenson (1956) used "striiformis" in their Check List of North American Rust Fungi. Most of the literature since 1956 has referred to the fungus as Puccinia striiformis. Hassebrauk (1965) gives a detailed discussion of the nomenclature of this fungus.

Uredospores and teliospores of P. striiformis are produced on gramineous hosts. Although teliospores will readily germinate in the laboratory, no alternate host has been discovered. Apparently the only functional spore produced by the fungus is the uredospore.

Host Range

Reports of the occurrence of P. striiformis on various members of the Gramineae have come from around the world (Hassebrauk, 1965). Only those reports from the United States and Canada are of interest here, however.

An early investigation of the host range of P. striiformis in the Pacific Northwest was made by Hungerford and Owens (1923). Their work was mainly done in the greenhouse where the reactions of a considerable number of grass species to isolates of P. striiformis from wheat, Bromus marginatus, Elymus glaucus, and Hordeum nodosum (brachyantherum)¹ were determined. Rust isolates from

¹The authors referred to this grass as Hordeum nodosum. Hitchcock (1950) states that nodosum is a misnomer for brachyantherum in this country.

the above three grasses all attacked wheat. They found that 59 grass species were hosts for P. striiformis. Sanford and Broadfoot (1932b) published results of a study on the host range of P. striiformis in Canada.

Since these early publications other host range lists have appeared. Fischer and Levine summarized the literature on the host range of stripe rust in 1941. The following year Fischer et al. published a host range based on observations in the Pacific Northwest during 1941 (Fischer et al., 1942). Many of the grasses which these authors found to be rusted were in nurseries at experiment stations or universities. The host lists of P. striiformis based on observations of grasses in the native habitat are considerably shorter than those given by Fischer et al. (1942) (Hendrix et al., 1965; Hungerford and Owens, 1923; Sanford and Broadfoot, 1932b; Tollenaar and Houston, 1967).

The most comprehensive and recent host list is that of Hassebrauk (1965). It is worldwide in scope. The list is based on published reports and so includes the findings of the authors previously mentioned. Hassebrauk distinguished between grass hosts that were inoculated with an isolate of rust from some other host species and grass hosts that were found to be naturally rusted. He did not distinguish between natural infections observed in nurseries and those observed in native habitats because this distinction was not always

made in the original papers. Again the list of species susceptible to stripe rust exceeds the number of species on which stripe rust has been found in the field. Hassebrauk also indicated whether a particular grass species had been found susceptible to an isolate of P. striiformis from wheat. Altogether there are 126 grass species distributed among 20 genera on which stripe rust occurs in the field in the United States, according to Hassebrauk's list. The most important genera, in terms of the number of species, are Agropyron, Bromus, Elymus, and Hordeum.

Physiologic Specialization

In this country there is limited information on physiologic specialization of P. striiformis. The European set of differential wheat varieties has not worked satisfactorily here and no other standard set has been developed and used by workers throughout the Pacific Northwest.

With a selected set of wheat varieties Tollenaar and Houston (1967) found no racial differences among their collections of stripe rust from wheat in California. Sharp (1962, 1965), using European differentials, reported an isolate of the fungus from Montana that did not conform to any of the races described in Europe. Purdy obtained evidence for three races of P. striiformis in Washington based on the reactions of a set of differential varieties of his

composition (personal communication, 1967). Because different varieties of wheat were used, the results of these workers cannot be compared. But it does appear that races of the fungus do exist in this country.

Physiologic specialization may also be considered at the host generic level. Isolates from Poa pratensis have infected only species of the genus Poa and two species of Alopecurus (Britton and Cummins, 1956). Although rust on Poa pratensis is commonly found in the Pacific Northwest (Hardison, 1963), it has no significance for the disease on wheat. Stripe rust on Dactylis glomerata in Great Britain and Europe was raised to varietal status by Manners (1960) on the basis of morphological characters. The rust on D. glomerata is confined to that grass. So far stripe rust has not been reported on D. glomerata in the western hemisphere.

In the United States stripe rust isolates from Bromus marginatus, Elymus glaucus, Hordeum jubatum, and Hordeum nodosum (brachyantherum) have infected wheat (Hungerford and Owens, 1923). Hordeum jubatum and Agropyron dasystachyum were commonly rusted in Canada, presumably from spores produced on wheat further south (Sanford and Broadfoot, 1932b). Hendrix et al. (1965) found stripe rust on several species in the genera Agropyron, Bromus, Elymus, Hordeum, Poa, and Sitanion in the mountains around the wheat producing areas of the Pacific Northwest. They implied that this rust

would infect wheat and was indeed the same race(s) involved in the epidemiology of the disease on wheat. No tests were made, however, to determine if the rust did infect wheat.

Tollenaar and Houston (1967) found that P. striiformis isolates from several grasses behaved the same toward their differential wheat varieties as did wheat isolates. The isolate from Poa pratensis was the only exception; it infected only P. pratensis. The commercial wheat variety Gaines was susceptible to all but the Poa isolate.

Zadoks (1961) investigated physiologic specialization of P. striiformis on grasses in the Netherlands. Rust from Agropyron repens attacked some cereal varieties, but these were not varieties commercially grown in Europe. Clones of A. repens differed in susceptibility to this isolate, indicating that stripe rust resistance was not uniform throughout the species. Wheat isolates of stripe rust failed to infect A. repens. Manners (1950) reported variability in the response of A. repens to a wheat isolate of P. striiformis in Britain. He failed to find an isolate of stripe rust on any grass in Britain that would infect wheat. Considering the findings of other European workers and his own findings, Zadoks (1961) concluded that the designation P. striiformis f. sp. agropyri was useful for the stripe rust on Agropyron in Europe. He felt that the development of stripe rust on Agropyron in the Netherlands was a separate phenomenon from the development of stripe rust on wheat. Similar

to the case with Agropyron, he found that stripe rust on barley was largely confined to species of Hordeum. Zadoks concluded that grasses in the Netherlands were not compatible hosts for the P. striiformis on wheat, and that those grasses which were hosts were not important in the epidemiology of the disease on wheat. Many of the instances where wheat races of P. striiformis have been found on grasses should be attributed to the unusual conditions in a rust nursery, according to Zadoks. This latter point as well as the evidence that variation in resistance may occur among populations of native grasses is important in analyzing the significance of host lists for P. striiformis at the species level. The occurrence of stripe rust on a native grass at one place does not necessarily mean that members of that species everywhere are susceptible. The limited evidence already cited for intraspecies differences in susceptibility means that this phenomenon should be looked for in other species. Also, if the occurrence of stripe rust on a grass is to be used as evidence that grasses play a role in the epidemiology of the disease on wheat, it must be clearly shown that the rust on the grass is the same race as that found on wheat. This has not always been done.

The Summer Survival of P. striiformis

Several possibilities for overwintering of the fungus have been explored. Grass hosts, which remain green throughout the

summer are one possibility for overwintering. Hungerford (1923), working in the Willamette Valley, reported that the fungus persisted through the summer on leaves of Elymus glaucus along a stream bank. In early June of 1917, the fungus was active on this host, but from June 8 until September 10 no rain fell in the Valley and the uredia dried up. In the fall he observed fresh uredia around the old, dry uredia and suggested that the fungus had survived the summer as dormant mycelium. He collected rusted leaves of Agropyron dasystachyum and Elymus condensatus on August 28, 1916 and September 5, 1916 respectively. Germination of spores from the former was 95 percent at the time of collection; germination of spores from the latter was 85 percent. From September 1917 to July 1918 he could collect viable uredospores in every month of the year on wheat or grasses. Among the grasses involved, in addition to the above two, were Hordeum nodosum (brachyantherum), Hordeum jubatum, Bromus marginatus, and Elymus canadensis.

Sanford and Broadfoot (1932b) reported abundant stripe rust on H. jubatum and Agropyron species in Canada in the summer. Prevalence increased until late September when frosts began to kill foliage.

Survival of the fungus on grasses during the summer is also common in the Sierra-Nevada of California according to Tollenaar and Houston (1967). On the basis of their report there seems to be

little question that these mountains are the source of rust for wheat in the fall. The severity of stripe rust on grasses above 6000 feet elevation increased during the summer. Pathogenicity of the rust on these grasses to wheat has already been mentioned.

Hendrix et al. (1965) searched the mountains around the wheat growing region of Washington for rusted grasses during the summer of 1963. In mid-July they found rust at several locations in the Blue Mountains, in the Nez Perce National Forest, and in the mountains of northern Idaho and western Montana. Most of these grasses were at elevations of 3500 to 6000 feet. Making additional searches in August and October in the Blue Mountains, they found fewer rusted grasses than in July. In October only two collections were made (5800 to 6000 feet elevation). The authors did not mention how much rust occurred at each site of collection. The decline of rust on these grasses (mostly species of Bromus and Agropyron) during the summer is in contrast to events in California and Canada. It is probably because of the different moisture and temperature conditions in the Blue Mountains compared to Canada and the high elevations of the Sierra-Nevada. Hendrix et al. (1965) grew wheat at a number of sites in the Blue Mountains. Rust developed on wheat at 6 of the 12 plots. The authors did not specifically state how near to these plots rusted native grasses were found, nor what species of grasses occurred in the plot areas. They presented no direct evidence that

the stripe rust on the grasses would infect wheat.

Volunteer wheat can serve as a summer host for P. striiformis (s'Jacob and Zadoks, 1957; Zadoks, 1961). In the Netherlands that is the means of oversummering since rust can often be found in abundance during the summer on these plants. The extent of oversummering by this method depends on weather during the summer, which affects emergence and survival of the volunteer crop as well as rust development. s'Jacob and Zadoks mentioned that at temperatures of 23 C and above mature plants were resistant to stripe rust. But at these same temperatures the seedlings were susceptible and carried the fungus through the summer.

Stripe rust resistance induced by high temperatures has been known for some time. Newton and Johnson (1936) reported that nine varieties of wheat susceptible to stripe rust at 12.9 C were "completely resistant" at 25.3 C. Sharp (1965) found that growing the normally susceptible variety of wheat "Omar" at a constant temperature of 24 C before and after inoculation resulted in a highly resistant reaction. He showed that mycelium in these leaves was dead rather than dormant. If Omar was grown at a nighttime temperature of 15 C and a daytime temperature of 24 C the induced resistance did not occur. This temperature regime has more relevance for epidemiology than a constant temperature of 24 C. Nighttime temperatures in Oregon rarely exceed 20 C. However,

volunteer wheat is rare in the Columbia Basin during the summer (Hendrix et al. , 1965).

In some parts of the world wheat produced at high elevations will bridge the gap between successive winter cereal crops (Ling Lee, 1945; Hassebrauk, 1963; Mehta, 1940; Zadoks, 1961). Mehta made a thorough study of this matter in India. He regularly found stripe rust to oversummer on wheat at 6000 feet or higher. Late in the summer rust was on self-sown plants. High temperatures on the plains of India (temperatures exceed 100 F daily for weeks at a time) eradicated the fungus from that area. Three to four months after the wheat was sown on the plains stripe rust appeared, although conditions were favorable for infection prior to that time. Mehta determined that races of rust at the high elevations and on the plains were the same. On the basis of these observations and the results of spore trapping experiments Mehta concluded that inoculum was reintroduced into the plains area each year anew from the mountains where the fungus oversummered.

A seasonal movement of stripe rust in 1958 in the midwestern United States was reported by Futrell et al. (1959). In that year stripe rust was epidemic in the midwest for the first time since the disease was recognized in the United States. The growing season for wheat is progressively later going north from Mexico to Canada. Judging by the first appearance of stripe rust at points along the wheat

belt, Futrell et al. concluded that the fungus was moving north from an original source in Mexico. Sanford and Broadfoot (1932b) felt that the stripe rust found in Canada was introduced each spring from northern Washington, Idaho, and Montana.

Another possibility for survival of P. striiformis during adverse conditions is survival apart from green host crops. The ability of uredospores to survive on stubble has received limited attention. Hungerford (1923) collected rusted leaves of wheat, A. dasystachyum, and E. condensatus and placed them in herbarium packets. The packets were stored at room temperature. The wheat was collected in winter; the grasses were collected in summer. Spores from all three sources gave a trace to 1 percent germination after 43 to 58 days of storage. Uredospores placed on a glass slide in the laboratory ceased to germinate between 23 and 25 days.

Mehta (1923) found that spores stored in the laboratory for one month gave 5 percent germination. Spores stored in a greenhouse where the temperature was maintained between 4.5 and 21 C gave 50 percent germination after 10 days and less than 10 percent germination after five weeks.

Raeder and Bever (1931) stored leaves with pustules at 23 to 26 C and 49 percent relative humidity. Spores remained viable for 42 days. Keeping leaves at 9 to 13 C and 49 percent relative humidity resulted in a spore longevity of 88 days. For all the storage

temperatures examined, 49 percent relative humidity was best for survival of spores. But their results with spores stored at 25 percent relative humidity and various temperatures did not differ greatly from results of storage at 49 percent relative humidity.

Dionigi (1937) speculated that survival of uredospores on soil and stubble could be a significant means of overwintering, but he had no experimental evidence in support of his view.

Ducomet (1925) suggested that uredospores might survive on soil and infect seedlings after being splashed on them by rain. He had no supportive data.

Apparently only one study has been done to determine how long uredospores of P. striiformis can survive on green foliage prior to infection. Burleigh (1965) was concerned with survival at low temperatures and found that at an average air temperature of 1 C spores retained infectivity for 18 days. He was unable to extend the experiment to the point of no infectivity. Rehydrated, vacuum-dried uredospores were used rather than fresh spores.

Leathers (1961), working with fresh uredospores of Puccinia graminis found that hydrated spores would last longer on foliage at 75 F (more than 40 days) than would non-hydrated spores, which lasted 40 days. Mohamed (1960) found that stem rust uredospores lost infectivity after 11 days on green foliage when temperatures ranged from 87 to 90 F.

Winter Survival

The overwintering of P. striiformis is better understood than the oversummering. Reports from around the world are in general agreement.

Three studies have been conducted in the Pacific Northwest on this aspect of the disease cycle. The first was Hungerford's (1923), done at Corvallis. During the winter he inoculated wheat in the greenhouse with stripe rust. After pustules developed the plants were taken outside. Five weeks later the wheat was returned to the greenhouse. Pustules were not evident at that time, but new pustules soon formed which indicated that viable mycelium had persisted for the five weeks. During the exposure period there was some cold injury to foliage. Hungerford also observed overwintering on certain native grasses, especially H. nodosum (brachyantherum), B. marginatus, and E. glaucus. The latter bore viable uredospores from September 1917 to July 1918.

Burleigh (1965), working in Washington, made a detailed study of the ability of P. striiformis to survive and develop at low temperatures. By periodically inoculating small plots of wheat in the field during the winter he could correlate infection with climatic data.

Burleigh found that P. striiformis could overwinter for certain periods as active uredia on host tissue, persist as mycelium within

host tissue, or survive as uredospores on dead or living tissue. Evidence for the latter was obtained by leaving excised, sporulating leaves in the field under snow cover. After 35 days a trace of germination was detectable. As he points out, however, the leaves remained green for 30 days under the snow so new spores may have been produced during that time. This method of survival was considered to be important when there was winter-kill of infected foliage.

In Montana, Sharp and Hehn (1963) found that P. striiformis could survive for five months during the winter as mycelium within leaves of a susceptible host. For two and one half months the plants were under snow cover. By periodically bringing some of these plants into growth rooms they found that the prevalence of disease decreased throughout the winter. The fungus survived most successfully on early-planted wheat (August or early September) which was in a protected situation during the winter.

Sanford and Broadfoot (1932a) reported that overwintering of P. striiformis was rare in western Canada because of winter-killing of fall-infected foliage. Rust did not reappear on these same plants until July, which indicated that uredospores also failed to overwinter. Apparently inoculum for the infection evident in July came from the northern United States where stripe rust developed earlier in the spring.

In Europe and Great Britain similar modes of winter survival

of P. striiformis have been reported. Pole Evans (1907) found pustules year-round at Cambridge, England. He noted that in the winter it was the leaves lying on or coming in contact with the soil that were most likely to have pustules.

Zadoks (1961) studied the overwintering of stripe rust in detail in the Netherlands. He reported that the first infections of the fall-sown crop became evident in late November. Frost could kill sporulating portions of leaves, but infected, non-sporulating tissues seemed as frost hardy as healthy leaves. Under conditions where he was working, Zadoks felt that overwintering of uredospores was unlikely because of their sensitivity to high humidity and repeated wetting. Zadoks consistently found stripe rust overwintering as mycelium in the normal crop or on volunteers.

Minimum Periods of Free Moisture Necessary for Infection

The moisture requirements for infection have been investigated by Burleigh (1965) and by Tu and Hendrix (1967). Burleigh found that three hours of free moisture were sufficient for infection at 11 C. At higher and lower temperatures the minimum periods were longer. Whether fresh or vacuum-dried, rehydrated or non-rehydrated spores were used was not indicated. He also reported that infection could take place through guttation droplets. When infection occurred through guttation droplets, sporulation was first observed on leaf

tips. Under field conditions Tu and Hendrix reported positive results from inoculations of wheat with P. striiformis uredospores when free moisture endured for three or more hours, either in the form of rain or dew.

Monteith (1957) found that dew on foliage could be deposited from atmospheric moisture or could be deposited from soil moisture by a distillation process. The latter method commonly occurred with short grasses on calm, clear nights which favor rapid cooling.

Latent Periods

Several investigators have provided data on latent periods (Appendix I-Glossary) observed with stripe rust.

Zadoks (1961) determined latent periods by noting the time required for pustules to form on wheat in the field that he had inoculated. He compared these times with mean daily temperatures based on hourly observations. The shortest latent period--11 days--occurred when mean temperatures were between 12 and 19 C. Below 12 C the latent period lengthened rapidly.

Burleigh (1965), using a similar experimental design, found much the same relation as reported by Zadoks.

Tollenaar and Houston (1967) investigated the influence of temperature on the latent period using growth chambers at constant temperatures. The curve they obtained was similar to those published

by Burleigh and Zadoks.

Tu and Hendrix (1967) determined latent periods in the field in the summer. None of the mean temperatures they reported exceeded 20 C, but they found latent periods to range from 12 to 44 days. The authors state that no close relationship existed between temperature and latent period, but that the longest latent periods for both 1963 and 1964 occurred in July. Temperature data were not given but possibly daily deviations from the mean temperature could explain why these authors found such long latent periods at mean temperatures of about 18 C while Zadoks found the latent periods to range from only 11 to 19 days at a daily mean temperature of 18 C.

Infectious Periods of Individual Leaves

The length of time that tissue remains infectious is of considerable importance in epidemiology. The systemic nature of the stripe rust mycelium in the infected leaf has a bearing on this. In the early part of this century the growth behavior of the fungus in leaves was investigated. Pole Evans (1907) found that the fungus produces runner hyphae capable of extending from an infection center 10 to 22 mm in either direction in 24 hours. In another 24 hours the beginning of a new pustule forms at the point of the growth apex of the day before. Marryat (1907) found that uredospores form successively from a single hyphal tip. She did not indicate how long

a single tip might produce spores, however. The size of the individual pustules does not increase with age, according to Allen (1928), since uredia have borders of sterile cells. About 14 uredia per centimeter of leaf are formed. Chains of 100 uredia are not rare. Between the last active uredium and the tip of the runner hyphae Allen found five or six juvenile uredia. She stated that the lifetime of an individual uredium is short, but did not indicate how short. Zadoks (1961) claimed that during the winter an individual pustule might only persist for three days.

Because the mycelium is systemic within individual leaf blades the sporulating life of an individual leaf is perhaps more important for this disease than for a truly local lesion disease. The entire leaf may eventually bear pustules as a result of a single infection. Zadoks (1961) found that individual leaves would remain infectious for a few days to a few weeks. Winter or summer dormancy could extend this period considerably.

Spore Movement

Studies on the movement of uredospores of P. striiformis have depended mostly on indirect means. Mechanical devices and plants have been used as spore traps. Race studies have given information on spore dispersal.

In India Mehta (1940) used these indirect means to study spore

movement. His best evidence for movement of spores from the hills to the plains and from the plains to the hills was the time of rust appearance in the two areas and the fact that races in the two areas were the same. On the basis of wind trajectories he surmised spore dispersal of as much as 1000 km.

From the appearance of a new race, Zadoks (1961) deduced effective dispersal of 200 km. Over a period of one or two years, a race which had originated in the Netherlands spread over 800 km. Zadoks compared this situation with that in the Great Plains of the United States where stripe rust covered 2400 km in a single season (Futrell et al., 1959).

In California Tollenaar and Houston (1967) concluded, on the basis of the time of symptom development in widely scattered plots, that effective dispersal of 150 miles could take place.

During the winter spores often do not travel far. Ducomet (1925) found that rust would not spread to healthy wheat 5 m from rusted wheat during January, although rust spread vertically during this time on the originally rusted wheat. Zadoks (1961) felt that spore dispersal in the winter was mainly by leaf-to-leaf contact. Many times he observed that during the winter rust would spread slowly down a row of wheat where there was direct contact between healthy and diseased foliage, while plants in adjacent rows, which had no contact with rusted tissue, would remain free of rust. It was difficult

for Zadoks to obtain data on medium distance spore dispersal in the Netherlands because of the endemic nature of the disease there. In two cases he found that spores moved at least 1.8 and 13 km respectively, in a single step.

Development of Epidemics

Few quantitative data on the buildup of stripe rust during a season have been published. Zadoks (1961) provided some such data, including results of an experiment where leaf area and percentage of attack were estimated with a planimeter. Using detailed data supplied by Zadoks, van der Plank (1963) calculated an apparent infection rate of 0.132 per unit per day. When the apparent infection rate was corrected for growth of the host during the course of the epidemic, a value of 0.149 per unit per day was obtained.

MATERIALS AND METHODS

Spore Preservation

For long term storage of uredospores the vacuum-drying technique of Hughes and Macer (1964) was used. Spores were vacuum-dried for three hours. While still under vacuum, the ampoules containing spores were flame-sealed. Ampoules were stored in the dark at 5 ± 0.5 C.

For short term storage of spores, unsealed ampoules were kept in a sealed glass container at 3 C. A small beaker of 45 percent sulfuric acid was also in the container which maintained a relative humidity of approximately 50 percent.

Dew Treatments

Puccinia striiformis requires free moisture for infection. The optimal temperature for infection is around 10 C. Virtually no infection takes place above 21 C (Bever, 1934).

For greenhouse and growth chamber work a dew chamber was constructed using a 32 gallon metal garbage can. The can was placed in a walk-in cold room maintained at 3 C. Water in the bottom of the can was heated to 25 C with a heating cable, resulting in an air temperature within the can of 12 C. Under these conditions a fine

layer of moisture would deposit on the leaves of the wheat within a half hour of being placed on a rack above the water in the can. Plants were left in the dew chamber for 8 to 15 hours. Then they were returned to the greenhouse or growth chamber where symptoms could develop.

Inoculation Techniques

Depending on the type of experiment, three different inoculation techniques were used in this study. For most work a suspension of uredospores in Freon-113 (trichlorotrifluoroethane) was used (Miller, 1965). Uredospores of P. striiformis in Freon-113 form a uniform suspension. Spores were applied with an atomizer. When the atomizer nozzle was held about 12 inches from the leaves being inoculated, the freon evaporated by the time the spores landed on foliage and an even deposition of spores resulted.

The most useful alternate method was the application of spores to leaves with a camel's hair brush. This method did not injure leaves and probably did not alter the spores structurally or physiologically. The brush was dipped into the spore source prior to inoculating each leaf. While the method was not quantitative, with experience it was possible to apply approximately equal amounts of spores to each leaf.

When the amount of inoculum was small, spores were spread over leaves with a scalpel.

Field Surveys

Much of this study involved observations of stripe rust in the field. Three general types of information were recorded when observing stripe rust in the field: reaction type, severity, and growth stage of the host.

The reaction type (RT) expresses the degree of compatibility between the host and the fungus. It is estimated by the amount of sporulation and attendant chlorosis and necrosis on the diseased leaf. Some workers refer to reaction type as infection type. However, much of the infection phenomenon is detectable only at the physiological level. To assert that two different host-parasite combinations which result in similar types of pustules and attendant symptoms are identical in all respects of the infection phenomenon is to assert far more than the evidence allows. Somewhat the same objections may be made to the term "reaction type," but the word reaction does not have such a specific meaning in plant pathology as does infection so it is not ambiguous to give it a more precise meaning for the present work.

The International Scale accepted by the First International Yellow Rust Conference (Zadoks, 1961) was used in the present

study, with some modification (Table 1).

Table 1. Reaction types.

i	= immunity
0	= no pustules, only chlorosis or necrosis
1	= some separated, very small pustules and also chlorosis or necrosis
2	= a few pustules, also chlorosis, perhaps necrosis
3	= normal pustule formation, also chlorosis
4	= normal pustule formation without chlorosis
z	= no symptoms observed

For recording severities of stripe rust on wheat in the field the International Scale, accepted by the First International Yellow Rust Conference (Zadoks, 1961), was used. It is given here for reference (Table 2).

The severity rating is referred to as the degree of attack (DA), following Zadok's notation (Zadoks, 1961). When DA values are translated into their corresponding percentages of leaf surface attacked, they become percentages of attack (PA).

Although the International Scale of severity estimation was routinely used, the Horsfall and Barratt (1945) system of severity estimation was also tried in the field. The small categories at the extremes of their scale were difficult to distinguish without the aid

of standard drawings. The systemic nature of the fungus in leaf blades means that there may be one or more areas on the blade that are heavily rusted, while other large areas appear healthy. The variability in this pattern renders standard diagrams useless for making severity estimations.

Table 2. International scale of disease severity.

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

I used the International Scale with more confidence. In a seed treatment rusticide trial using spring wheat the initial infection was rather uniform within plots of susceptible wheat. As disease developed I found that good agreement existed between my severity estimates of replicated treatments.

For making a severity estimate of a plot or a field an overall

examination was made to determine the uniformity of severity. If the plot or field was uniformly attacked then several representative tillers were examined with more care to arrive at an average DA for the plot or field. When considerable non-uniformity existed, as commonly occurred early in the season, DA estimates were made on foci (Appendix I-Glossary) or heavily rusted single plants. Then the average DA was determined for the entire area being considered, by assuming that the level of rust non-evenly distributed was actually spread out uniformly over the area. Thus if foci, which made up 10 percent of the area of a field, were at DA 8 (50% severity), then the field DA would be 5 (5% severity). All visible leaf symptoms and signs were included in the DA estimate. In considering a DA value the RT is also important, since it indicates the extent of sporulation on symptomatic tissue. A DA of 6 with an RT of 3 means that more inoculum is available to infect healthy tissue than in the case of a DA of 8 and an RT of 1.

The growth stage of wheat was estimated according to the Feekes scale as presented by Large (1954).

Field observations were made both in the Willamette Valley and in northeastern Oregon. Most observations in the Willamette Valley were made at two locations near Corvallis. One was Hyslop Agronomy Farm, the site of winter cereals research of Oregon State University in the Willamette Valley. The farm is seven miles north

of Corvallis. The official meteorological station for Corvallis, Oregon is located at Hyslop Farm. The second area of field observations in the Willamette Valley was at another university farm--East Farm. East Farm is located about one mile east of Corvallis, directly across the Willamette River. It is the site of the spring cereal research in the Willamette Valley. Much of the author's field work, both observations of disease increase and experimental work, was carried out at these two locations.

Studies were also carried out in northeastern Oregon. I made frequent trips to this area, at all times of the year to observe commercial wheat fields and other areas where stripe rust might occur. County extension agents and branch experiment station personnel also assisted in this study. During 1964 cooperators in all the northeastern Oregon wheat-producing counties made regular observations of several fields in their respective counties. They made notes on growth stage, DA and RT. They also exposed spore traps regularly, which were sent to Corvallis for evaluation. In the following years cooperators continued to expose spore traps.

Mountain Plots

Plots of wheat were established at several locations in the mountains adjacent to wheat growing regions of Oregon to study spore dispersal and physiologic specialization (Table 3). Ten varieties of

wheat differing in their susceptibility to stripe rust were grown at each site.

Table 3. The locations of the Mountain Plots

Plot	County	Legal description	Elevation, feet
Dale	Grant	Sec. 32, T7S, R33E	5 300
Mary's Peak	Benton	Sec. 20, T12S, R7W	3200
Meachum	Umatilla	Sec. 36, T1S, R36E	4000
Tollgate	Umatilla	Sec. 20, T4N, R38E	5000
Tupper	Morrow	Sec. 9, T6S, R27E	4300

The varieties of wheat were as follows:

Suwon × Omar ²	Nord Desprez
Gaines	Hymar × Orfed
Moro	Omar
Druchamp	Golden
Heines VII	173438 × Elgin

Gaines, Moro, and Omar are varieties commercially grown in northeastern Oregon. Gaines and Druchamp are grown in the Willamette Valley.

A plot consisted of one row each of the ten varieties. Dimensions of the plots were approximately 6 × 12 feet. The rows ran the width of the plot. Two plots, oriented at right angles to one another, were established at each location.

To prevent grazing by animals, wire cages were placed around the plots (Figure 2). These consisted of a rodent shield of sheet metal, 24 inches wide and buried 15 inches in the soil, plus sides and a top constructed of poultry wire. Six steel fence posts provided structural support for the wire. The height of the cage was about four feet.

Wheat was sown in late September or October. After covering the seed with soil, 16-20-0 fertilizer was applied. In the following spring and summer the wheat at these locations was examined for stripe rust.

Spore Traps

To study the dispersal of uredospores in the air, spore sampling devices were constructed that were similar to those used by Bromfield et al. (1959). The spore trap consisted of a stainless steel rod fitted permanently into a rubber base (Figure 3). A rain shield was constructed of a galvanized metal disc, with a nut soldered in the center for attachment to the rod. The rods were exposed in the field by inserting the base into the top of a pipe which served as the stand (Figure 4).

Bromfield et al. (1959) recommended the development of some better method than the one they employed for making spore counts after exposing rod traps. The rods used in this study were wrapped

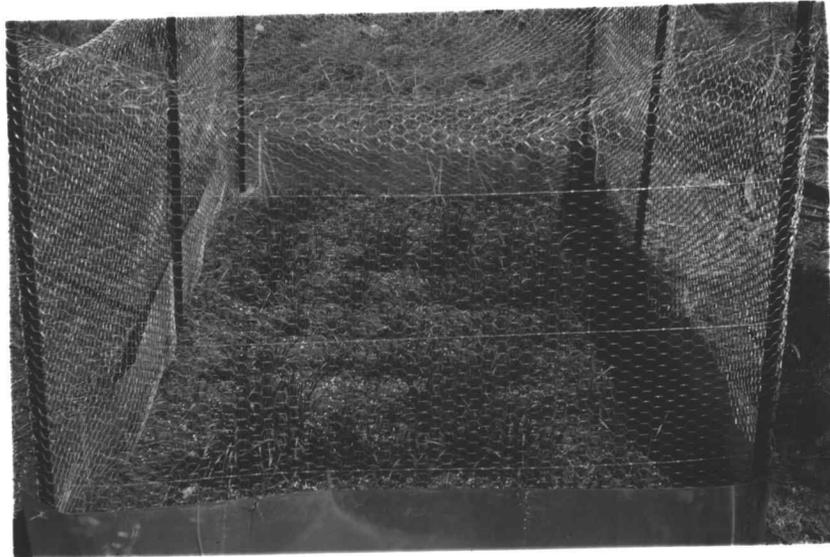


Figure 2. The layout and construction of Mountain Plots--Tupper location.

Figure 3. The rod-type spore trap with the rain shield in place. The black bands indicate where clear cellophane tape was wrapped around the rods prior to dipping them in glycerine jelly.

Figure 4. The spore trap in the field. The trap stand is about four feet high. The upper 8 inches were painted fluorescent red to facilitate detection in the field. The white line, evident on the trap base was oriented northward during the exposure period.



in two places, indicated by black bands in Figure 3, with clear cellophane tape (3/4 inch width). The two ends of the tape just met. With the tapes in place, rods were dipped in molten glycerin jelly. After allowing the excess glycerin jelly to drain, the rods were placed in cardboard mailing tubes until time for exposure.

A white line, painted on the base of the trap from the rod to the perimeter of the base, was oriented toward north during exposure. The first step in examination of the trap was to notch each tape on the lower edge with a scalpel at a point corresponding to north, which was determined from the white line. Using a scalpel and forceps, the tape was separated along the juncture and peeled from the rod. It was placed on a drop of glycerine on a microscope slide with the exposed surface up. Gentle heat was applied to smooth the tape. A drop of glycerine was added to the surface and then a cover slip applied. The tape was examined under the microscope directly.

The entire surface of the tape was scanned for uredospores. This was done by starting at one corner and scanning in a vertical direction, with respect to field orientation. Then the tape was moved horizontally one microscope field width and scanned again vertically. At a magnification of $100\times$ nine scans were required to observe the entire tape. Thus there were nine sectors on the tape, each covering 40° . The total number of spores in each sector was recorded. By noting in which sector the notch occurred and considering the

relation between the tape's position on the trap in the field and its position on the slide, it was possible to assign a compass direction to each sector. Both tapes on each trap were examined in this way.

RESULTS

Host Range

Stripe rust occurs on grasses as well as on wheat in Oregon. Observations were made to determine the extent of stripe rust on grasses and experiments were conducted to determine whether grasses play a role in the epidemiology of stripe rust on wheat.

The Oregon State University Mycological Herbarium was consulted for a record of hosts in Oregon upon which stripe rust has been found. The grasses bearing stripe rust are listed in Table 4. The list is short, especially in terms of the number of species. The times of collection should be noted. With two exceptions the grasses were collected at the time of year when stripe rust is active on the wheat crop. The earliest specimens of wheat with stripe rust in the herbarium were collected by F. Kølpin Ravn in June of 1915.

During the course of this study I observed stripe rust on 15 species distributed among five genera of the Gramineae (Table 5). Twenty-six of the observations were made in the Corvallis area, and with one exception were in nurseries. Most of the grasses with stripe rust in the nurseries were in the genus Agropyron. Although species of Agropyron are common throughout northeastern Oregon stripe rust was never observed on them. Agropyron cristatum (L.) Gaertn. is

Table 4. Grasses with stripe rust in the Oregon State University
Mycological Herbarium

Grass	County where collected	Date of collection
<u>Elymus glaucus</u>	Benton	June, 1923
<u>E. glaucus</u>	Benton	June 18, 1926
<u>E. glaucus</u>	Benton	May 2, 1935
<u>E. glaucus</u>	Benton	May 8, 1935
<u>E. glaucus</u>	Benton	June, 1936
<u>E. glaucus</u>	Marion	May 25, 1935
<u>E. glaucus</u>	Marion	April 21, 1938
<u>Elymus species</u>	Jackson	May 8, 1919
<u>Agropyron cristatum</u>	Sherman	May 15, 1934
<u>A. cristatum</u>	Clatsop	October 3, 1935
<u>Hordeum vulgare</u>	Sherman	1923
<u>Hordeum gussoneanum</u>	Jackson	June 16, 1915
<u>Hordeum jubatum</u>	Lake	August, 1914
<u>Sitanion hystrix</u>	Crook	June 24, 1912

Table 5. Observations of stripe rust on grasses in Oregon, 1965 through 1967.

<u>Grass</u>	<u>Location</u> ^a	<u>Months in which stripe rust found</u>
<u>Agropyron cristatum</u>	Nursery, OSU	Apr.
<u>A. cristatum</u>	Hyslop	May
<u>Agropyron elongatum</u>	Nursery, OSU	Apr. , Jun.
<u>Agropyron riparium</u>	Nursery, OSU	Apr.
<u>A. riparium</u>	Hyslop	May
<u>Agropyron sibiricum</u>	Nursery, OSU	Apr. , Jun.
<u>A. sibiricum</u>	Hyslop	May
<u>Agropyron spicatum</u>	Nursery, OSU	Jan. , Feb. , Apr. , Jul. , Sep. , Dec.
<u>A. spicatum</u>	Hyslop	May
<u>Agropyron trachycaulum</u>	Nursery, OSU	Apr
<u>Bromus marginatus</u>	Malheur Co.	Aug.
<u>B. marginatus</u>	Grant Co.	Jun.
<u>B. marginatus</u>	Union Co.	Jun.
<u>B. marginatus</u>	Morrow Co.	Jun.
<u>B. marginatus</u>	Wallowa Co.	Aug.
<u>Bromus species</u>	Union Co.	Jul.
<u>Elymus canadensis</u>	Nursery, OSU	Apr. , Jun.
<u>Elymus cinereus</u>	Col. Basin	Jun. , Sep.
<u>E. cinereus</u>	Union Co.	Aug.
<u>E. cinereus</u>	Wallowa Co.	Jun. , Aug.
<u>Elymus glaucus</u>	Nursery, OSU	Apr.
<u>E. glaucus</u>	Benton Co.	Aug.
<u>Elymus species</u>	Col. Basin	Mar. , Jul.
<u>Hordeum brachyantherum</u>	Union Co.	Jan.
<u>Poa ampla</u>	Nursery, OSU	Jul.

Table 5. (continued)

Grass	Location	Months in which stripe rust found
<u>P. ampla</u>	Hyslop	Sep.
<u>Poa species</u>	Deschutes Co.	Sep.

^aExcept for the grasses at Hyslop Farm or the nursery on the Oregon State University Campus, the grasses listed were in their native habitats.

common along roadsides and around wheat fields in the Columbia Basin. Several pastures in the area have been planted with this species. Even when nearby wheat had severe stripe rust, none could be found on this grass. But when grown in irrigated nurseries, stripe rust could be found on A. cristatum. Also when A. cristatum was grown in the greenhouse from seed collected in Umatilla and Wasco Counties and inoculated, infection occurred, resulting in RT's which ranged from 0 to 3. In its native habitat A. cristatum is quite resistant to stripe rust, but under conditions of artificial cultivation the resistance is not evident.

Elymus cinereus Scribn. and Merr. is a grass that is common along roadsides and streambanks throughout the shallow valleys of northeastern Oregon. Since Hungerford and Owens (1923) did their work on the host range of P. striiformis, the variety of Elymus condensatus occurring in Oregon was placed in synonymy with

E. cinereus (Hitchcock, 1950). Therefore, the grass referred to as E. condensatus by these early workers is probably the same as that referred to as E. cinereus in the present work.

Elymus cinereus is one of the only two grasses upon which stripe rust was found with any regularity in northeastern Oregon (Table 5). In the spring the fungus could be seen sporulating abundantly on the leaves (RT 3), but as the season progressed the reaction type diminished to a 2 or 1. Finally only small necrotic stripes could be seen. Stripe rust was not observed to rejuvenate on such foliage with the advent of cool, moist weather in the fall.

Although a number of observations of stripe rust were made on E. cinereus during the past four years, most of the plants of this species examined were apparently free of the disease. Therefore plants were raised from seed in the greenhouse and inoculated with a wheat isolate (Appendix I-Glossary) of P. striiformis. The seed was collected from five locations in northeastern Oregon from plants which showed no evidence of having stripe rust. All of the plants were uniformly susceptible (RT 3).

Bromus marginatus Nees, is the other grass which was observed several times to have stripe rust (Table 5). This grass occurs in the wheat producing area and also at higher elevations. In 1967 stripe rust was seen on this grass at the Tupper Mountain Plot. When plants were grown in the greenhouse from seed collected

from this location, they were found to be susceptible to a wheat isolate of P. striiformis.

Bromus breviaristatus Buckl. occurs in the Blue Mountains which separate the wheat growing area of Umatilla County from the Grande Ronde Valley (Union County). This grass was examined for stripe rust periodically, especially in the late summer and fall. None was ever found. However, when grown and inoculated in the greenhouse it was found susceptible to a wheat isolate of P. striiformis. Of seven plants inoculated, all seven rusted, exhibiting RT's of 2 and 3. The PA for all inoculated leaves was over 70 percent.

Agropyron dasystachyum (Hook.) Scribn. was seeded in the area of the Meachum Mountain Plot by the Forest Service. It was never observed to have stripe rust in the field. Again, when plants of this species grown in the greenhouse were inoculated with a wheat isolate of P. striiformis, they did rust (Table 8).

Elymus glaucus Buckl, does not give consistent RT's as a result of stripe rust infection (Table 6).

The E. glaucus from Benton County is worthy of special discussion. These plants were collected along the bank of the Mary's River on August 9, 1967. Stripe rust was on the plants at the time of collection, but severity and prevalence (Appendix I-Glossary) were low. Spores from these plants were inoculated to wheat seedlings in the greenhouse. Of 50 inoculated primary leaves, 13 developed

symptoms: seven were RT 0, five were RT 1 and one was RT 3.

Twenty six uninoculated leaves showed no symptoms. The rust on

the one plant showing RT 3 proved to be a contaminate (probably a

wheat isolate) since it failed to infect new healthy leaves of the same

E. glaucus from which it was presumably isolated, but did infect

wheat. Since the remaining 12 symptomatic wheat plants showed RT 0

or 1 the isolate on E. glaucus was apparently not a race found on

wheat in the area.

Table 6. Reactions of E. glaucus to P. striiformis infection.

Source of grass seed	Source of inoculum	Reaction type
Dale Mountain Plot	wheat	3
Battle Mountain Summit, Umatilla Co.	wheat	i - 0
Meachum Mountain Plot	wheat	i
Benton Co.	wheat	i
Benton Co.	wheat	i
Seed lab ^a	Agropyron	4
Seed lab	wheat	2-4
Seed lab	wheat	3
Seed lab	Elymus	2
Seed lab	Elymus	4

^aOregon State University Seed Testing Laboratory. The original source is not known.

When a wheat isolate of P. striiformis was inoculated to healthy leaves of these same E. glaucus plants, no symptoms developed.

The E. glaucus obtained from the seed testing laboratory was susceptible to wheat isolates but in any particular experiment many inoculated plants did not show symptoms suggesting there was variability in resistance.

A difference was noted in the RT's of E. glaucus collected from the Battle Mountain Summit and the Dale Mountain Plot when they were inoculated with the same wheat isolate of P. striiformis. These two locations are about 30 miles apart. Rust was not found on either of these grasses where they occurred in the field.

Isolates from Agropyron spicatum (Pursh.) Scribn, Agropyron sibiricum (Willd.) Beauv., E. glaucus and wheat all from the nursery on the OSU campus infected wheat, Agropyron desertorum (Fisch.) Schult., A. sibiricum and E. glaucus in the greenhouse. Apparently in the nursery situation all of the grasses observed to have stripe rust had been infected by a wheat race of P. striiformis. But in their native habitats these grasses are apparently resistant to wheat races of the fungus.

Several isolates of P. striiformis from grasses in their native habitats infected wheat. Uredospores collected from B. marginatus (Tupper Mountain Plot) were single-spore inoculated to Baart wheat

with success. Stripe rust found on this species in Wallowa County and in Malheur County also infected wheat, including commercial varieties used in Oregon. When uredospores collected from E. cinereus were single-spore inoculated to Baart wheat, a number of infections resulted. Thus the two grasses on which rust was most often observed (Table 5) in northeastern Oregon were susceptible to wheat races of P. striiformis.

Although rust was often found on species of Poa in the Willamette Valley isolates from Poa consistently failed to infect wheat. Stripe rust was not seen on any Poa species in northeastern Oregon. One collection of stripe rust was made from a Poa species near Madras, Oregon which also failed to infect wheat.

Stripe rust was never observed on Dactylis glomerata L. by the author although numerous plants of this species were examined over the past four years.

Mountain Plots

The Mountain Plots were established to determine if wheat at those locations would become infected with stripe rust. Differential varieties were used to determine whether any stripe rust that did occur differed from the rust on commercial wheat at lower elevations. The results of three years of observation of the wheat varieties are given in Table 7.

Table 7. Reaction types of the wheat varieties grown at the Mountain Plots.

Variety	RT for each location and year													
	Tollgate			Meachum			Dale			Tupper			Mary's Peak	
	1965	1966	1967	1965	1966	1967	1965	1966	1967	1965	1966	1967	1966	1967
Suwon x Omar ²	z	z	z	z	z		z	z	z	z	z	z	z	z
Gaines	+ ^a	3	3	+	3		+	3	3	z	4	3	2	3
Moro	z	z	z	z	z		z	z	z	z	z	z	2	z
Druchamp	z	z	z	z	z		z	z	z	z	z	z	z	z
Heines VII	+	2-4	z	z	z		+	z	3	z	z	3	3	z
Capelle Desprez	z			z			z			z				
Nord Desprez		2	NS ^b		z			z	3		4	z	NS	z
Omar	+	3	z	+	3		+	3	3	3	3	3	4	3
Hymar x Orfed	+	3	z	+	4		+	2	4	3	4	4	4	3
Golden	z	2	z	z	4		+	3	3	z	z	3	3	3
173438 x Elgin	z	2	z	z	3		z	2	4	z	4	3	3	z

^aIn 1965 only the presence or absence of stripe rust on a variety was noted, except at Tupper.

^bNS = no stand

It was not possible to inspect the Meachum Plot in 1967.

Stripe rust was seen on Gaines and Omar at all locations and in all years with the exception of Tupper in 1965 when no rust was seen on Gaines and Tollgate in 1967 when none was on Omar. Rust was never seen on Suwon × Omar² or Druchamp. One plant of Moro had stripe rust in 1966 at the Mary's Peak Plot. In commercial fields of Moro occasional plants are found with stripe rust, indicating that there is some genetic impurity in the variety.

The occurrence of rust on the varieties Heines VII, Capelle Desprez, Nord Desprez (which replaced Capelle Desprez after 1965), Golden, and 173438 × Elgin was inconsistent. For any given year or any given Plot there was an irregular pattern of infection for these five varieties. The variability may be due to environmental modification of susceptibility. The important conclusion to be drawn from these data is that the rust found at all of these Plots in every year was capable of infecting Gaines or Omar, the main commercial varieties of Oregon. The three varieties which were resistant have likewise been resistant in the wheat growing area.

On the basis of the total number of observations of rust at the eastern Oregon Plots for each year, 1966 was the most favorable year for stripe rust development at high elevations. In general stripe rust could be found on wheat at the Mountain Plots from late June through September in each year.

Although rust was found every year on wheat at the Mountain

Plots, it was found on nearby grasses on only one occasion. This was in 1967 at the Tupper Site (B. marginatus, Table 5). The rust was seen in June, but on subsequent visits to the area in the summer and fall rust could no longer be found on this grass.

Several grass species occurred in the immediate area of the wheat at the Mountain Plots some of which have been reported as hosts for P. striiformis. Some of these grasses were raised from seed in the greenhouse and tested for susceptibility to wheat isolates of P. striiformis (Table 8).

Table 8. Response of grasses found at the Mountain Plots to wheat isolates of P. striiformis.

Grass	Source	Reaction type
<u>Agropyron dasystachyum</u>	Meachum	2-3
<u>Elymus glaucus</u>	Meachum	i
<u>Agropyron inerme</u>	Dale	1-2
<u>Elymus glaucus</u>	Dale	3
<u>Poa species</u>	Dale	i
<u>Elymus cinereus</u>	Tupper	2-3

These data indicate that the grasses at the Mountain Plots behave similarly to the grasses in the wheat growing area toward stripe rust infection. In their natural habitat they are generally resistant, but in the greenhouse they can be infected by wheat isolates of P. striiformis in some cases.

Evaluation of the Rod-Type Spore Trap

The method of counting spores in each sector of the tapes on the spore trap was described in the Materials and Methods section. Spores were counted in this way to determine the direction from which spores impacted. The assumption was that the number of spores in a sector reflected the number of spores coming from the direction faced by that sector. To determine whether this assumption was valid two types of experiment were performed.

First, traps were exposed in the greenhouse to a freon-spore suspension spray. The nozzle of the atomizer was held 18 inches from the trap and aimed midway between the tapes. One trap was exposed at a time, for 75 seconds. The tapes were then examined in the same manner as described for traps exposed in the field. The numbers of spores caught on upper tapes were much lower than the numbers of spores caught on the lower tapes. But the frequency distributions were similar (Figure 5). Most spores impacted in the sector normal to the direction from which they came. Although spores came from a single direction, they impacted in as many as eight sectors of a single tape.

In another experiment eight trap stands were placed in a line in an area of severe stripe rust in the field. Trap stands were placed 10 feet apart. Twenty-four hour exposures of spore traps

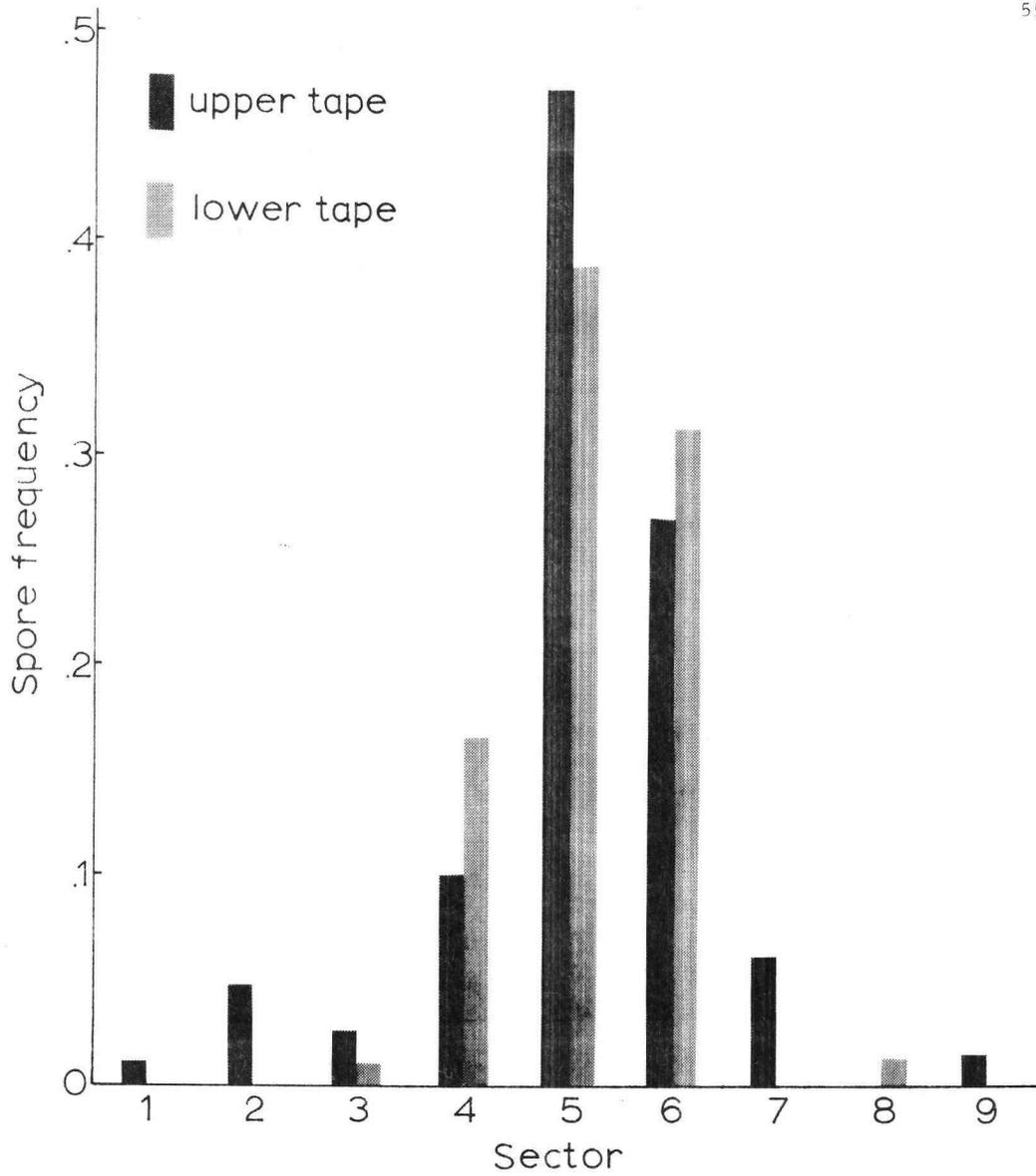


Figure 5. The frequency distributions of spores trapped on upper and lower tapes of the rod-type spore trap. Each curve is the average of three tapes. Sector five was normal to the direction from which spores came.

made on July 14 and July 20, 1964. Several comparisons can be made from the spore counts. On the July 14 exposure significantly more spores were trapped on upper than on lower tapes, but on the July 20 exposure the difference was not significant (Table 9).

Table 9. A comparison of the spore counts on upper and lower tapes of replicated spore traps exposed at East Farm during July 1964.

Trap no.	Spore Counts			
	7-14-64		7-20-64	
	Upper tape	Lower tape	Upper tape	Lower tape
1	68	14	47	18
2	170	55	84	73
3	108	109	113	53
4	360	240	215	119
5	493	134	206	214
6	559	94	215	314
7	317	171	98	149
8	760	318	132	129
Total	2835	1135	1110	1069
Mean	354	142	139	134
	LSD _{0.05} = 152 spores		No significant difference shown at 5%	

Another comparison that can be made between replicated traps is that of the average number of spores counted on each trap. When the average spore counts of the eight spore traps for the July 20

exposure were ranked according to their magnitude, some statistically significant differences were detected (Table 10). The differences were not related to trap position. They apparently reflect differences in spore densities in the air. A comparison of the mean spore counts for the eight traps exposed on July 14 failed to reveal any significant differences between them.

Table 10. Variation in the number of spores caught on the traps exposed on a single date at East Farm.

	Trap Number							
	1	3	2	7	8	4	5	6
Average spore no.	32.5 ^a	58.0	78.5	123.5	130.5	167.0	210.0	264.5

^aMeans underscored by a common line do not differ significantly at the 5% level.

For each of the eight traps the directions of spore impaction are compared in Table 11. The mean sectors of each of the traps for an exposure time are all within three adjacent sectors.

Table 11. The variability in mean sectors for the traps exposed at East Farm during July, 1964.

Exposure date	Mean sectors for the indicated traps								
	1	2	3	4	5	6	7	8	mean
7-14	4.5 ^a	3.5	5.9	5.0	5.2	4.9	3.2	5.4	4.7
7-20	5.4	6.7	6.1	5.2	-	5.0	-	5.0	5.0

^aThe mean sector was determined by summing the products of the frequency of spores in each sector and the sector number. For all traps sector 5 is north.

The replicated trap experiment was repeated in 1965. Four trap stands were placed in a row at Hyslop Farm. Severely rusted wheat was in the area. On the first exposure date all of the traps had rain shields. On the second and third exposures the first and third traps were exposed without rain shields to see if the shield altered the trapping efficiency of the rod. When the total spores caught on the rods without rain shields were compared with the total spores caught on rods with rain shields, no significant difference was shown.

The mean sectors for the spore traps at Hyslop Farm in 1965 are given in Table 12.

Table 12. The variability in mean sectors for the traps exposed at Hyslop Farm, 1965.

Exposure date	Mean sectors for the indicated traps				
	1	2	3	4	mean
6- 5	5.2 ^a	5.2	5.6	4.6	5.2
6-15	5.6	5.0	4.8	4.7	5.0
6-28	4.1	4.6	4.9	4.3	4.5

^aThe mean sector was determined by summing the products of the frequency of spores in each sector and the sector number. For all traps sector 5 is north.

In this experiment the agreement between mean sectors was better than in the 1964 experiment. From these comparisons it is concluded that sectors can be grouped into the four cardinal directions without serious error. Thus, when sector 5 is north sectors 4, 5,

and 6 form the north quadrant; 7 and 8 form the west quadrant; 9 and 1 form the the south quadrant; 2 and 3 form the east quadrant.

The Estimation of Infectivity

Because P. striiformis becomes systemic within individual leaf blades it is not practical to count pustules to estimate the infectivity (Appendix I-Glossary) of a population of spores. Therefore the prevalence (Appendix I-Glossary) of rust on seedlings was used to make these estimates. An experiment was performed to examine the effect of spore density on prevalence. Three lots of uredospores, weighing 0.5, 2.5, and 5.0 mg respectively, were each suspended in 5 ml of freon and sprayed over 20 plants. Microscope slides, coated with glycerine jelly, were exposed horizontally among each group of plants during inoculation. These were examined microscopically to estimate the relative density of spores deposited on leaves. For each group of plants prevalence, PA, and RT were recorded (Table 13). The PA measured 11 days after inoculation best detected differences in inoculum density. But differences were also evident when prevalence was measured. Since inoculations using freon ordinarily involved spore concentrations of 3 to 5 mg per 5 ml of freon, it was reasonable to use prevalence to detect differences in infectivity between populations of spores.

Table 13. The effect of inoculum density on prevalence, PA and RT.

Initial inoculum, mg/5 ml freon ^a	Prevalence	Mean PA		Mean RT	Relative spore density, spores/cm ²
		11 days	13 days		
	%	%	%		
0.5	40	3.5	6.8	2.75	28
2.5	90	14.8	25.3	2.89	56
5.0	100	30.0	47.5	2.95	144

^aTwenty leaves were inoculated with each spore density.

Freon as a Spore Suspending Agent

Because there is little published information on the use of freon for applying uredospores some experiments were undertaken to learn more about the use of freon as a spore suspending agent. Miller (1956) found that uredospores of Puccinia graminis tritici were most susceptible to freon injury if their moisture content exceeded 15 per cent.

It was necessary to answer two questions about the use of freon. Would the customary rehydration period of vacuum-dried spores described by Sharp and Smith (1952) render them too sensitive to freon injury? How long would uredospores, either vacuum-dried or fresh, remain viable in freon?

Spores were applied to foliage after having been suspended in freon for various periods of time. No significant difference was shown

for prevalence of rust on plants inoculated with spores which had been in freon for 0, 10, or 20 minutes prior to application to foliage. This was so for both fresh and vacuum-dried spores. In routine work plants were inoculated within three minutes of putting the spores in freon. The results of these experiments indicate that within that time freon would not reduce the infectivity of spores.

Five experiments were conducted to determine the relative infectivities of rehydrated and non-rehydrated spores. Vacuum-dried spores were rehydrated by exposing them to a saturated atmosphere at 20 C for 12 hours. When the results of all five experiments are considered together, 65 percent of the leaves inoculated with rehydrated spores developed rust; 73 percent of the leaves inoculated with non-rehydrated spores developed rust. These values are not statistically different (5 percent level). Considering the experiments individually, in one case significantly more leaves inoculated with rehydrated spores developed rust than did leaves inoculated with non-rehydrated spores. In two experiments the reverse was true and in the other two experiments there was no difference. The amount of germination of stripe rust uredospores is notoriously inconsistent for reasons not entirely understood (Burleigh, 1965; Schröder and Hassebrauk, 1965). But factors such as environmental conditions during spore production, spore age at the time of collection, and perhaps environmental factors other than light,

temperature, and moisture during germination influence the germination of uredospores (Tollenaar and Houston, 1966). The spores used in these five experiments were collected at different times from different sources and were stored for different periods of time. This may have influenced the behavior of the spores when used as inoculum. But since no consistent advantage was obtained by rehydrating vacuum-dried spores prior to inoculation with freon the procedure was not used.

Minimum Dew Period Experiments

Since free moisture, preferably in the form of dew, is required for infection of plants by P. striiformis, the minimum period of free moisture on leaves necessary for infection was determined.

Inoculated seedlings were placed in the dew chamber which had been turned on previously to equilibrate. At various times after being put in the dew chamber, groups of pots were returned to the greenhouse bench. The moisture on the leaves evaporated naturally within a few minutes after the plants were removed from the dew chamber. For each dew duration treatment the prevalence and RT were recorded. Altogether 13 such experiments were conducted (Table 14).

None of the inoculated plants became infected with a dew period of two hours or less. Infections of plants receiving no dew treatment or a one hour dew treatment took place when plants were raised in

Vermiculite in the growth chamber. Under these conditions guttation droplets formed on leaf tips of many plants and provided the moisture necessary for infection. The small pustules (RT 2) were confined to the leaf tips.

Table 14. The influence of the length of the dew duration period on the prevalence of stripe rust.

Experiment number	Prevalence of rust after indicated dew period (hours)								
	0	1	2	3	4	5	6	7	≥ 8
	%	%	%	%	%	%	%	%	%
1	0			5		100		95	55
2	0	0	0			8			4
3 G ^a	21	3	0	82					97
4 G	0	0	0	38					88
5 G	8	0	0	0					92
6 G	0	8	0	17					100
7	0	0	0	70	60				60
8	0		0	0	0	6			75
9	0		0	12	58	61			100
10	0		0	7	0			64	
11	0		0	0 ^b 13				87	
12	0	0	0		0			6	
13	0			0		30			60

^aG indicates that the experiment was performed in the growth chamber. Otherwise the experiments were conducted in the greenhouse.

^bA group of pots was removed from the dew chamber after 2.5 hours.

With dew periods of three hours some infection occurred in the majority of experiments, but with three hours of dew the prevalence was usually lower than with longer dew periods. This may reflect variability in the time of dew formation on individual leaves. Also spores probably differ in the length of exposure to moisture needed to produce a germ tube. Dew chamber air temperatures in these experiments ranged from 12 to 16 C with variations of ± 0.5 C during any given experiment. Therefore, within this temperature range the minimum dew period necessary for infection can be taken as between two and three hours.

At the same time the above experiments were conducted, spore germination was evaluated on agar and leaf surfaces (Table 15). When freon was used to apply spores, agar-coated slides were exposed horizontally among the plants being inoculated. The slides were then placed in a dark, saturated atmosphere at 15 C. At the same time that pots were removed from the dew chamber, slides were removed from the incubator and examined microscopically to determine the percentage germination. A spore was considered germinated if the germ tube length exceeded the spore diameter. Germination of spores on the leaf surface was also determined. A thin film of glue (Testor's Formula B model cement) was spread with a glass rod over the leaves to be sampled. After drying for about a minute the glue strip was pulled off and placed on a slide over a

drop of lactophenol cotton blue. The strip was then examined for germinated spores, which were pulled off the leaf with the glue. Germination on agar was detected after one or two hours of incubation at 15 C. Germination could be detected on leaves of plants which had been in the dew chamber for only two hours. As with prevalence of rust on plants, germination of spores on leaves increased with increasing dew periods. In experiments 9 and 10 it appears that leaves in the dew chamber form a better substrate for uredospore germination than does agar under the conditions described.

Table 15. The germination of uredospores on agar or leaf surfaces.

Experiment number ^a	Substrate	Germination after the indicated moist periods (hours)						
		0	1	2	3	4	5	≥7
		%	%	%	%	%	%	%
7	agar		0.3 ^b	0.3	0.3	0.7		37.0
8	agar			0	0	1.0	5.3	22.6
9	agar	0		0	1.0	0.3	19.3	
9	leaf	0 ^c		33.3	49.3	43.8	23.4	
10	agar	0		0.7	0.3	0		0
10	leaf	0		0.7	8.3	23.0		31.4
12	leaf	0	0	0.3		2.3		7.9

^aThe experiment numbers correspond to those given in Table 14.

^bThe germination percentages for spores on agar were based on 300 spores.

^cThe germination percentages for spores on leaves were based on as many spores as could be found. This varied from 20 to 200 spores.

Survival Studies

Because of the scarcity of active stripe rust during the summer months in Oregon, investigations into the ability of P. striiformis uredospores to survive apart from a living host were carried out.

Survival of Uredospores on Stubble

After harvest of the wheat crop stubble is allowed to stand until the following spring. If this stubble was rusted during the growing season, then a considerable amount of inoculum might possibly remain on the crop after maturity. To determine how long these spores survive on stubble, leaves that had been rusted were collected and used as a source of spores to inoculate wheat seedlings in the greenhouse. On June 10, 1965 rusted leaves of Omar wheat were collected from Hyslop Farm and placed in envelopes. One lot was stored in the greenhouse, one in the coldroom (37 F) and one outside the greenhouse in a cold frame. When seedlings of Gaines, Omar and Michigan Amber were inoculated with spores from stubble on the day of collection (June 10), all developed rust. Twenty six days later only spores from leaves that had been stored in the cold room produced infection.

In other experiments leaves were placed in a cage in the field. The sides were constructed of several layers of cheesecloth; the top was of plate glass. The cage was placed in the field directly on the

ground.

In the first such experiment spores lost their infectivity within seven days. In the second experiment spores on leaves in the cage lost infectivity between 5 and 11 days. The mean maximum temperature in the cage during the first experiment was 45 C; that during the second experiment was 37 C. These were far above ambient temperature.

In the final experiment some wheat at Hyslop Farm was used as a source of rusted stubble. The leaves were left in situ until the time of spore assay. Observations and the exposure of seedlings during the summer indicated that movement of infective inoculum through the air was insignificant during the summer. Therefore contamination of test materials was not a problem. By June 15 the leaves were dried out so that rust development ceased. Beginning July 12 eight flag leaves from fully ripened Omar wheat were periodically taken into the laboratory. Spores from these leaves were used to inoculate seedlings of Baart wheat (Table 16). Another group of seedlings was inoculated at each assay time with either freshly collected or vacuum-dried spores. An uninoculated group of seedlings was also included. Beginning August 14 eight flag leaves of Druchamp wheat were also collected. Druchamp is an immune wheat and so served as a check for contamination of stubble in the field by uredospores from some other source. From this experiment there is evidence that spores

can survive on stubble for at least 51 days in the field. The infectivity observed on August 24 is inconclusive since freon washings of Druchamp leaves evidently contained infective uredospores.

Table 16. The survival of uredospores on stubble at Hyslop Farm.

Date stubble collected	Prevalence of rust on inoculated plants			
	Spore source			Uninoculated control
	Omar stubble	Druchamp stubble	Fresh spores	
	%	%	%	%
7-12-67	12 ^a	-	88	0
8- 4-67	4	-	100	0
8-14-67	0	0	100	0
8-24-67	5	5	100	0
8-29-67	0	0	100	0
9-11-67	0	0	91	0
9-24-67	0	5	65	0

^aEach figure is based on 20 leaves.

The loss of infectivity of spores on stubble was reflected in the RT as well as prevalence. On both the July 12 and August 4 assays the mean RT for plants inoculated with spores from stubble was less (2.71 and 2.00 respectively) than the mean RT for inoculated controls (3.00).

Dried flag leaves of wheat with rust pustules were collected from several fields in northeastern Oregon during September of 1967.

Spores from leaves from Wasco, Sherman, Gilliam, and Union Counties were assayed. Only one of 26 plants inoculated with spores from Wasco County developed rust. Although the controls were free of rust a contaminant cannot be ruled out as the one infective spore. None of the spores from the other locations gave any evidence of infectivity. It is concluded that by mid-September very few, if any, infective spores remained on the stubble in northeastern Oregon.

Survival of Uredospores on Soil

During the course of rust development on wheat spores fall to the soil in great quantity. Thus the soil surface is another place where uredospores might survive for some time during the summer.

Greenhouse soil, screened through a 24 mesh-to-the-inch sieve, was placed in petri plates, without lids, and packed while in a moist condition. The soil was allowed to air dry for at least five days. Uredospores, freshly collected from foliage, were placed on the dry soil surface. The plates were placed on the greenhouse bench. At appropriate intervals spores on the soil in the plates were assayed for infectivity.

Four experiments of this type were carried out (Table 17). The variability in survival times can be explained in part by differences in greenhouse temperatures during the experiments. The maximum survival time was 31 days. The decrease in prevalence of rust on

plants inoculated with spores from soil after various times is shown in Figure 6. For the first 10 days the prevalence was high. Thereafter prevalence decreased at an increasing rate until it became 0 at 30 days.

Table 17. Survival of uredospores on dry soil.

Date spores applied to soil	Number of days until last detection of infective spores	Number of days until next assay	Mean maximum daily temp. °C
7-25-66	11	24	29
12-19-66	31	43	24
6-24-67	0	5	40
10-15-67	25	30	22

It was observed during the above experiment that RT's ranged from 0 to 3. The mean RT for the plants inoculated with spores from soil and the plants of the control group are plotted for each assay time in Figure 7. The trends of both groups are similar, but the mean RT for the group inoculated with spores from soil drops sooner and further than the RT for the control group. The pattern of RT for the plants inoculated with spores from soil is the same as the pattern of infectivity as measured by prevalence (Figure 6).

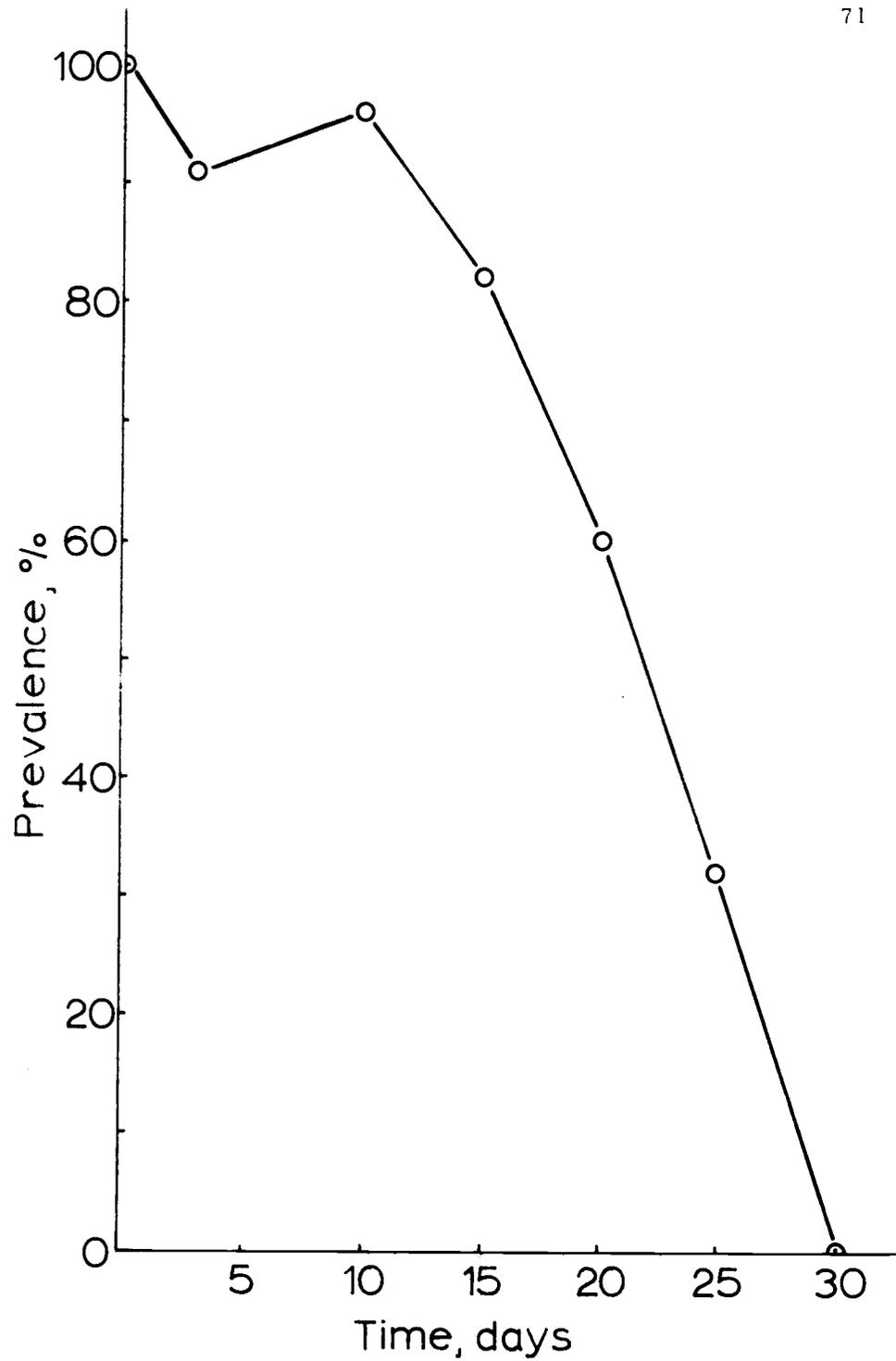


Figure 6. The decrease in prevalence of rust on plants inoculated with spores that had been on a dry soil surface for various lengths of time. Data are from the October 15, 1967 experiment (Table 17). Each point is based on the response of 25 leaves.

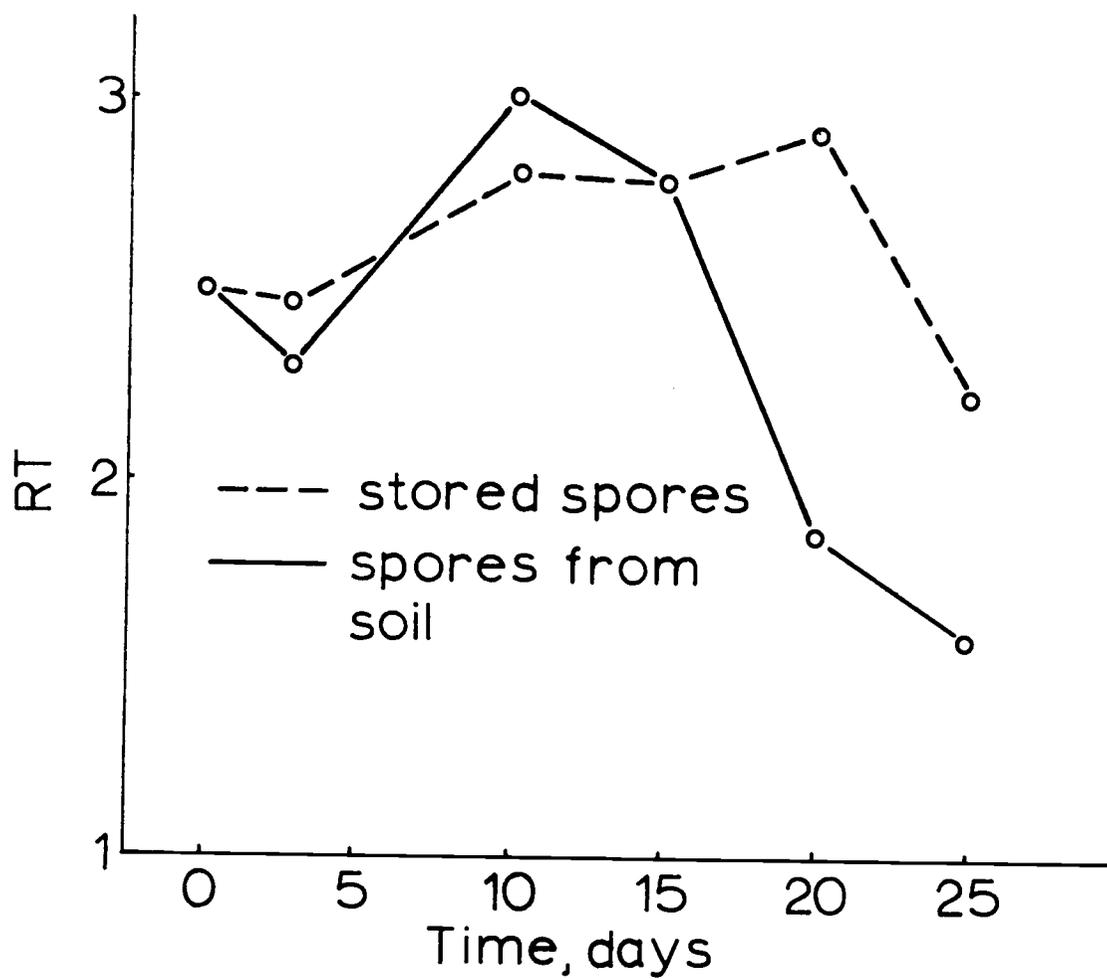


Figure 7. Mean RT's for plants inoculated with spores from a dry soil surface or with fresh uredospores. Data are from the October 15, 1967 experiment (Table 17).

Survival of Uredospores on Green Foliage

Conditions for infection do not always follow immediately the deposition of spores on foliage. Therefore the ability of spores to survive on green foliage influences the effectiveness of air-borne inoculum.

Eight experiments were conducted in the greenhouse to investigate the ability of uredospores to survive on foliage prior to infection (Table 18). When the mean maximum greenhouse temperature was 20.5 C some spores retained infectivity for 16 days. Even at a mean maximum temperature of 43.0 C spores retained infectivity for five days. Spores applied with freon did not survive as long as spores applied by brush or scalpel, but the difference was not great.

The relationship between prevalence and the delay in the dew period is presented graphically for two experiments in Figure 8. The pattern is similar to the one for the survival of spores on dry soil, but the period of survival is shorter.

Latent Periods

Although other workers have published data on the latent period (Appendix I-Glossary) for stripe rust, it was felt that this should be investigated under the climatic conditions of Oregon and with isolates of the fungus from this area.

Table 18. The survival of uredospores on green wheat foliage.

Exp. no.	Inoculation method	Mean maximum temperature °C	Prevalence at first day %	Number of days to last detection of infectivity	Prevalence at last day %	Number of days to no detectable infectivity
1	freon		86	5	2	
2	freon	28.3	92	3	9	4
3	freon	23.2	81	5	10	
4	brush	43.0	100	5	5	
5	brush	30.7	25	3	5	4
6	scalpel	23.0	90	5	30	
7	brush	20.8	88	8	84	
8	brush	20.5	100	16	36	18

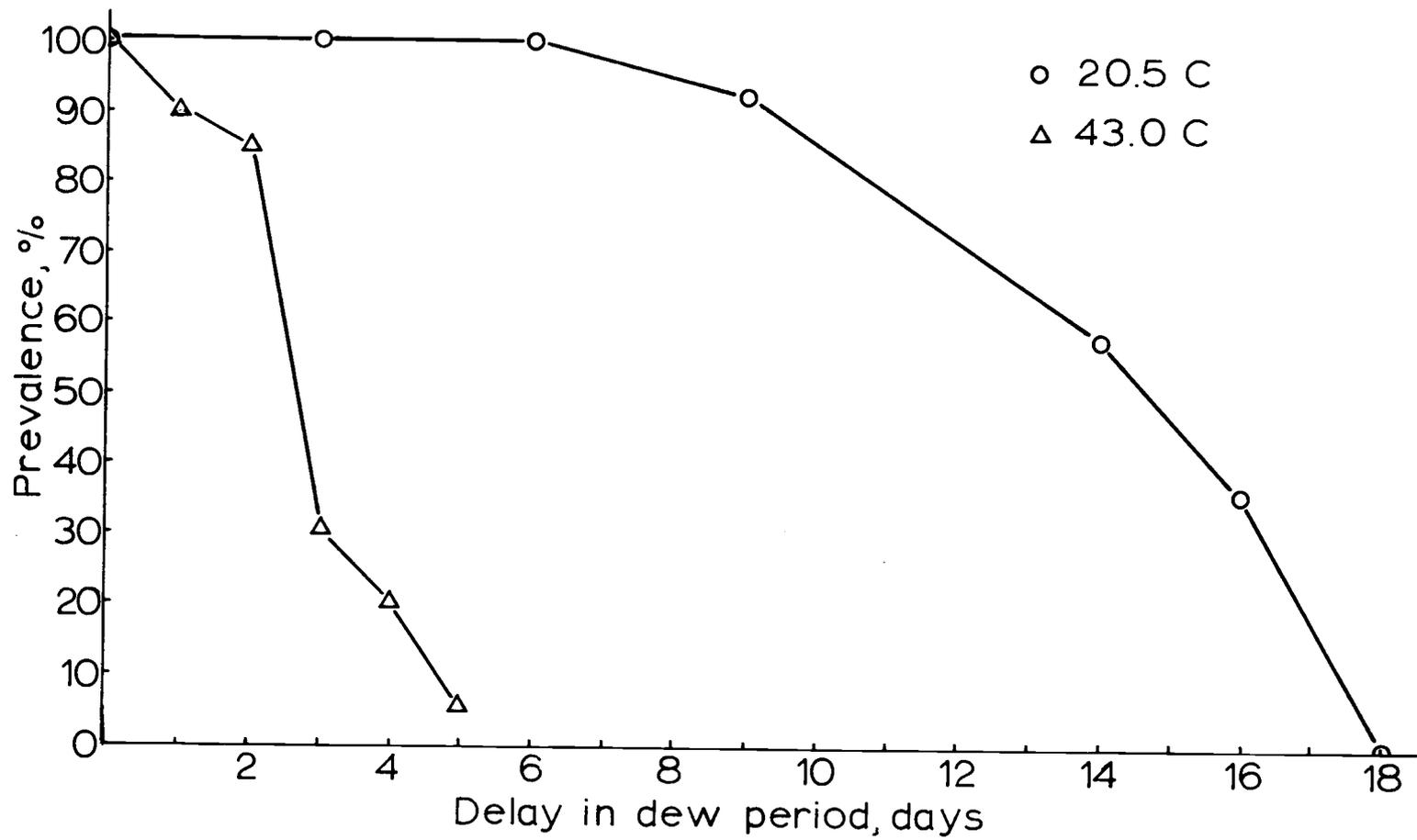


Figure 8. The relationship between the prevalence of rust and the delay in the dew period. The data are from the fourth and eighth experiments of Table 18.

Wheat seedlings (Gaines or Omar) were inoculated periodically throughout the year. After inoculation and a dew treatment half of the plants were placed outside and half were left in the greenhouse as controls. The plants were inspected regularly and the first appearance of pustules was noted. These experiments were conducted for about two years beginning in September of 1965. Plants were exposed at Corvallis or at East Farm.

The relation between mean daily temperature and the latent period is expressed in Figure 9. There is close agreement between Figure 9 and the figures published by other authors relating latent period to temperature (Burleigh, 1965; Tollenaar and Houston, 1967; Zadoks, 1961).

In less compatible race-variety combinations the latent period may be protracted. Limited evidence for this was obtained in race studies. When groups of differential varieties were inoculated, resistant varieties often required longer to show the final reaction type than more susceptible varieties (Table 19).

Three groups can be discerned in this list of varieties. The first three varieties showed their highest RT at 10.5 days after inoculation. The next three varieties were equally susceptible, in terms of RT, but did not show their highest RT until the twelfth day. The last three varieties were resistant to the rust isolate used and did not develop their highest RT until 12 or 14 days after inoculation.

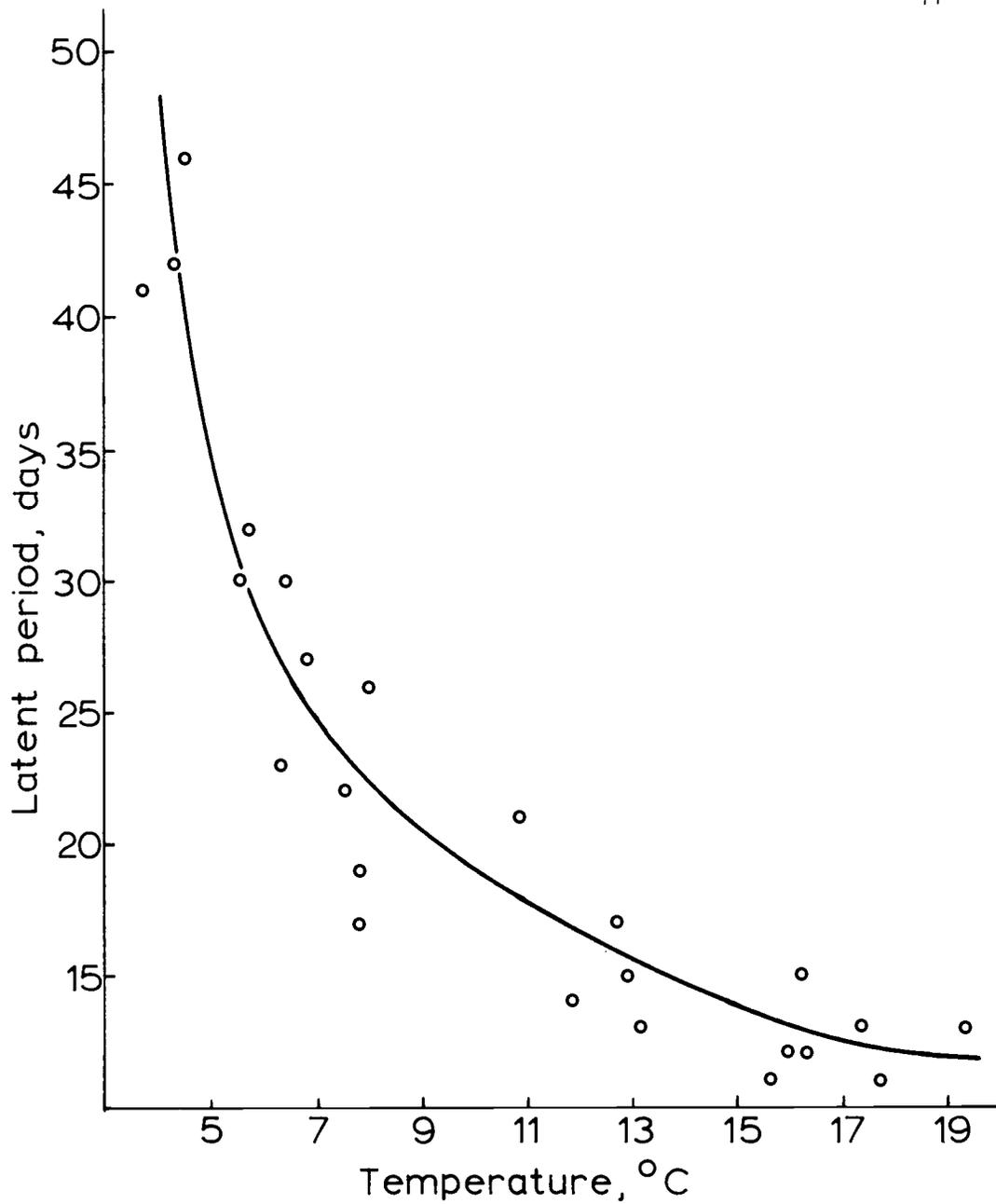


Figure 9. The influence of temperature on the latent period. Each point represents the minimum latent period for a group of inoculated plants. The mean daily temperature for each latent period was calculated by averaging the mean maximum and mean minimum temperature for the number of days in the latent period.

The extension of the latent period as an expression of resistance does not appear to be great.

Table 19. The extension of the latent period as an expression of stripe rust resistance.

Variety	RT at the indicated number of days after inoculation		
	10.5	12	14
Michigan Amber	4	4	
Omar	4	3 ⁺	
Rubis	3 ⁺	3 ⁺	
Lucas	2	4	3 ⁺
Dippes Triumph	1	3 ⁺	3
Harvest Queen	1	3 ⁺	3
Alba	0	2	2
Heines VII	0	1	2
Little Joss	z	2	

The latent period can also be plotted against the calendar time of infection to see more directly the change in the latent period during the year. This kind of relationship would vary more from year to year since it is indirect, being dependent on the consistency of the weather. In Figure 10 latent periods are compared with the time of year that infection took place. The data have been divided into three groups so that year-to-year variation is apparent. A fact evident from Figure 10 is that the shortest latent period was not reached until mid-July. During the period of greatest disease increase

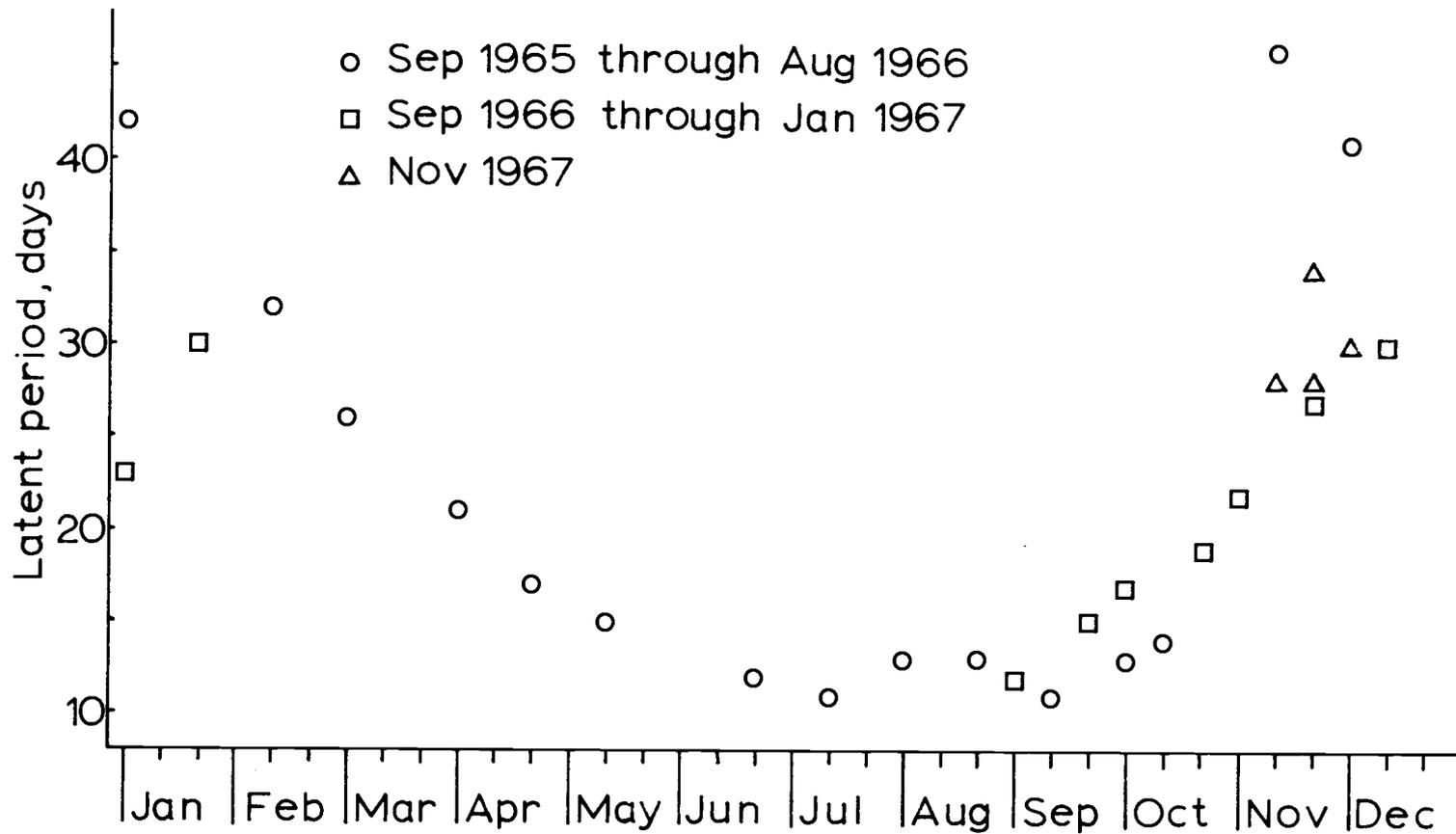


Figure 10. The relation between the latent period and the time of year when infection takes place.

on wheat (March through May) latent periods ranged from 26 to 15 days. In the first ten day period in January of 1966 and 1967 there was a considerable difference in latent periods. The mean temperature for that period in 1966 was 4.3 C; that for 1967 was 6.3 C.

The slight extension of the latent period during August may be significant. At constant temperatures of 21, 22 and 23 C Tollenaar and Houston (1967) found progressively longer latent periods. At a constant temperature of 24.5 C only chlorotic flecks appeared, which according to Sharp (1965) would indicate that the mycelium was killed within the leaf.

To investigate the influence of high temperatures on the latent period an experiment was performed in the greenhouse and growth chamber. The growth chamber was programmed for a 14 hour photoperiod (0600 to 2000 hours). The night temperature was 10 C (1830 to 0730 hours); the day temperature was 31 C (0830 to 1830 hours). These conditions were chosen to simulate the warm days of July and August. August temperatures in Corvallis may occasionally exceed 31 C for eight hours and reach a maximum of 35 to 38 C. This was especially so in the summer of 1967. The mean greenhouse temperature was 18 C (12 C minimum, 25 C maximum). When the second leaf emerged, the seedlings of Gaines were inoculated with uredospores and given dew treatments. Immediately after the dew treatment, a group of these seedlings was transferred from the

growth chamber to the greenhouse. A reciprocal transfer was also made. Such transfers, each time with a different group of the inoculated seedlings, were repeated at intervals for 21 days. When stripe rust developed, prevalence and RT were recorded (Table 20).

Table 20. The influence of a temperature of 31 C for 10 hours per day on development of stripe rust.

Group	Initial Environment	Time when transferred (days after inoculation)	Prevalence %	RT
1	chamber	0	64	3
2	chamber	1	24	3
3	chamber	5	4	2
4	chamber	8	4	oo ^a
5	chamber	11	0	
6	chamber	14	0	
7	chamber	16	0	
8	chamber	21	0	
9	chamber	not transferred	0	
10	greenhouse	0	100	oo ^{y b}
11	greenhouse	not transferred	100	3
12	greenhouse	0 (uninoculated)	0	
13	greenhouse	8	60	0 ^c
14	greenhouse	14	100	3-2
15	greenhouse	not transferred, uninoculated	0	

a = small chlorotic flecks; b = small necrotic flecks; c = chlorotic patches

Post infection high temperatures decreased prevalence and RT. Infections were eradicated between five and eight days in the high temperature regime. Plants left for more than eight days at the high temperature failed to develop symptoms. Pustules failed to develop on plants which were incubated eight days in the greenhouse and then transferred to the growth chamber. Apparently seven or eight consecutive days of these high temperatures anytime during the incubation period, can kill the mycelium within leaves.

Growth of Mycelium in Leaves

To determine the epidemiological consequences of a single infection by P. striiformis, growth rates of mycelium in leaves were estimated by measuring the increase in the length of the sporulating area on each leaf, as suggested by Allen's (1928) work which indicated that there was a rather constant distance between the edge of the visible lesion and the tips of the runner hyphae. This work was done in the greenhouse to prevent secondary infection.

In one experiment spores were applied to leaves with a camel's hair brush in a band about 1/2 cm wide, in the middle of the leaf. The length of the sporulating zone which developed on each leaf was measured. The first measurement was 15 days after inoculation; the second was 10 days later. On the basis of 19 leaves measured, the growth rate was calculated to be 8.9 ± 1.6 mm per day (95 percent

confidence limits). The mean temperature during the 10 day interval was 21.4 C.

In another experiment growth rates of lesions resulting from single spore inoculations were determined (Figure 11). In this case measurements were made daily for a 10 day period beginning 12 days after inoculation. A chlorotic region could be seen at either end of the sporulating region of the leaf. Measurements were made from one edge of the chlorotic zone to the other. Measurements were also made of the length of the sporulating zone. During the 11 day period that measurements were made the mean temperature was 25.1 C. Over the interval of the experiment the increase in the length of the sporulating zone of the lesion and the total lesion were linear. The rates for both were about 5 mm per day. In this experiment and the one above lesions were growing in two directions.

Infectious Periods of Individual Leaves

The systemic growth of P. striiformis mycelium within leaves is of epidemiological significance. Throughout the period October 1966 to June 1967 field observations were made on the length of time that individual leaves bore active pustules at Corvallis, Oregon. Leaves that were beginning to show symptoms of stripe rust were marked with string tags and observed at intervals until senescence. Once tillers began elongating in the spring the position of leaves on

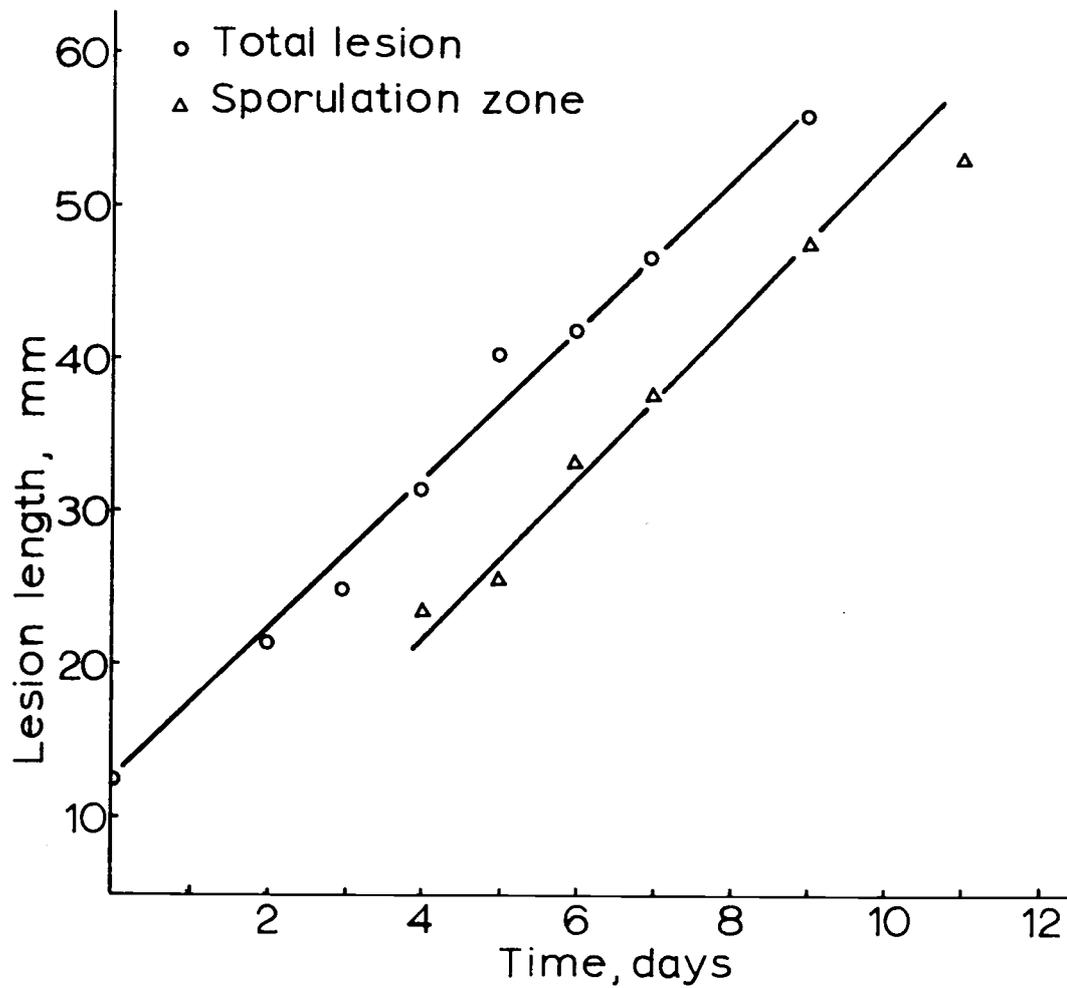


Figure 11. The growth of lesions resulting from single spore infections. Each point is the average of measurements on six leaves.

the tiller was recorded.

During the winter the development of the fungus was retarded, but sporulation occurred at all times (Table 21). RT's of 3 were often noticed during the course of spore production, but there was generally more necrosis associated with the pustules than in the spring. Commonly the first symptoms of rust were observed at leaf tips. There would first be a chlorotic patch, followed by abundant sporulation (RT 3). The sporulating zone would then progress down the leaf, similar to the manner observed in the greenhouse, but growth was in one direction only. As the sporulating zone progressed down the leaf, the original zone of sporulation would become necrotic. Thus there was a series of stages of rust development along the leaf: pre-pustule chlorosis, an area of active pustules, and finally tissue that had passed the infectious stage and was necrotic. At any one time sporulation usually occurred over less than half the length of the leaf. In the last column of Table 21 are some latent periods determined from Figure 10. They are latent periods for infections that take place on the dates given in the first column of Table 21. Thus the latent periods indicate the time required for a second infection locus on the leaf to sporulate if the infection locus resulted from a spore produced at the first infection locus. The similarity of the infectious periods of individual leaves in the winter and latent periods in the same season means that new infections on a leaf already bearing

pustules would not shorten the infectious period nor increase the rate of inoculum production. In the winter multiple infections were apparently not common, as evidenced by the rarity of more than one infection locus on the leaf.

Table 21. The rate of rust development on individual seedling leaves of winter wheat at Hyslop Farm.

Date of tagging	RT when tagged	Number of days until leaf senescence	Corresponding latent periods (from Fig. 10)
10-26-66	0	17	19
11- 3-66	1	17	22
11-29-66	2	34	27
12-20-66	2	35	30
1-15-67	2	42	30
2-18-67	2	35	32
2-26-67	2	25	30
3-18-67	2-3	20	24

During the spring, observations were made on the development of rust on the stem leaves of individual tillers (Figure 12). The periods of active rust development for these leaves were about as long as the infectious periods reported in Table 21. But during the spring the PA increased on stem leaves, whereas it remained nearly constant on the seedling leaves owing to necrosis. The entire stem leaf was commonly invaded and bore pustules before any one portion became necrotic. This was probably due to multiple infections and a

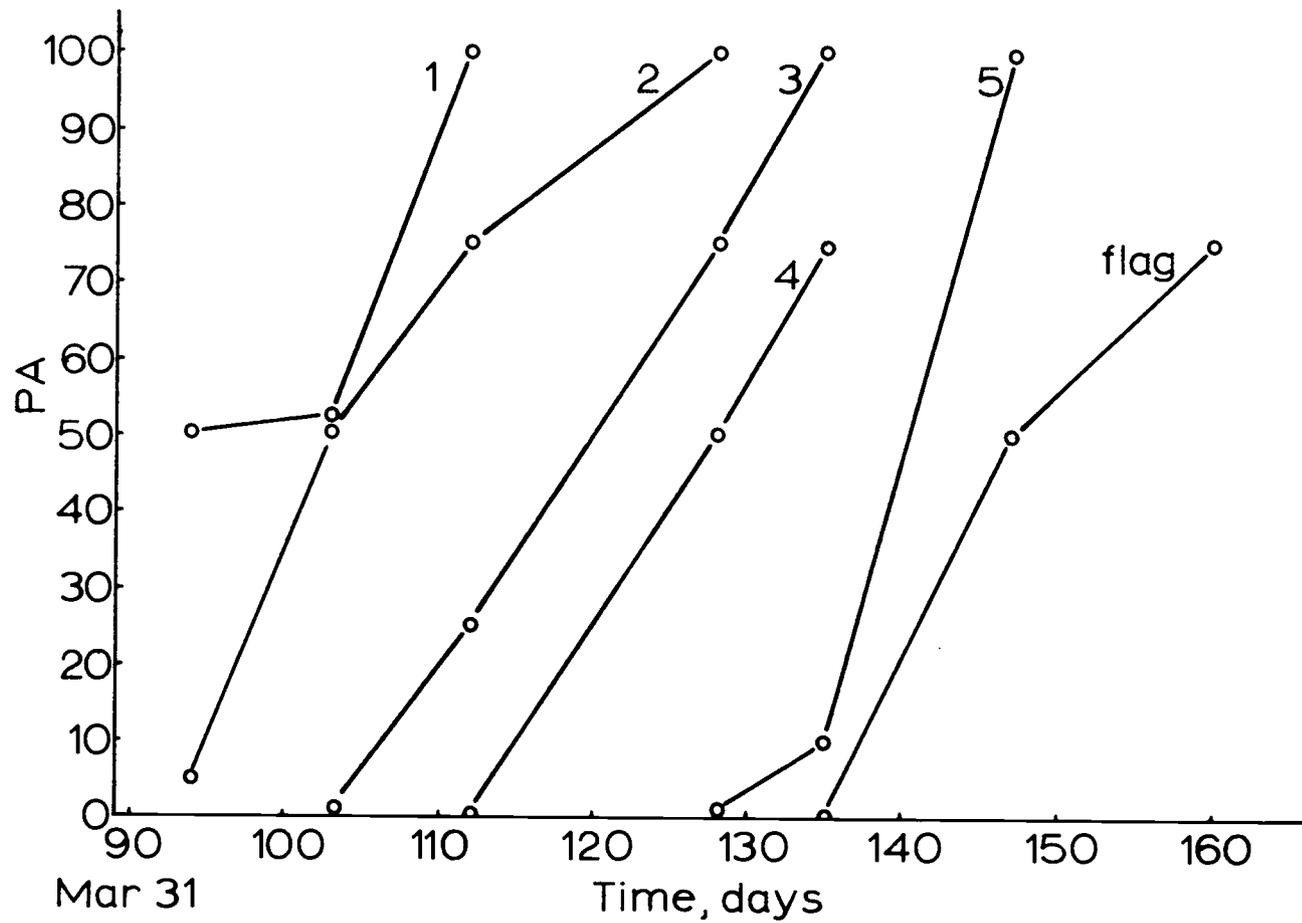


Figure 12. The development of rust on stem leaves on an individual tiller of Omar wheat. The leaves are numbered consecutively.

higher growth rate of mycelium within the leaf because of higher temperatures.

Natural Infection Conditions

An experiment was designed to determine the frequency of days favorable for infection of wheat by P. striiformis in the field. Wheat seedlings (Bart), grown in four-inch pots, were exposed for 24 hours at East Farm. Nineteen exposures were made, each time with fresh seedlings, from April 20, 1967 to June 24, 1967. To permit distinction between days when inoculum was limiting and days when climatic factors were limiting, one group of seedlings was inoculated and the other was not. The seedlings were exposed in the field near a plot of wheat with severe stripe rust.

The duration of free moisture during the exposure period was measured with a Wallin-Polhemus dew recorder (Wallin and Polhemus, 1954). Temperature and relative humidity were recorded with a hygrothermograph. These instruments were placed on the soil surface near the seedlings. Spore trap exposures were also made during the 24 hour period. Following the exposure period the plants were returned to the greenhouse. The prevalence of rust in each group was recorded. A similar experiment was commenced on October 14, 1967 using Omar and Gaines winter wheats.

Of the 19 exposures made during the spring (Table 22) the

Table 22. The development of rust on inoculated and uninoculated wheat seedlings after a 24 hour exposure at East Farm in the spring of 1967.

Date	Spore Count	Free Moisture Period, hours	Prevalence of Rust		Mean Temp. °C
			Inoculated %	Uninoculated %	
4-20	19	12	50	10	10.9
4-22	92	11	15	2	9.8
4-24	135	10 R ^a	4	0	12.3
4-27	16	- R	11	0	7.0
5- 1	7	-	92	2	10.6
5- 5	-	11	8	2	15.3
5- 9	2	13 R	6	0	9.3
5-13	5	10	54	4	14.2
5-17	21	5	4	2	18.3
5-20	217	5	0	0	22.9
5-23	81	4	0	0	15.1
5-26	97	4	0	0	13.1
5-29	257	11 R	2	4	10.5
6- 2	323	7 + 7 R	10	28	13.5
6- 6	3732	0	0	0	15.5
6- 9	2314	8	100	100	12.7
6-14	1023	9	98	100	19.0
6-19	2410	0	0	0	20.6
6-24	1442	7	84	98	20.7

^aR indicates that moisture was in the form of rain; otherwise it was in the form of dew.

inoculated group of plants developed rust on 14 occasions. The uninoculated group of plants developed rust on 11 occasions. Most nights from April to late June, 1967 were favorable for infection assuming that the times of exposure were representative of weather during the period of the experiment.

During the fall and winter of 1967, 16 exposures were made (Table 23). Rust developed on the inoculated plants on 13 occasions. Rust was found on uninoculated plants only three times. Spore trapping data shows that the amount of inoculum moving in the air could account for the difference between the results with uninoculated plants in these experiments and those in the spring. In the fall, until December 11, there was no active rust detected in the area of exposure. From December 11 until the termination of the experiments, there were actively sporulating plants within five feet of the plants used in the experiment. But even then spore movement in the air was not detected.

The mean prevalence of rust on inoculated plants was 28 percent in the spring; the mean prevalence of rust on inoculated plants was 43 percent in the fall. So, although infection conditions were more frequent in the spring, when they did occur in the fall, a higher prevalence resulted.

A second objective was to examine more closely conditions which favored infection in the field. In Figure 13 the prevalence of

Table 23. The development of rust on inoculated and uninoculated wheat seedlings after a 24 hour exposure at East Farm in the fall of 1967.

Date	Spore Count	Free Moisture Period, hours	Prevalence of Rust		Mean Temp.
			Inoculated	Uninoculated	
			%	%	°C
10-14	0	-	15	0	8.7
10-17	0	18	76	0	7.8
10-24	0	19 R ^a	98	0	6.9
10-26	0	15 R	2	0	7.9
10-28	0	19 R	90	0	6.2
11- 1	0	6	0	0	5.8
11- 6	0	12 R	84	0	8.3
11- 9	67	7 R	14	0	9.0
11-17	5	-	94	0	5.6
11-22	0	4	6	0	2.6
11-28	2	- R	18	2	6.0
12- 7	-	13	10	0	2.5
12-16	0	11 R	0	0	0.6
12-19	0	24 R	0	0	1.2
12-27	0	14	100	8	7.9
1-13	0	24 R	86	12	8.0

^aR indicates that moisture was in the form of rain; otherwise it was in the form of dew.

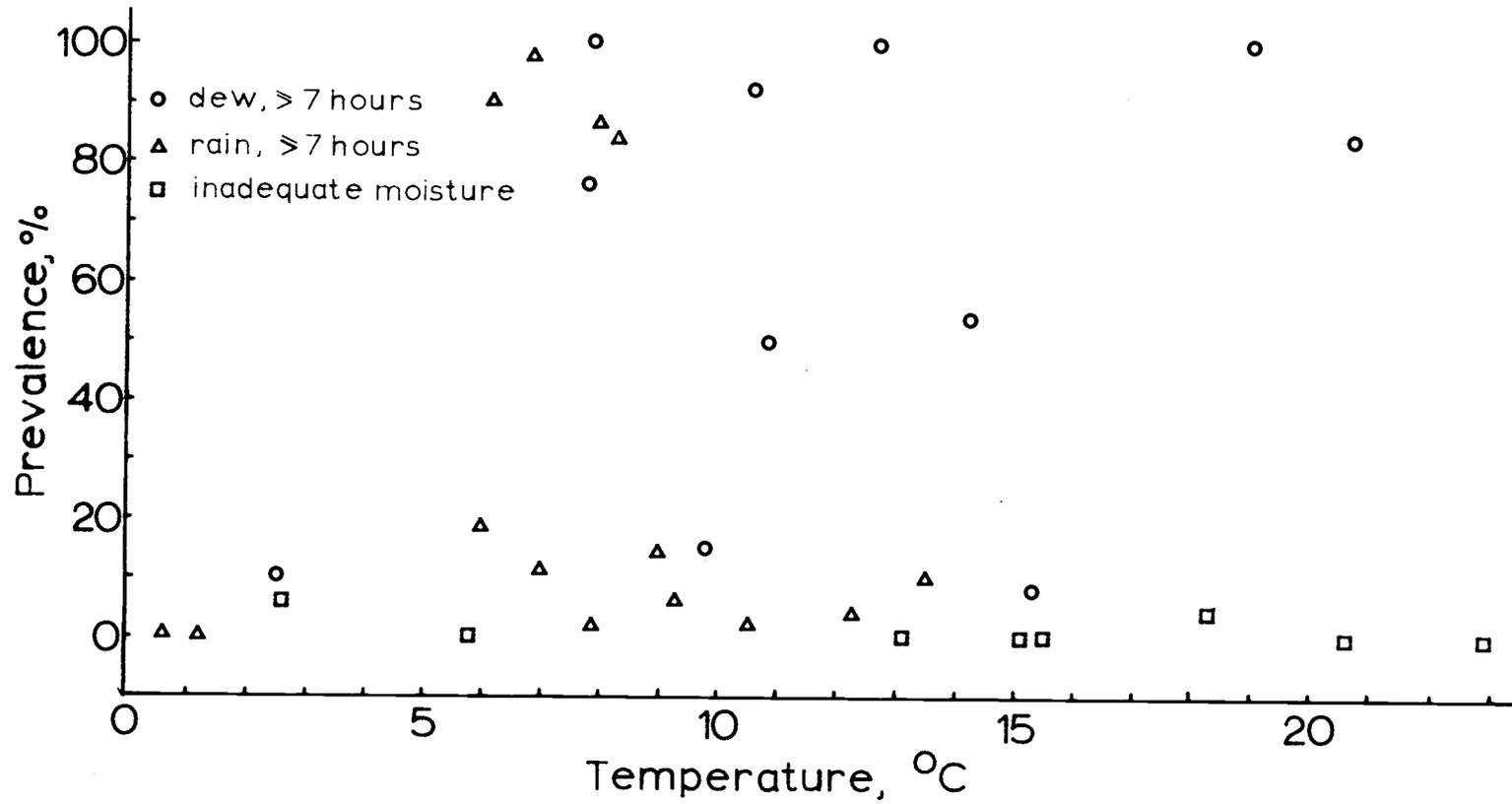


Figure 13. The influence of temperature and moisture on infection of inoculated plants in the field. Each point is based on 50 leaves.

rust on inoculated seedlings is compared with temperatures and moisture conditions during the exposure period. For 50 percent or more of the inoculated plants to become infected moisture had to persist at least seven hours. These prevalences occurred more often when the seven or more hours of moisture were in the form of dew rather than rain. Good infections were obtained when mean temperatures fell between 6 and 22 C. Beyond these limits the data are insufficient to draw conclusions about temperature and infection. In the case of the one point in Figure 13 where moisture was deemed inadequate, frost had formed on the leaves. The recorder may not have reflected moisture conditions on leaves under these conditions.

To investigate the possibility that rain washed spores from foliage an experiment was performed in the greenhouse. Three groups of wheat plants were inoculated with uredospores. Two of these groups were placed in a mist chamber. With the water on, a heavy mist filled the chamber and rapidly wet the plants. Within half an hour water was running off the foliage. The plants were left in the mist chamber for eight hours. The third group of inoculated plants and an uninoculated group of plants were left on the greenhouse bench. At the end of the eight hours one group of pots was removed from the mist chamber and placed on the greenhouse bench. The other group, along with the two groups which had been on the bench all day were given a 16 hour dew treatment. The prevalence of rust

on each group was recorded. None of the plants that received a mist treatment was infected. Of the group that received a dew treatment only, 94 percent of the inoculated leaves developed rust. These results indicate that freon-applied uredospores can be washed from foliage. It is possible that chlorine in the municipal water supply interfered with infection, but complete inhibition does not seem likely since municipal water was used instead of freon on other occasions to apply uredospores with resulting high levels of infection.

Another objective of the field experiments was to compare counts of spores on traps with prevalence of rust. Considering the times when moisture was adequate, there was a sharp difference between prevalences when spore counts were less than 100 spores and when they were greater than 1000 spores (Figure 14). When spore counts were intermediate between these values, moisture conditions were not favorable for infection. On one occasion when rain fell and the spore count was 340, 28 percent of the plants developed rust. A high prevalence of rust might have resulted if dew rather than rain provided the moisture when a spore count of 340 was recorded.

Quantitative Epidemiology

One of the most useful ways to examine the records of disease severity increase is to plot the severity of disease against time. But

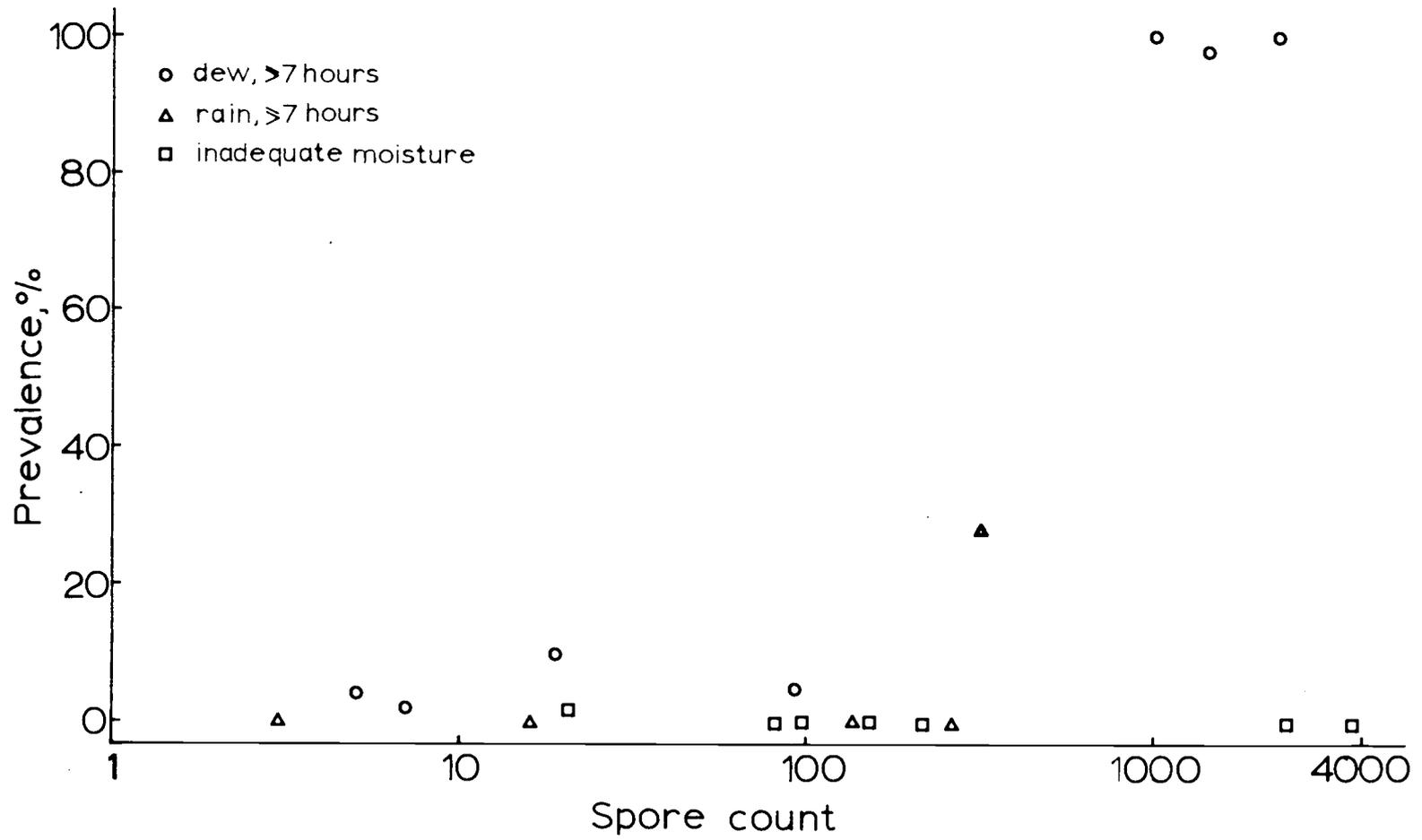


Figure 14. The relationship between the number of spores caught on the rod spore trap and the prevalence of rust on uninoculated seedlings during a 24 hour exposure. Each point is based on 50 leaves.

rather than simply plotting the DA against time, the logit transformation of van der Plank (1963) can be used. Van der Plank's basic equation for disease increase is:

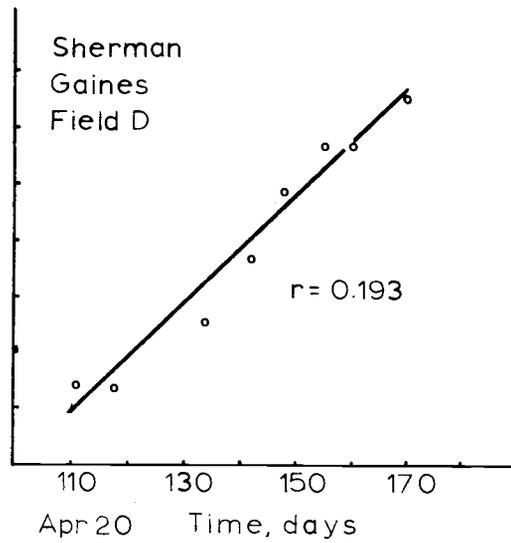
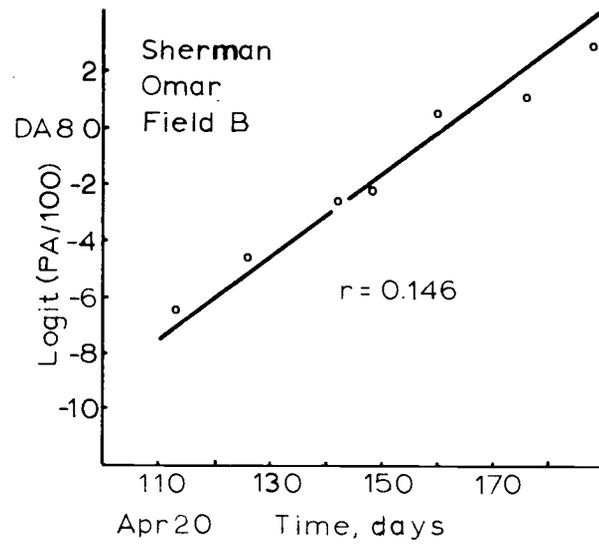
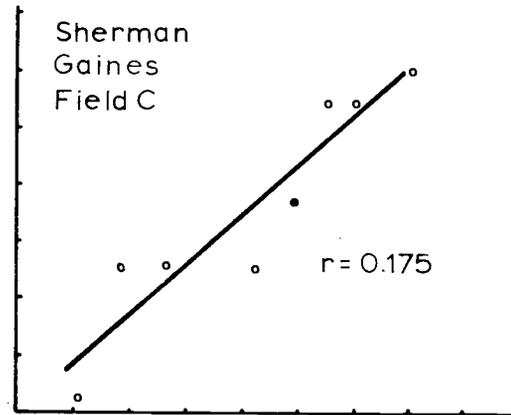
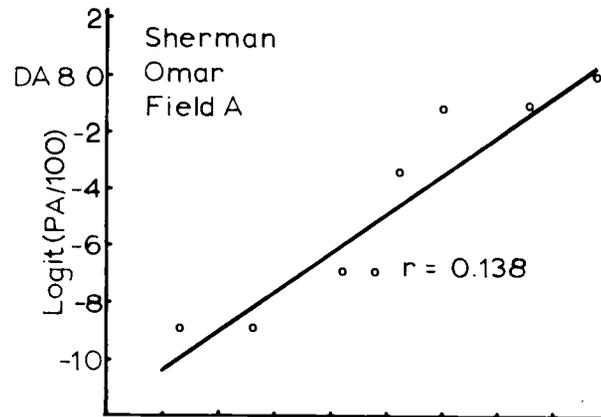
$$dx/dt = rx(1-x) \quad (1)$$

which when integrated between the intervals t_1 and t_2 gives:

$$r = 1/(t_2 - t_1) [\log_e x_2 / (1 - x_2) - \log_e x_1 / (1 - x_1)] \quad (2)$$

In these equations t is time. For stripe rust time (t) is measured in days. The term x is the proportion of diseased tissue (PA/100). Equation (2) is that of a straight line of slope r . The slope characterizes the rate of disease increase. Van der Plank calls it the apparent infection rate. The apparent infection rate need not remain constant throughout an epidemic. The term $\log_e x / (1 - x)$ is referred to as the logit of x . This definition of logit is not the same as that used by Zadoks (1961), but the definition used by van der Plank has priority (van der Plank, 1963).

Some disease progress curves for individual fields in which the logit transformation was used are given in Figure 15. The apparent infection rate (r) was determined for each curve by calculating the regression coefficient. An abrupt and obvious change in the disease progress occurred in one field (Figure 15G). Therefore the data were divided into two groups and regression coefficients



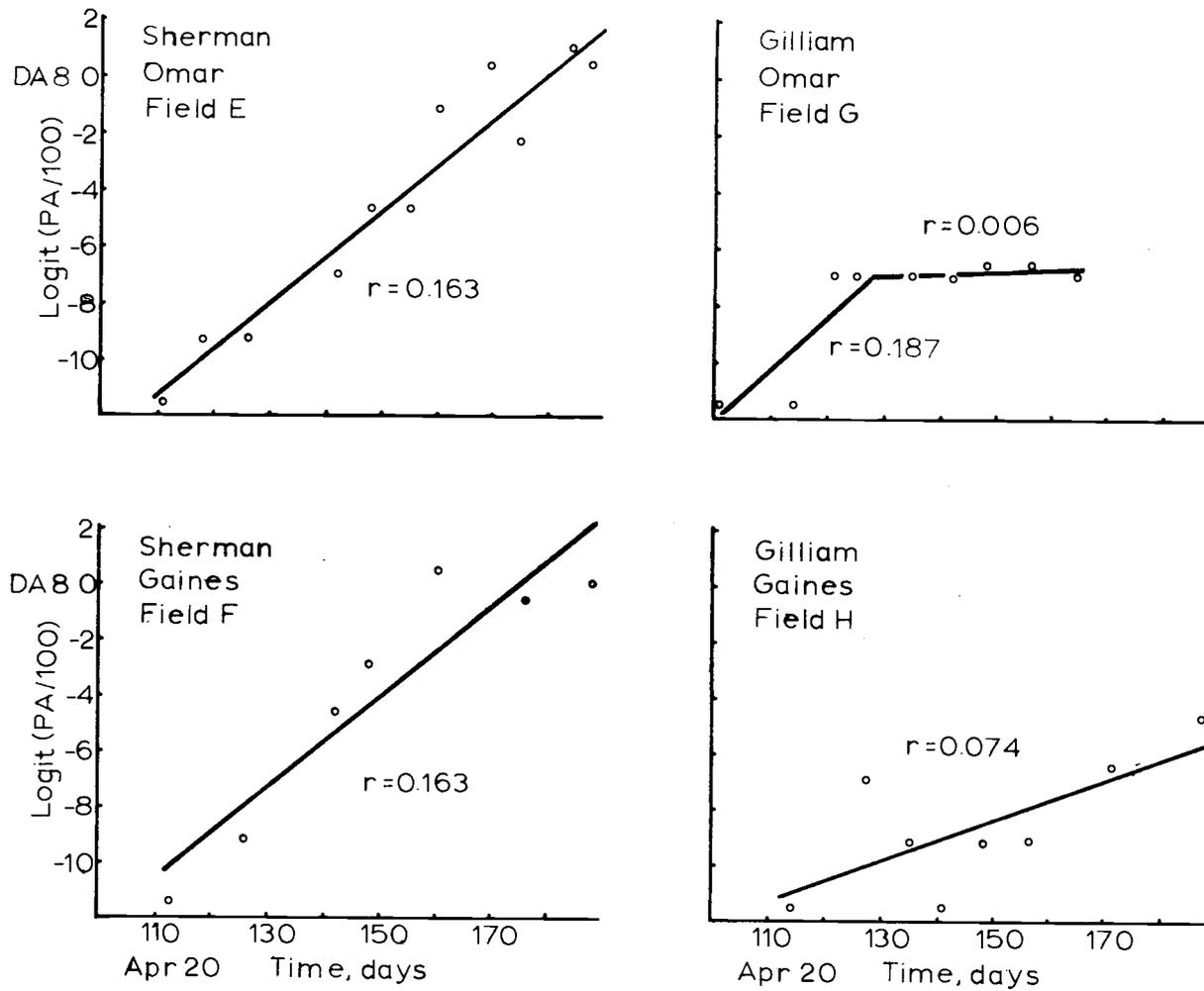


Figure 15. The development of stripe rust in eight fields of winter wheat in northeastern Oregon in 1964.

were calculated for each group.

The value of plotting disease in this way is that the apparent infection rate is a quantitative character useful for comparing epidemics and analyzing them with respect to environmental factors. This approach opens the way for a more careful analysis of the development of an epidemic.

Considering the eight curves of Figure 15 it is apparent that conditions were more favorable for disease development in Sherman County than in Gilliam County. The two varieties of wheat can likewise be compared. Considering only Sherman County, the mean apparent infection rate for Gaines wheat was 0.177 per unit per day; that for Omar wheat was 0.149 per unit per day. This is interesting since Gaines is regarded as the more resistant variety of the two. Its resistance is based on the RT of plants at about the time of head emergence.

Another feature of the eight disease progress curves is that the final level of disease was similar in all fields. The exception was the field depicted in Figure 15B where the final PA was 95 percent. In the other fields it was 50 or 75 percent and these levels were not reached until late in the epidemic.

The Basic Infection Rate (R)

Equations (1) and (2) give a simplified view of disease increase. But they are a starting point for developing more realistic expressions. The following discussion derives mostly from van der Plank (1963) and is given here for a background to a treatment of data on stripe rust epidemiology.

The apparent infection rate (r) is so named because it does not account for two features of disease increase. These are the latent period and the infectious period. Equation (1) assumes that infected tissue becomes immediately infectious. This is not true for stripe rust or probably for any other plant disease. The existence of a latent period means that the amount of tissue which is infectious at any given time is less than the amount of infected tissue. If the latent period is denoted by p , then at time t , x_t is the proportion of infected tissue and x_{t-p} is the proportion of infected tissue which has gone through the latent period and is therefore infectious. To account for the latent period van der Plank writes:

$$dx/dt = Rx_{t-p}(1-x_t) \quad (4)$$

The term R is the basic infection rate. It is determined from r by the expression:

$$R/r = x_t/x_{t-p} \quad (5)$$

It is evident that to know x_{t-p} one must know p . Then from disease progress curves such as appear in Figure 15, for any time (t) one can determine the value of x , p days prior to t . This value of x is then the proportion of infectious tissue at time t . When van der Plank discusses the relation of R to r , he assumes that the latent period remains constant or varies only by a day or two around some mean value. However, as shown in Figures 9 and 10, the latent period for stripe rust progressively changes during the season. Thus for Oregon a constant latent period cannot be assumed when calculating R .

Using the progress of disease in an Omar wheat field in Sherman County (Figure 15B) as an example, the influence of a changing latent period can be determined. This field was chosen because the points come very near to falling on the regression line so that r for this field was indeed nearly constant throughout the epidemic. When r is constant, R will vary with the increase in x even if p is constant. This is a property of the relation between r and R . Therefore R has been calculated in Table 24 for various times during the epidemic using $r = 0.146$ per unit per day, $p = 12$ days, and equation (5). Note that R always exceeds r . The values of R illustrate that with r constant, conditions continually become less favorable for disease development. With p continually decreasing the change in R with time was increased. Taking the

change of p into account shows that conditions for infection decreased to a greater extent than would have been apparent if a constant latent period were assumed.

Table 24. The effect of a changing latent period on the rate of change of R with time when r is constant (0.146 per unit per day).

Time (t) days	x_t	Latent period ^a (p), days	R with p variable	R with p constant (12 days)
10	0.0006	24	4.42	0.92
30	0.010	19	2.16	0.86
50	0.167	15	1.11	0.76
70	0.786	13	0.32	0.32
90	0.985	12	0.16	0.16

^a Latent periods were determined for the date of each time (t) from Figure 10.

The Apparent Infection Rate Corrected for Growth of the Host (ρ)

The basic infection rate (R) although accounting for the latent period, is like the apparent infection rate (r) in that it measures the rate of increase of disease, not the growth rate of the pathogen on the host. If the amount of host tissue remains constant throughout an epidemic, r and R are measures of the pathogen's growth rate on the host. But if the host grows during the epidemic, then r measures the growth rate of the pathogen relative to the growth of the host. In this case r may be near zero or even negative, yet

the pathogen may be actively growing, but with a growth rate less than that of the host. Van der Plank gives an equation for the apparent infection rate corrected for the growth of the host:

$$\rho = 1/(t_2 - t_1) \log_e [y_2 x_2 (1 - x_1) / y_1 x_1 (1 - x_2)] \quad (6)$$

In this equation y is some measure of susceptible host tissue, preferably an estimate of area. Growth of the host may be important in analyzing stripe rust epidemics. Puccinia striiformis often becomes established while the host is in the seedling stage and continues to develop until the host matures. During this time both the total area of host tissue and the area of infected tissue increase. But at any time the estimate of x is based only on tissue present at that time. Thus the basis on which x is estimated changes throughout the season. To correct for this by equation (6) estimates of the total area of susceptible host tissue need to be made each time x is estimated. It is difficult to estimate y in a relative manner. A direct measurement is needed. Zadoks (1961) followed the increase in susceptible tissue area by measuring the area of all leaves on a number of representative tillers at each observation time with a planimeter. The PA was estimated by the same method. By knowing the planting density and row spacing for the fields observed he arrived at estimates of leaf area in terms of cm^2/ha . From these data van der Plank (1963) calculated a corrected apparent infection

rate (ρ) of 0.149 per unit per day, for the disease increase from April 20 to June 1. The apparent infection rate (r) for the same period was 0.132 per unit per day. The y_2/y_1 ratio in these calculations was 2.1. Making the assumption that this ratio of wheat growth applies in Oregon during the same period, infection rates corrected for host growth for the fields represented in Figure 15 can be calculated by adding 0.018 to r .

It was not feasible to accurately measure y for several fields or plots at intervals of a few days throughout the season. But in one experiment detailed notes were kept on the number of leaves and tillers per plant. Although this is not as precise a measurement of susceptible tissue as an area estimate, the information can be used to estimate y_2/y_1 . For the disease progress curve of this plot of wheat (Figure 17) the initial value of r was 0.217 per unit per day. The y_2/y_1 ratio based on the average number of leaves per plant at 96 and 117 days was 2.26. This is close to Zadoks' measurement. Using this ratio the apparent infection rate corrected for growth of the host (ρ) was calculated to be 0.256 per unit per day.

As long as the different fields being examined are growing at about the same rate the correction factor is not needed. But if different varieties or chemical treatments are being compared, and where there are resultant differences in growth rates of hosts, the correction factor is needed to provide the most accurate distinction

between disease development on the various hosts.

Calculation of r When Disease Increase Is Due to Growth of Mycelium within Leaves

Although r , R , and ρ measure disease increase, they do not specify the manner by which disease increases. For most rust diseases x is increased by inoculum dispersal and new individual infections. Stripe rust is different, however, in that the growth of mycelium in a single leaf can be extensive and rapid. Sporulation can occur over the entire leaf surface from a single infection. Thus the proportion of diseased tissue can increase by systemic growth of mycelium within leaves, as well as by new infections. In a greenhouse experiment the increase in the amount of rust on leaves with time was measured (Figure 11). Since only one dew treatment was given the increase in x was due solely to mycelial growth. Taking the total length of the primary leaf to be 80 mm the length of the sporulating zone divided by 80 is an estimate of x . By this method x at day 4 was 0.262 and at day 10 was 0.656. Then by equation (2), r equals 0.28 per unit per day.

In Table 13 PA estimates are entered for groups of plants inoculated with different inoculum densities. From the two PA estimates for each treatment apparent infection rates have been calculated. They are 0.349, 0.344, and 0.374 per unit per day

respectively for the 0.5, 2.5, and 5.0 mg spore doses. These values of r for individual leaves are generally higher than the values of r calculated for disease increase in fields.

The increase in PA for six stem leaves was given in Figure 12. Infection rates have been calculated from these data (Table 25).

Table 25. Apparent infection rates for individual stem leaves in the field, ^a

	Leaf					
	1	2	3	4	5	flag
x_1	0.50	0.25	0.25	0.50	0.25	0.50
x_2	0.80	0.80	0.80	0.75	0.80	0.75
$t_2 - t_1$	11	20	18.5	7	15	13
r	0.127	0.125	0.135	0.157	0.227	0.085

^aThe disease increase on these leaves is shown in Figure 12. The disease progress curve for the plot of wheat which the above plant was in is given in Figure 16C.

Here again the apparent infection rates for individual leaves are greater than the apparent infection rate for disease increase in the entire plot. During the time of observation of the individual leaves, r for the whole plot was 0.030 per unit per day (Figure 16, 1967). By determining x for the whole tiller (Figure 12), for each observation time, on the basis of the PA for each leaf, r for the whole tiller was determined. For the interval April 4 to May 6

(day 94 to day 126 in Figure 12) r is 0.029 per unit per day. This agrees very well with r for that period determined from Figure 16, 1967. After May 6 the value of x for the plant dropped about 0.3 logit units. This drop was not detected in the plot as a whole.

Development of Stripe Rust in the Willamette Valley

The seasonal development of stripe rust was followed in plots of Omar wheat at Hyslop Farm. The disease progress curves for four years appear in Figure 16. Most of the disease progress curves plotted for northeastern Oregon are straight lines up to the termination of the epidemic (Figure 15). At Hyslop, however, the apparent infection rates decreased abruptly during the season. The change in r occurs between $\logit x = 0$ (DA 8) and $\logit x = -1$ (DA 7). This point was reached earlier at Hyslop than in the northeastern Oregon fields.

A constant value of r means that conditions steadily deteriorate for disease development (R continually decreases). A decrease in r signifies an even greater deterioration. It appears that at DA 8 conditions for development of stripe rust in a wheat field become less favorable. At DA 8 the balance of an epidemic shifts. More tissue is diseased than is healthy. Part of the decrease in r may be because of undercorrection of the term $1-x$ in equations (1) and (2). Microclimatic changes may also be involved.

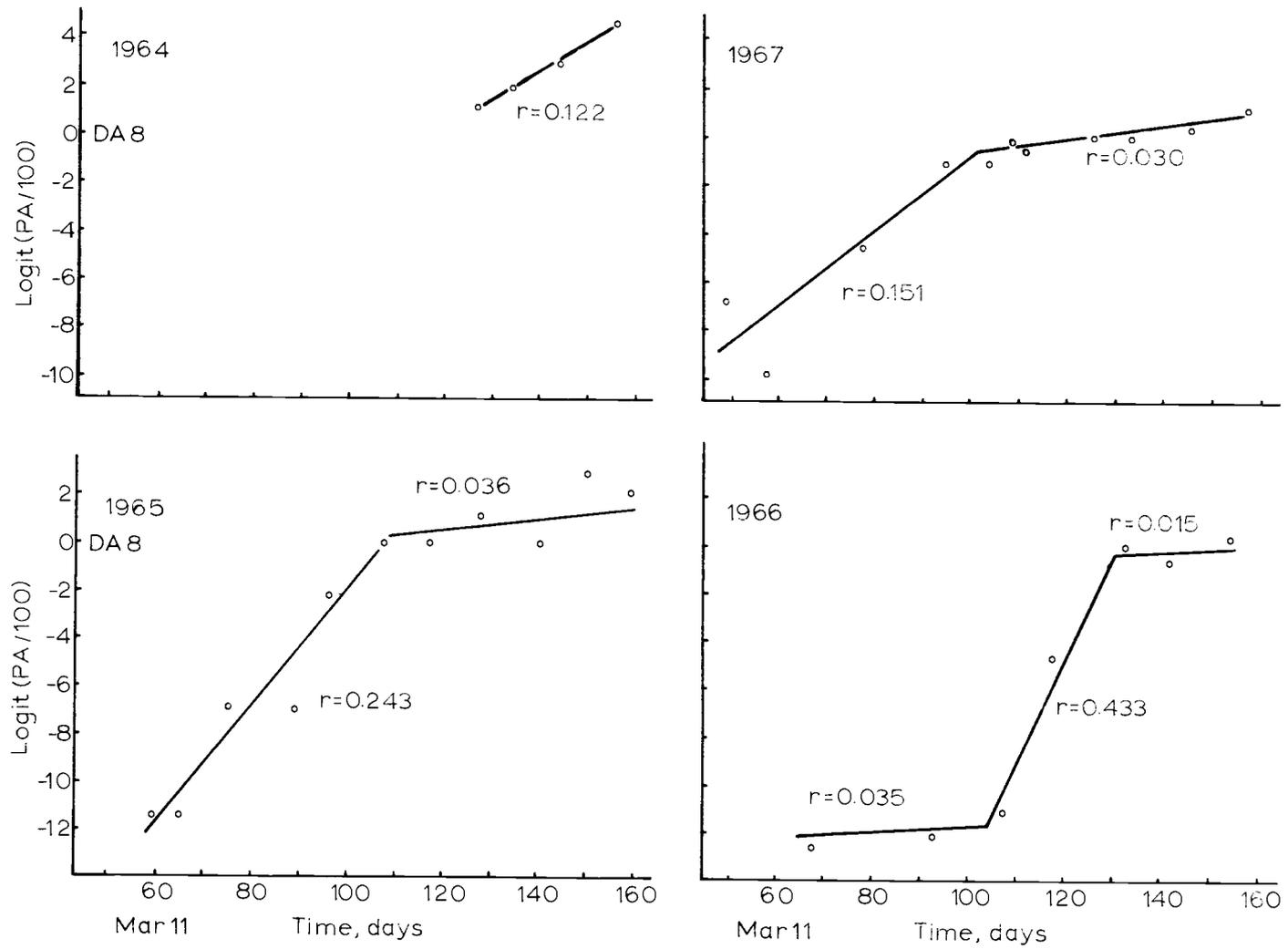


Figure 16. The development of stripe rust on Omar wheat at Hyslop Farm.

A change in the apparent infection rate was also detected during an epidemic in a spring wheat at East Farm (Figure 17). The shift was at PA 69 (DA 8.8) and occurred on June 16. Comparison of the 1967 curve of Figure 16 and Figure 17 shows that long after the reduction of r in the winter wheat at Hyslop, the epidemic in the spring wheat at East Farm was still in the fast phase. This argues that the change in r was not due to some macroclimatic factor, but rather to some consequence of x . The reason that the shift in r is not seen in the northeastern Oregon disease progress curves (Figure 15) is that DA 8 was usually not reached until the termination of the epidemic. Disease in the field depicted in Figure 15B did progress beyond DA 8. Although a straight line was fitted to all the points, a tendency for r to decrease can be seen.

The curves of Figure 16 indicate something of the length of time that rust is active on wheat in the Willamette Valley. The first points for the years 1965 and 1966 represent the first observations of rust. Rust was seen first on December 31, 1966 in the 1967 crop year. Severity remained near DA 1 until about the middle of February when activity of the fungus increased. Evidence for fall infection is difficult to find in the Willamette Valley.

Plots of wheat at Hyslop Farm were inoculated in the fall of 1965 and the development of rust followed through the winter (Figure 18). The level of rust remained low throughout the winter.

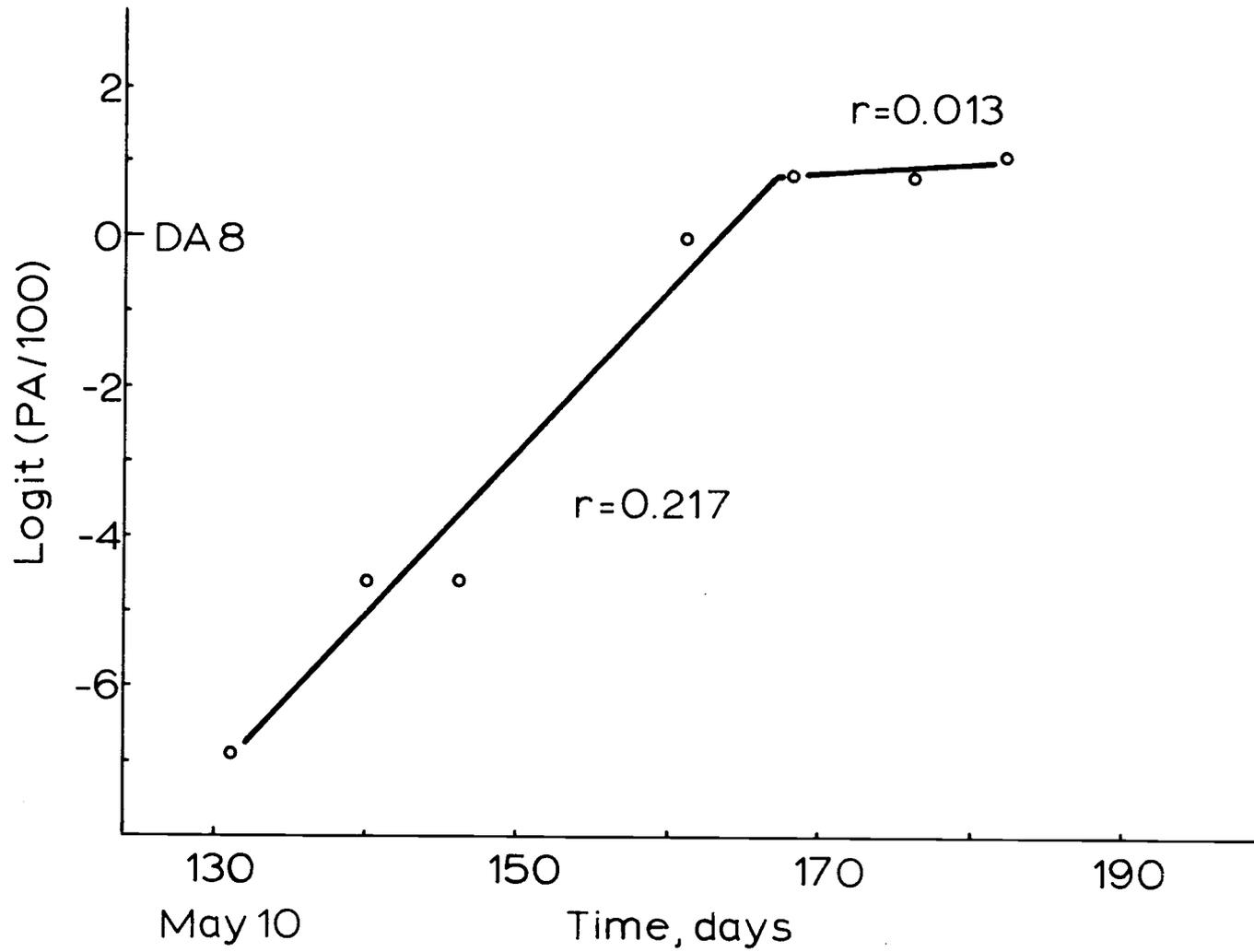


Figure 17. The development of stripe rust on a spring wheat (Bart) at East Farm in 1967.

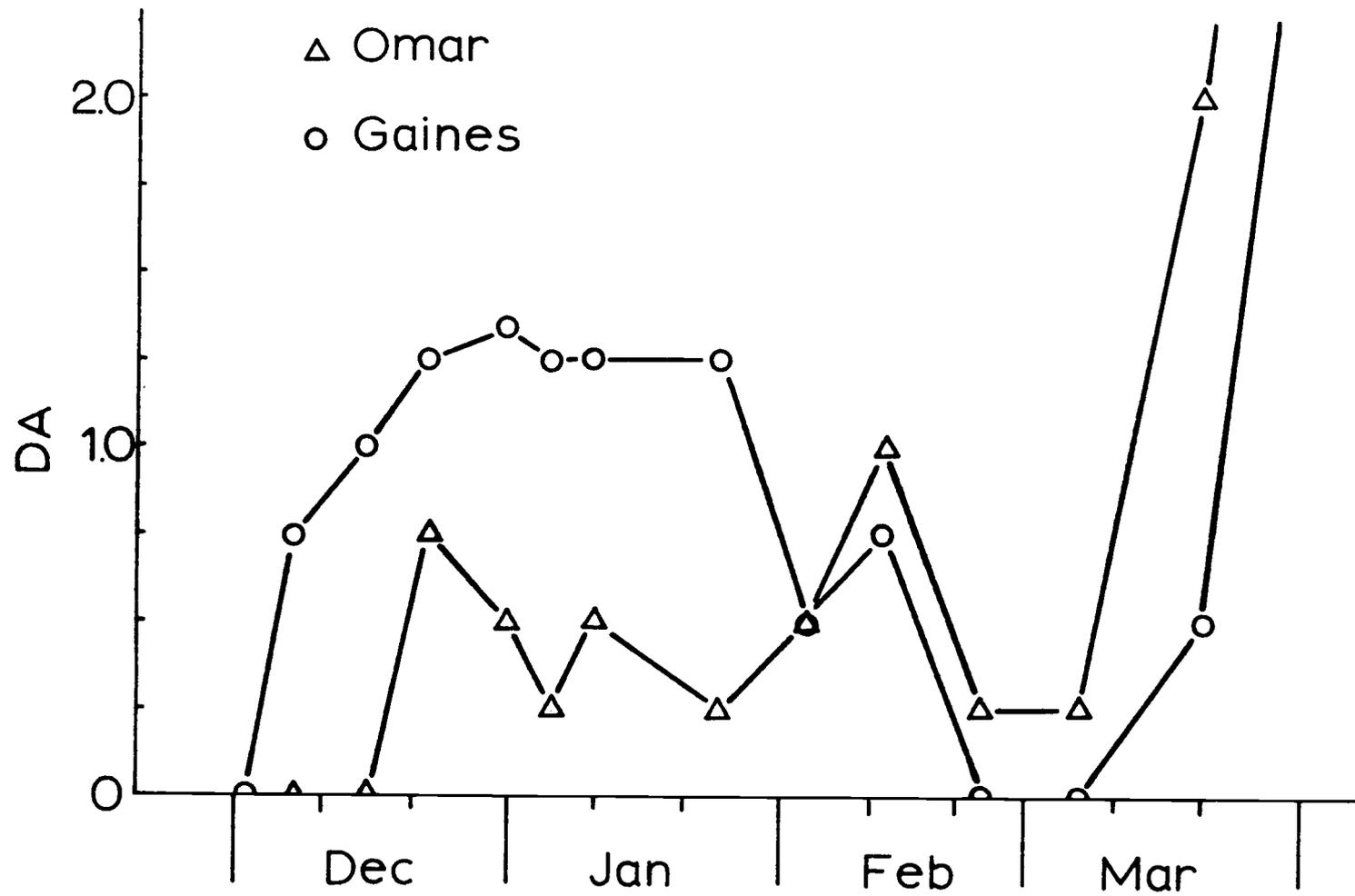


Figure 18. The level of overwintering stripe rust in two varieties of winter wheat at Hyslop Farm in 1965-66. The plants were inoculated on November 19, 1965.

Symptomatic tissue was nearly eradicated by late February, but with the advent of warmer weather in March the amount of rust rapidly increased.

Another plot of wheat was heavily and uniformly inoculated on September 27, 1966. Eleven days later stripe rust infection was evident (RT 0). Thirteen days after inoculation the RT was 3 but the severity had not changed (Figure 19). If mycelium did not grow within leaves this initial level of disease would have remained until a second latent period had passed. But 21 days after inoculation a large increase in the DA was detected. This could only have been from growth of mycelium within leaves. An outside spore source could be ruled out because the nearby plot of uninoculated wheat remained rust-free. After reaching the level observed at 21 days, the DA increased little for the remainder of the fall and winter. During this time there was some host growth and new infection. But senescence of lower leaves, after they were beaten to the soil by rain, removed infected tissue from the population.

Spore Trapping

Spore trapping was carried out during the four years of this study in northeastern Oregon (Tables 26 through 29). The most extensive spore trapping was done in 1964 which was a year of severe stripe rust. By April spores were already moving in the Columbia

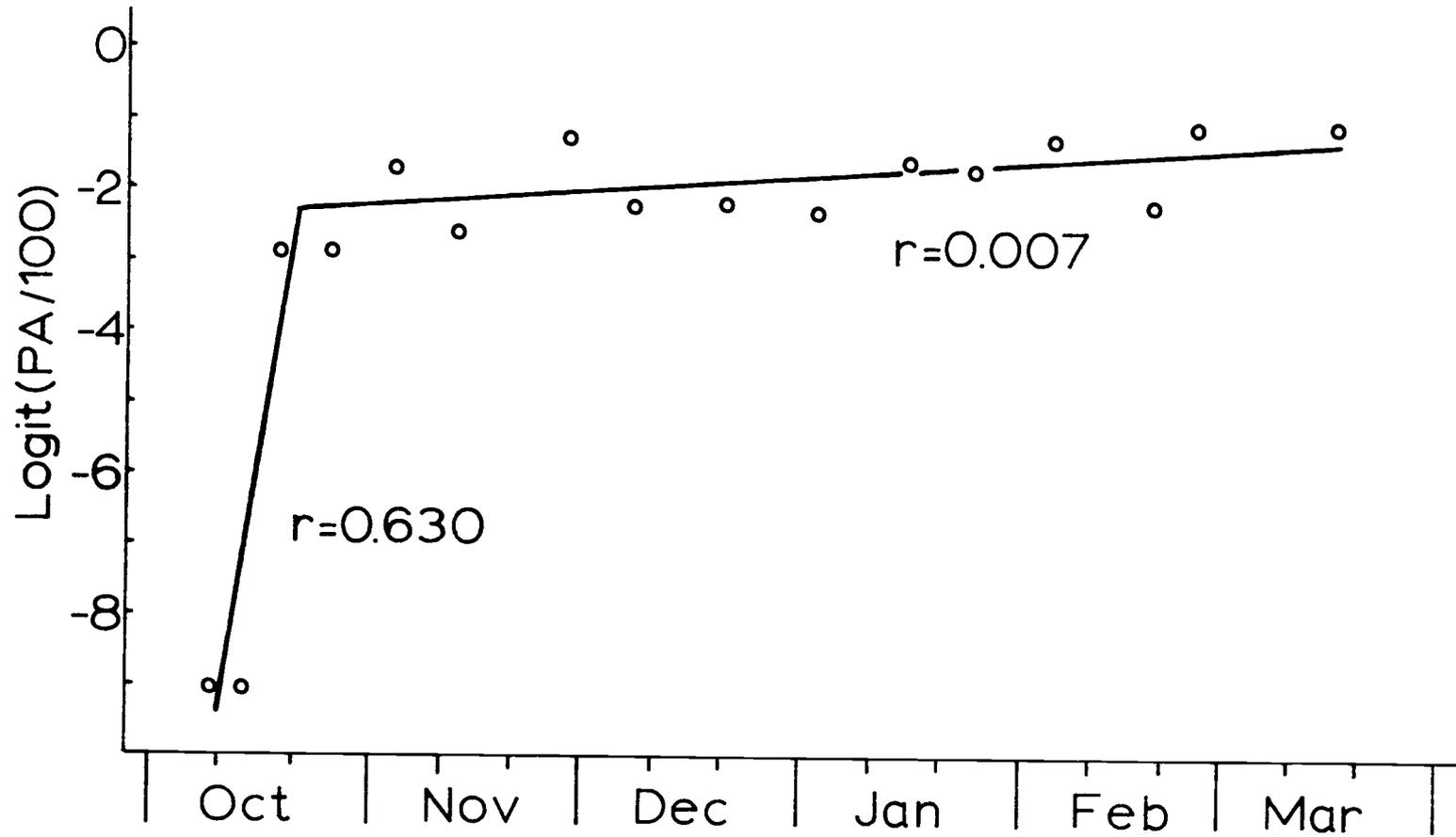


Figure 19. The level of overwintering stripe rust on Omar wheat at Hyslop Farm in 1966-67. The wheat was inoculated on September 27, 1966.

Table 26. Spore trapping summary for northeastern Oregon in 1964.

County	Month	Number of Exposures	Number of Spores Trapped	Average Number of Spores per Trap
Wasco	April	4	16	4
	May	6	2937	489
	June	4	201	50
	July	1	28	28
Sherman	April	11	54	5
	May	14	425	30
	June	14	1102	79
	July	8	427	53
	August	8	2	1
	September	8	6	1
	October	6	14	2
	November	6	0	0
Gilliam	April	6	77	13
	May	6	1224	204
	June	6	52	9
	July	3	150	50
	August	2	3	2
Morrow	April	6	16	3
	May	6	44	7

Table 26. (Continued)

County	Month	Number of Exposures	Number of Spores Trapped	Average Number of Spores per Trap
Morrow	June	4	116	29
	July	2	3	2
Umatilla	April	19	57	3
	May	19	40	2
	June	24	316	13
	July	13	26	2
	August	8	0	0
	September	8	0	0
	Union	April	2	0
Union	May	11	8	1
	June	6	122	20
	July	4	4	1
	August	4	0	0
	Wallowa	April	2	0
Wallowa	May	6	2	1
	June	9	142	16
	July	10	2102	210
	August	2	698	349
	September	2	7	4

Table 27. Spore trapping summary for northeastern Oregon in 1965.

County	Month	Number of Exposures	Number of Spores Trapped	Average Number of Spores per Trap
Wasco	April	0		
	May	3	7	3
	June	9	410	46
	July	3	108	36
Sherman	April	3	1	1
	May	9	25	3
	June	3	26	9
	July	1	8	8
Gilliam	March	2	0	0
	April	5	75	15
	May	9	1116	124
	June	6	5355	830
	July	3	53	18
Morrow	March	2	0	0
	April	0		
	May	1	0	0
	June	3	11	4
Umatilla	March	12	0	0
	April	14	12	1

Table 27. (Continued)

County	Month	Number of Exposures	Number of Spores Trapped	Average Number of Spores per Trap
Umatilla	May	16	14	1
	June	28	332	12
	July	1	13	13
Union	March	1	0	0
	April	3	0	0
	May	4	7	2
	June	1	117	117
	July	2	25	13
Wallowa	May	1	0	0
	June	5	25	5
	July	2	39	20

Table 28. Spore trapping summary for northeastern Oregon in 1966.

County	Month	Number of Exposures	Number of Spores Trapped	Average Number of Spores per Trap
Sherman	February	3	0	0
	March	15	849	57
	April	9	569	63
	May	9	3966	441
Gilliam	April	3	10	3
	May	2	56	28
Umatilla	February	3	3	1
	March	6	7	1
	April	6	24	4
	May	9	539	60
	June	6	425	71
	July	5	28	6
	August	3	12	4

Table 29. Spore trapping summary for northeastern Oregon in 1967.

County	Month	Number of Exposures	Number of Spores Trapped	Average Number of Spores per Trap
Sherman	February	9	215	24
	March	9	94	10
	April	4	7433	1858
	May	8	14238	1780
	June	10	448	45
Umatilla	February	6	26	4
	March	9	27	3
	April	3	135	45
	May	9	9427	1047
	June	6	870	145
	July	2	8	4
	August	0		
	September	0		
	October	1	0	0
	November	2	0	0
	December	2	0	0

Basin counties. In May there was a sharp increase in the aerial spore density in the western counties; spores appeared for the first time in Union and Wallowa Counties. In the Columbia Basin spore counts reached a maximum in May or June. In July spores were still being trapped. The lateness of the epidemic in Union and Wallowa Counties was reflected in the spore counts.

The data summary for 1965 (Table 27) reflects the general absence of stripe rust in that season. Only in two counties did spore counts get very high (Gilliam and Union Counties). These two counties were the ones where disease reached its greatest development in 1965.

Spore counts in the spring of 1966 reached levels similar to those of 1964 (Table 28). This reflects the development of disease during the spring. The March spore counts in Sherman County were the highest of the four years. The disease ceased to develop in May because of unfavorable weather and spore trapping was discontinued at most locations.

Spore counts in 1967 (Table 29) reflect the fact that stripe rust appeared early and in the spring was as serious as in the epidemic year of 1961. The highest spore counts of the four years were obtained in 1967. The spore counts decreased in June and by July were quite low. This corresponds to the termination of the epidemic in June because of the advent of an unusually hot and dry summer.

The spore trapping data for Sherman County for the past four

years are presented in graphical form for a more direct comparison of the events in each year (Figure 20). The curves depict the pattern of disease development in Sherman County for each year. The highest level of spore counts for each year indicates the level of disease severity in that year. The earliness of the epidemic in each year can also be seen from the curves. That the pattern of spore counts during each season follows the development of the disease on the crop in the area of the spore trap indicates that the spores trapped are locally produced. Further, the spore trapping indicates that a large influx of outside inoculum does not occur in the spring. The disease can be detected on wheat in an area before spores begin to appear on the traps.

The relation between spore counts and local disease increase is further indicated by examining the spore count data in the manner of Romig and Dirks (1966). They found that the logit transformation of percentage cumulative spore count gave the best fit to a straight line when such logits were plotted against time. This argues that the number of spores trapped is related to local disease increase, rather than to events at some other place. For some of the fields for which disease progress curves have been given, the spore trapping data have been treated as in Romig and Dirks (1966) in Table 30. With one exception (field H) the ranking of slopes of the cumulative spore count curves is the same as that of the apparent infection rates. The

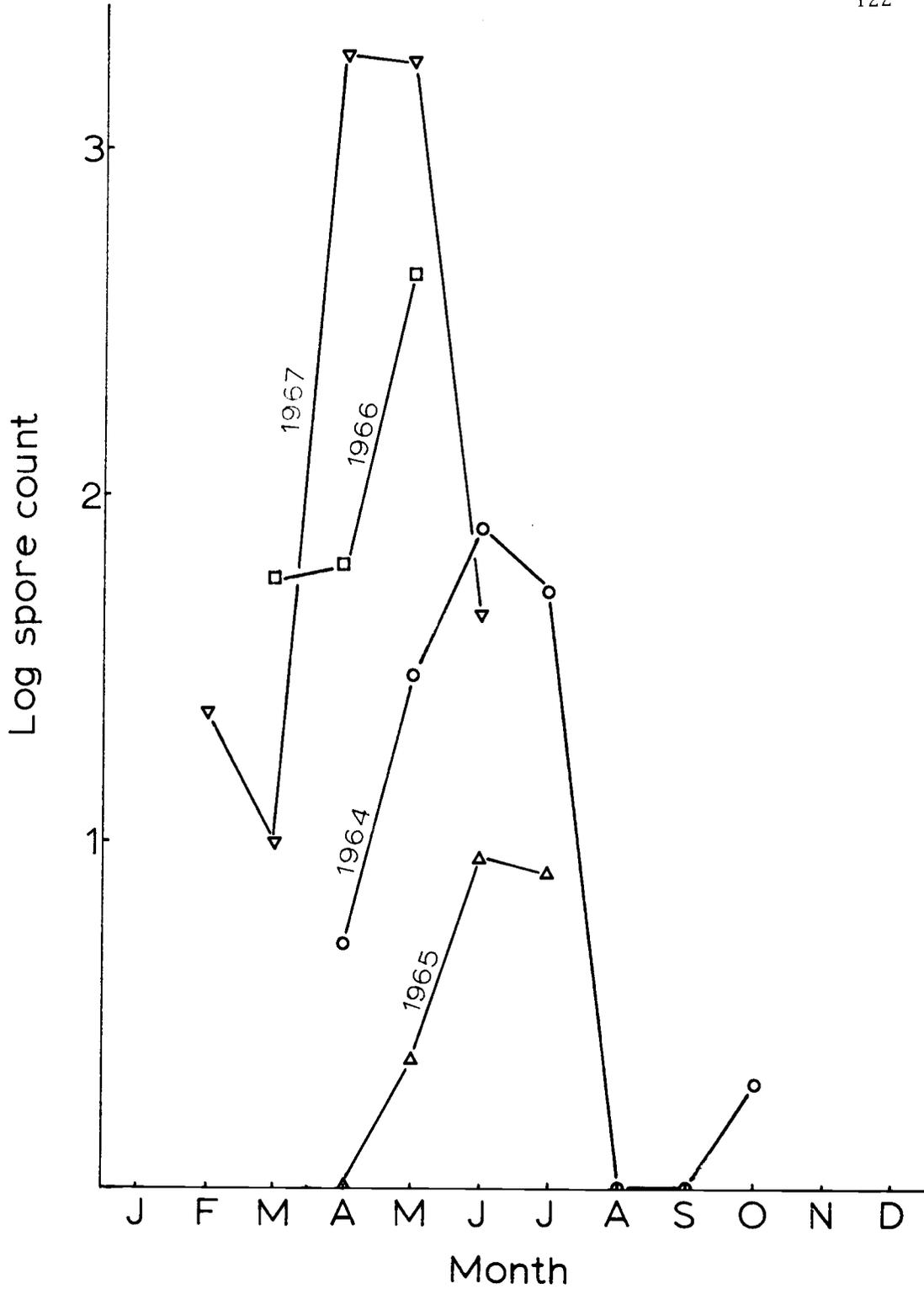


Figure 20. The average number of spores caught per trap for each month during four years in Sherman County.

absolute values of spore counts for the trap at field H were quite low compared to the other traps which may explain the discrepancy. This relationship between the slopes and apparent infection rates lends support to the hypothesis that the spores trapped come from the local area of production and not from massive outside spore showers. The cumulative spore trapping data for the Baart field are given in Figure 21. Comparison of Figure 21 with Figure 17 shows that in the case of the spring wheat, spores were trapped prior to the rapid buildup of the disease on the wheat, but the cumulative spore counts leveled off until disease did begin to increase on the wheat (day 130).

Table 30. A comparison of the slopes of the regression lines of logit (percent cumulative spore count/100) versus time and the apparent infection rates for disease progress curves of fields in which the spores were trapped.

Field ^a	Apparent infection rate	Slope of the regression line	Coefficient of correlation
E	0.163	0.093	0.978
C	0.175	0.095	0.992
G	0.187	0.099	0.938
H	0.074	0.109	0.936
D	0.193	0.129	0.965
Baart	0.217	0.130	0.928

^aThe fields identified are those whose disease progress curves are given in Figure 15. The disease progress curve for the Baart field is given in Figure 17.

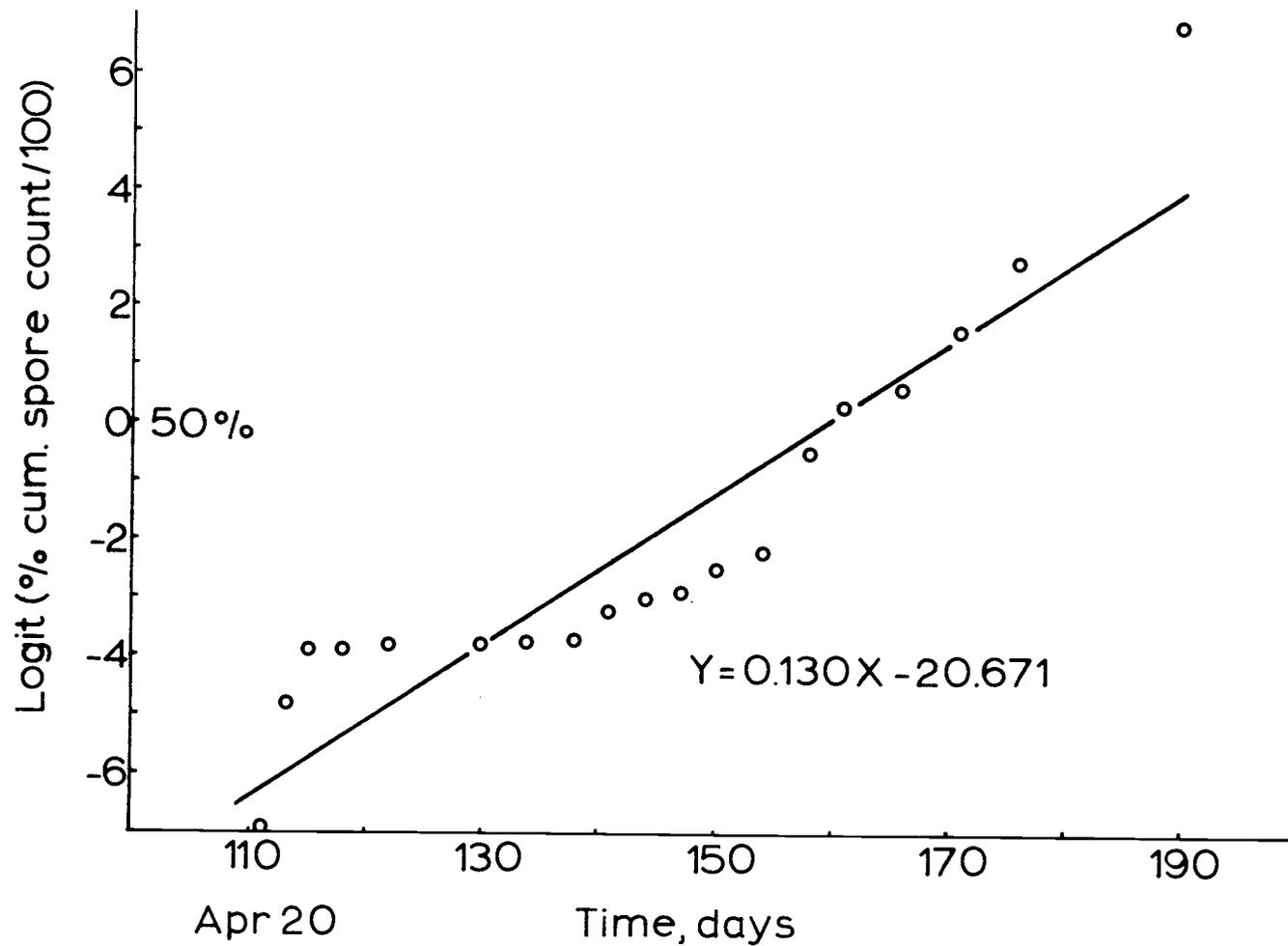


Figure 21. The logistic increase of cumulative spore counts for traps exposed at East Farm during the spring of 1967. The disease progress curve for the plot of Baart wheat near the trap is given in Figure 17.

After maturity of the wheat crop the number of spores trapped decreased sharply (Tables 26 through 29). Counts remained low until the next spring, even if active rust was present in the winter. The wheat inoculated in the fall of 1966 (Figure 19) provided some information on spore dispersal in the winter. Situated 165 m east of this plot was the west edge of another plot of wheat. Rust did not appear in the second plot until December 31, 1966, although active pustules were present in the inoculated plot continuously from October 13. On the basis of latent periods, infections taking place anytime from October 13 through the middle of November should have been evident before December 31. This indicates that few spores were moving from the inoculated plot. Spore traps exposed between the two plots verified that few spores moved through the air until April. The highest spore count for a 24 hour period was three spores. The development of stripe rust in the second plot was focal, indicating that a few outside spores initiated infections but that subsequent buildup of the disease was from spores produced within the plot.

The direction of spore movement can be surmised from the spore trapping data from northeastern Oregon. For all exposures in that area for each of the past four years, the percentage of spores impacting from the four cardinal directions was calculated (Table 31). In all years nearly half of the spores impacted in the west-facing sectors. The predominant winds come from the west and west winds

are likely to carry the greater spore load because air moves over a considerable wheat acreage in a west-east trajectory.

Table 31. The percentage of spores impacting from the four cardinal directions on the spore traps exposed in northeastern Oregon.

Year	Percentage of spores trapped from the indicated directions			
	North ^a	West	South	East
	%	%	%	%
1964	19	47	18	16
1965	13	52	32	5
1966	16	54	22	8
1967	16	48	21	15

^aThe odd sector was included in the north quadrant. Therefore spore totals for that quadrant were multiplied by two-thirds before calculating percentages.

Descriptive Epidemiology

The most serious outbreak of stripe rust in the Pacific Northwest in many years occurred in 1961. Although detailed observations of the increase of severity with time were not made it is useful to include an account of that epidemic. Monthly field reports of R. L. Powelson, then extension plant pathologist at Oregon State University, provided some information on the development of the 1961 epidemic. When stripe rust was first observed in the Willamette Valley in March, prevalence was low. By April the disease was severe on a

susceptible winter wheat. The disease was described as epidemic in May. The first mention of stripe rust in the Columbia Basin was in the May report and it was described as epidemic there at that time. Seventy to 80 percent of the wheat acreage in the Columbia Basin was planted with the susceptible variety Omar in 1961. On the basis of the May survey, wheat in the Columbia Basin was divided into three severity classes (Table 32). Warm weather in June probably increased losses from stripe rust by dessicating diseased plants.

Table 32. The severity of stripe rust in the Columbia Basin during 1961.

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

^aSevere = flag leaf rusted

^bModerate = no rust pustules on flag leaf

^cLight = some rusted leaves present

Again in 1964 stripe rust caused losses to growers in the Willamette Valley and the Columbia Basin. In the Columbia Basin stripe rust was prevalent early in the spring. But high temperatures and low rainfall suppressed disease development, particularly in the eastern part of the Columbia Basin. Disease did continue to increase

in Sherman County. A brief period of rainfall in late May and early June resulted in increased disease severities, but a subsequent dry period retarded further development.

Throughout the spring conditions were favorable for stripe rust in the Willamette Valley.

During limited surveys in the summer of 1964 stripe rust could not be found on late wheat tillers or grasses which were still green in the Columbia Basin.

Weather in the winter of 1964-65 was particularly severe in northeastern Oregon. By mid-March much of the wheat had not yet tillered. Losses from winter-kill were heavy so that much reseeding was done. No stripe rust was seen in March. Very little stripe rust developed during the spring of 1965. Most observations of rust were not made until late in the season. Weather was not unfavorable for disease development during the spring however, on the basis of comparisons with years in which the disease had developed. The main limiting factor was probably the failure of inoculum to overwinter. The loss of fall-infected foliage during the winter eradicated the fungus from many fields. As brought out in the Review of Literature such fall infections are the chief means of overwintering of P. striiformis. Some early rust development occurred in Union County where wheat was protected from winter-kill by snow cover, but inoculum apparently did not move from that area into the Columbia Basin. Winter-kill did not occur in the Willamette Valley and the

disease developed rapidly there (Figure 16). Stripe rust was found on maturing wheat and late season tillers throughout northeastern Oregon in mid-July of 1965. A nearly mature field of Omar south of The Dalles (Wasco County) had a DA of 4.

The first reports of stripe rust on wheat of the 1966 crop year were from Wasco and Umatilla Counties in December of 1965. The winter of 1965-66 was mild. By March stripe rust was prevalent throughout the Columbia Basin and appeared to be as severe as in 1961. Stripe rust could be found in most fields examined. Foci were still evident. In one field, where rust was still confined to the lowest leaves, it was those leaves which were in contact with the moist soil surface that bore pustules. The warm soil surface and higher humidity probably created a more favorable environment for infection and incubation than that to which most leaves were exposed. After March stripe rust ceased to spread. As the wheat crop grew, severity actually decreased in most fields. Only traces of rust were evident in June. However, rust was noted on late tillers, especially in Union and Umatilla Counties, in mid-July. Late tillers and grasses throughout northeastern Oregon were inspected for rust in late September. The only rust seen was on the wheat at the Tollgate Mountain Plot. When all of the Mountain Plots were again visited in October, no rust was seen on the grasses in the area. The wheat had matured.

During a survey of wheat in the western Columbia Basin on December 30, 1966 stripe rust was found (DA 2, RT 3) in a wheat cover crop in some orchards south of The Dalles (Wasco County).

The cover crop was at a more advanced stage of growth than the wheat sown in the fall by the wheat growers, indicating that it had been planted earlier than the regular wheat crop. Rust on upper leaves indicated that the fungus was active in the fall.

Cover cropping in The Dalles orchard area is an old practice (Thompson, personal communication). Rye was used initially, but wheat (variety "Golden") has been used for the past 10 years or more. Golden is an old commercial variety of northeastern Oregon. In 1960 and 1961 Golden was resistant to stripe rust. Since 1964 Golden has become progressively more susceptible to stripe rust until now it is as susceptible as any commercial variety in Oregon. Very little acreage is still planted to this variety by wheat producers. Prior to 1965 irrigation was available for only a small portion of the total orchard acreage. Therefore, the cover for most orchards was sown at about the same time as the ordinary wheat crop was sown--anytime from September through November. Since 1965 most of the 5000 or more acres of orchards in the area have had irrigation water available. Since that time wheat has been sown in August or September. Thus only in the last few years have the orchards been an area of an extensive, early-sown, stripe rust susceptible wheat. It may be important that some orchards have been irrigated since before 1965, because the cover crops could have been planted in August in them as is now done throughout the area.

On the same survey of December 30, 1966, in which stripe rust was found in the orchards, stripe rust was found (DA 2, RT 3) in an

advanced wheat border around a stubble field. The wheat had evidently been seeded in August or September as an erosion control measure. In the wheat fields to the south and east of this source, small rust foci were found. The wheat fields south of the orchards could not be inspected because of snow cover. By the end of January rust could be found in most wheat fields of Wasco and Sherman Counties. These observations and those from subsequent surveys are summarized in Table 33.

Table 33. The development of the 1967 stripe rust epidemic in the Columbia Basin.

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

^aPrevalence is given as the fraction of fields inspected in which stripe rust could be found.

The last evidence of active stripe rust in the summer of 1967 was found in early August. A few tillers with stripe rust were found in Wasco County. A late, irrigated field of spring wheat in Sherman County had some stripe rust, and the maturing crop in Wallowa County

still had some active stripe rust. On this trip some rust was also seen on native grasses in the area of the rust on wheat. The summer of 1967 was exceptionally dry and hot.

The first observation of rust in the winter of 1967 was again in the cover crops in the orchards of Wasco County. This was on December 7, 1967. Inspections of the orchards in September and October had failed to reveal stripe rust. By late February stripe rust could still not be found in most of northeastern Oregon, in contrast to the previous year. The disease was spreading within the orchards, but still distinctly focal. Single foci were seen in two fields, one in Wasco County a few miles south of the orchards, and the other in western Sherman County. Each focus involved only about three plants. Surveys in March and April revealed a situation similar to that in February. Stripe rust continued to spread within the orchards. Foci were beginning to lose their identity by March 21. The cover crop was plowed under in April but tillers which had not been turned under still bore active pustules of stripe rust. The focus in the wheat field in Wasco County had increased in size by April but no new foci were seen in that field or in any other. Three factors probably account for the poor disease development in the 1968 season. The prolonged spell of heat and drought the previous summer eradicated overwintering inoculum. The winter in northeastern Oregon was also unusually dry, so that the development of the wheat

crop was retarded. The dry conditions would not have been favorable for infection. Unusually cold weather in March, both in northeastern Oregon and in the Willamette Valley lengthened the latent periods so that existing infections were slow to produce inoculum.

DISCUSSION

One of the chief obstacles to an understanding of the epidemiology of stripe rust of wheat in the Pacific Northwest is the lack of knowledge concerning the way in which P. striiformis survives the summer. Three general modes of overwintering have been suggested in the literature: (1) survival on wild grass hosts, especially at high elevations, (2) survival on residual green wheat, or (3) survival of the uredospores. All three possibilities were considered in the present study.

Observations of grasses near wheat and in the mountains were made at all times of the year over a period of four years. The incidence of stripe rust on grasses in their natural habitats in northeastern Oregon was low especially in the summer (Table 5). Of the grasses upon which stripe rust was found naturally in northeastern Oregon, two might have a role in the epidemiology of stripe rust on wheat. These are Bromus marginatus and Elymus cinereus. Both occur throughout the area, near wheat fields and at higher elevations. But even on these species the incidence of rust was low, particularly considering the large number of specimens examined. When stripe rust was found on these and other grasses (Table 5), it was always after the disease was well established on the wheat crop (May and June). During July and August the incidence of stripe rust on grasses

near wheat and at higher elevations decreased until by autumn it could not be found in eastern Oregon. This contrasts with the situation in California where disease severity increased on grasses during the summer and autumn at high elevations (Tollenaar and Houston, 1967). The rust that was isolated from B. marginatus and E. cinereus did infect wheat, however, and appears to be the same as the rust found on wheat.

Most plants of E. cinereus examined in the field did not have stripe rust. Plants raised from seed of such plants, when inoculated with an eastern Oregon wheat isolate of P. striiformis were susceptible. Also, some of the species of grass upon which stripe rust was never found in northeastern Oregon were susceptible to stripe rust in the greenhouse or nursery. Thus several of the common grasses appear to have a high level of resistance in the field which is not always expressed in the greenhouse or irrigated nursery indicating that the resistance is modified by environment. It would be expected that under suitable conditions in the field, stripe rust would occur on many of the grasses which are usually resistant. This view is supported by the report from a county agent that in the spring of 1961, when conditions were unusually favorable for the disease on wheat, a pasture of Agropyron cristatum surrounded by wheat fields in Umatilla County did have stripe rust. Inspections of this same pasture during the past two years have failed to reveal stripe rust,

even though wheat in the area did have the disease.

When plants of Elymus glaucus, raised from seed in the greenhouse, were inoculated with various isolates of P. striiformis, they were often susceptible (Table 6). But in the field stripe rust was seen on this species only in an irrigated nursery and along a river bank in Benton County (Table 5). Unlike the situation reported by Hungerford (1923) new pustules did not form in the fall around old, dry pustules. Also, the rust on those plants was evidently not a wheat race. The varieties of wheat now grown are different from those of Hungerford's time. It is reasonable to suspect that the pathogenic capabilities of the fungus are different too. But since the P. striiformis now present in Oregon does not infect E. glaucus in the field, the fungus was evidently not depended on this grass for its summer survival.

Since the resistance of many grasses is apparently horizontal (Appendix I-Glossary), records of stripe rust on these grasses which are growing in nurseries have little relevance to the epidemiology of the disease on wheat, except to indicate that under some conditions the grasses will be infected. Because the grasses are usually resistant in the field, but are susceptible under some environmental conditions, there has apparently been a lack of selection pressure on P. striiformis for increased pathogenicity on these grasses. Either the grasses do not have a significant role in the oversummering of

P. striiformis or the levels of rust that are seen on them are sufficient to carry the fungus over the summer.

Residual green wheat is not common in either northeastern Oregon or the Willamette Valley during the summer. Because of the dryness of the summers volunteer wheat does not emerge until about the time that the fall-sown crop emerges. Post harvest late tillers can be found, sometimes with stripe rust, but the latest observation of rust on such hosts was early in August. Examination of these tillers late in the summer failed to reveal stripe rust. Thus there is a period from August until rust is found on the fall-sown crop in which no active rust can be found. Conditions for infection in late summer may not often be favorable because of the dryness. Tu and Hendrix (1967) found that of eight inoculations in the field at Pullman, Washington from mid-July through August only two gave positive results. The results of the growth chamber experiment on high temperatures and incubation (Table 20) indicate that infections that do occur in late summer may not result in the production of inoculum if the weather is too hot. Thus one limiting factor for the over-summering of stripe rust as mycelium within residual green wheat in Oregon may be the high daytime temperatures. Even if infection of these hosts occurred the fungus might fail to sporulate.

Another possibility to be considered in the oversummering of P. striiformis is the late wheat season in Wallowa County. Fields

may still be ripening in August there, and in early August stripe rust can be found, although severity is low. Oversummering on wheat at high elevations on late-developing wheat was described in India (Mehta, 1940) and in China (Ling, 1945). Zadoks (1961) suggested such a mechanism for the Alps. But the pattern of spore movement (Table 31) and the fact that the disease is usually first seen in the fall in the western Columbia Basin argues against the idea that the fungus oversummers in Wallowa County. Rather the spore trapping data and the pattern of disease development indicate that a spore source in the western Columbia Basin would be more important than one in the eastern part of the state. This lends greater significance to the stripe rust seen in the orchard cover crops and the other early-sown wheat in Wasco and Sherman Counties. Another fact suggests that the orchard cover crop now plays a role in the oversummering of P. striiformis. In 1961 the variety Golden was resistant to stripe rust on the basis of RT (2) and PA. Since that time its susceptibility has increased until now it is one of the most susceptible varieties grown. The change in susceptibility was also evident at the Mountain Plots. In 1965 Golden was resistant at three of the eastern Oregon Plots, but in 1966 and 1967 its susceptibility increased (Table 7). This suggests selection pressure for increased pathogenicity on Golden which could be brought about in the early fall when that variety makes up a major portion of the available host material.

Uredospores have a limited ability to withstand high temperatures. On stubble in the field during the summer infective spores lasted for 51 days (Table 16). Maximum survival of spores on soil was only one month (Table 17), perhaps because the soil surface can reach temperatures considerably above the air temperature. But the ability of spores to survive a month to six weeks in the absence of a living host could be sufficient to bridge the period between the disappearance of stripe rust on residual hosts and the emergence of the new wheat crop. Active rust was found in late July and early August in the Columbia Basin. Some early plantings of wheat emerge during September. This is particularly so of the orchard cover crops in Wasco County. In the 1967 and 1968 crop years rust was found in these orchards as early as it was found anywhere in the Columbia Basin. In 1968 this was the only area where evidence of infections could be found until March. It is possible that infections occurred in early September, but escaped detection until December when development of rust within the orchards was sufficient to make detection more likely. When rust was found in December of 1966 there was evidence that there had been as many as three infection cycles of the fungus. In December of 1967 the development of the fungus was not so extensive as in the previous year. Scattered, single leaves bore pustules. Not until February were obvious foci seen, which indicated that conditions in the winter of 1968 were not as favorable

for spread of the pathogen as they were in the winter of 1967.

Whatever the source of inoculum that infects wheat fields, the initial level of inoculum entering fields is not heavy. Disease is usually detected before spores appear on the spore traps and the development of the disease in individual fields is focal. Also, the pattern of spore trapping indicates that the number of spores caught is a function of the level of disease in the immediate area of the trap. The logit transformation of cumulative spore counts was linear with time, and the slopes of such curves reflected the apparent infection rates (r) of the fields in which the traps were placed (Table 30). The significance of inoculum production on early-sown wheat and long distance spore dispersal is that initial infections at some distance from these sources are provided in fields from which disease rapidly develops locally, provided climate is favorable. Once several foci are established the level of inoculum produced locally exceeds that coming in from outside sources so that these more distant sources assume diminishing importance.

One of the problems concerning studies on the means of survival of the fungus during the summer and winter pertains to the level of inoculum required for a successful epidemic in the spring, given favorable climate. The quantitative examination of stripe rust epidemics in the Columbia Basin can offer some information on how much infected tissue must be present to initiate an epidemic. The

development of stripe rust in several fields in Sherman County in 1964 was followed during the spring (Figure 15). The mean apparent infection rate (r) for these fields was 0.165 per unit per day. For purposes of calculation the date at which rust reached the level of DA 8 (logit $x = 0$) can be taken as June 18 (day 170). With this figure and the apparent infection rate the level of rust at some earlier time can be calculated using equation (2). On February 15 the level of rust would have been 7.9×10^{-8} per unit (7.9×10^{-6} percent). To convert this to a specific area of foliage the data of Zadoks (1961) can be used. The amount of foliage in February would be about $10^7 \text{ cm}^2/\text{ha}$. Thus $0.79 \text{ cm}^2/\text{ha}$ or $0.32 \text{ cm}^2/\text{acre}$ would be the area of diseased tissue. Because of the systemic growth habit of the stripe rust mycelium one infected leaf in five acres could bear pustules over enough of its surface to make up this level of disease. Actually infected leaves would probably be more frequent because the calculation assumes an even distribution of inoculum. In a year of little winter-kill the level of disease, in terms of the number of leaves infected, could be nearly the same as the level of fall infection. In a mild winter there could be some increase in the number of infected leaves from the time of fall infection until February 15. The level of rust in February points out the difficulty of adequately determining the level of fall infection. If the expected frequency of infected leaves is only perhaps one leaf per acre, then several hundred acres of

wheat would have to be carefully scrutinized to determine the actual level. This is an impossible task for one or two workers.

From Figure 10 it can be seen that infections evident on February 15 could take place any time prior to the first week in January. In Sherman and Wasco Counties this level of inoculum could probably be provided by the orchard cover crop and other early-sown wheat. Thus the level of rust in mid-February probably does not reflect the level of oversummering inoculum, but the level of inoculum produced during the fall. In the orchards themselves there was less than one focus per five acres indicating an even lower inoculum density provided the initial inoculum in them. Therefore only a few infected grasses or a few infected late tillers, not too far removed from the orchards might carry enough inoculum through the summer to successfully initiate an epidemic in the spring, with an intermediate stage on early-sown wheat. Even if the fungus mycelium died within these leaves prior to emergence of early-sown wheat the spores could survive for up to six weeks. But the longer the "wheat-free" period the fewer the number of infections that would occur. It is possible that remote sites in the Cascades would carry over sufficient inoculum, but the further removed the oversummering site is from the wheat, the larger it must be. Early-sown wheat, such as the orchard cover crop, even if not a necessary link in the disease cycle, permits the buildup of inoculum during the early winter, which can

increase the number of early infections in the wheat fields.

Van der Plank (1963), in discussing sanitation as a disease control measure, points out that the value of sanitation diminishes as the product rt increases, where t refers to the entire period of disease development. The analysis of sanitation can be applied to the analysis of natural survival of inoculum. Both are concerned with the inoculum available to initiate an epidemic. Stripe rust has a moderately high apparent infection rate and the period of disease development is long. Because of this, the destruction of inoculum, especially prior to infection in the fall will have little effect on the final outcome of the epidemic unless the destruction is very thorough. Thus even a summer such as that of 1967, during which much inoculum was certainly destroyed, would not prevent the development of an epidemic the following spring, if climatic conditions during the winter and spring were favorable for disease development. As already discussed, the winter and spring of 1968 were not favorable for infection or incubation and this more likely accounts for the poor disease development in that year, rather than the hot summer. The later in the season that the destruction of inoculum occurs, the less thorough it must be to achieve a given setback to the epidemic. A severe winter, in which much fall-produced foliage is destroyed is more likely to prevent an epidemic than is a hot summer. The events during the 1965 crop year would bear this out. The summer of 1964

was not unfavorable for the overwintering of stripe rust. But the winter of 1965 was severe, and there was much winter-kill of fall infected foliage. The development of stripe rust in northeastern Oregon was retarded that year although climatic conditions in the spring were not unfavorable.

Regardless of how favorable the summer and winter are for the survival of the fungus, conditions in the spring must be such that r is high in order for an epidemic to develop. Climate and host susceptibility influence the magnitude of r . Either of these may influence r through the latent period. As the temperature decreases the latent period increases (Figure 9). Although there was a general relation between the length of the latent period and the time of year, variation existed especially in the winter (Figure 10). Unusually cold weather in the winter, although it may not destroy infected foliage, can retard disease development by lengthening the latent period. The susceptibility of the host affects the latent period in some cases (Table 19), but the effect is not great. The values of the basic infection rate (R) were calculated for field B of Figure 15 in Table 24, taking into account the changing latent period. The effect of an extended latent period can be determined, using those values of R , by recalculating r using latent periods that are longer than those given in Table 24 (Table 34).

The evidence from the inoculation of seedlings in the greenhouse

suggested that the latent period might be extended by two days (Table 19). But from the value of x at day 190 (Table 34) it can be seen that the advantage gained from a two day extension of the latent period would not be great enough to warrant use of such an extended latent period as a sole source of resistance. Even a six day extension does not have a large effect.

Table 34. The influence of an extension of the latent period, due to resistance of the host, on the apparent infection rate (r).

	Latent period (p), days		
	p	p + 2	p + 6
r	0.146	0.138	0.123
x_{190}^a	0.985	0.958	0.723

^aThe value of x at day 190 was calculated assuming an initial level of severity on February 15 of 5.07×10^{-8} per unit.

The frequency of conditions for infection also influences the magnitude of r . On the basis of the experiments on natural infection conditions, a high level of infection can be expected if mean daily temperatures fall between 5 and 22 C, if dew persists for seven hours or more and if spore counts on the rod traps reach 500 or more spores. During the fall and spring such temperature conditions are common. Periods of sufficient free moisture and high enough spore

densities apparently limit infections in these seasons more than does temperature. The minimum period of dew for infection was three hours with temperatures of 12 and 16 C. In the experiments pertaining to natural infection in the field, no dew periods of three hours were recorded so that it is not possible to say whether that is the minimum dew period under field conditions. However, on several nights dew persisted for four or five hours. On some of these nights a few infections occurred; on others none took place. Thus the minimum in the field under the temperature conditions encountered there, may be three hours, but the prevalence would be low, as in the dew chamber experiments. The requirement for spore counts of 500 spores in a 24 hour exposure would not apply strictly to infection of wheat growing in the field, because spores could accumulate on foliage for several days. But under conditions when seven hours of dew formed nightly, spore counts would have to exceed 500 in a 24 hour period to expect heavy infection each night.

Since observations were made over a four year period at Hyslop Farm (Figure 16), the apparent infection rates for the four years can be examined with respect to climate. A distinctive feature of the disease progress curve for 1966 is the period of slow disease development early in the season, from March 5 (day 64) to April 14 (day 104). If the precipitation data for the period January through March are examined, it is seen that in 1966 that period had more

precipitation, in terms of total and frequency, than 1965 and 1967 (Table 35). The reason for considering precipitation data from January through March when analyzing disease development in the period March through mid-April is that disease seen in this period was the result of infection and spore dispersal from January on, because of the latent period. The effect of high rainfall is probably to hinder the movement of spores through the air. Also lower leaves bearing pustules are beaten to the soil by rain and rapidly rot there. The reports of disease development in 1961, discussed earlier, indicate that the disease was slow to become evident in the spring. This would be expected because of the heavy winter rainfall that year. Heavy rainfall in the winter is not deleterious to the epidemic, however. Although early spread is restricted, the additional moisture in the soil makes conditions more favorable in the spring, probably by providing moisture for dew formation by the distillation process (Monteith, 1957).

Table 35. Precipitation during the period of January through March at Hyslop Farm.

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

The disease progress curves for Omar wheat at Hyslop Farm (Figure 16) bent sharply at about DA 8 (logit $x = 0$). The disease progress curve for the field that reached DA 8 before the end of the epidemic in California also deflected, at DA 9 (Tollenaar and Houston, 1967). Reasons for the deflection were already suggested. The abrupt decrease in r was ascribed to the level of x which in turn could affect the microclimate, average lesion age, and probably other factors. But it might be expected that weather conditions in the spring could determine how much the curve deflected. Increasing temperatures could begin to hinder development of the disease. Sharp (1965) demonstrated that at a constant temperature of 24 C the mycelium of P. striiformis could not survive in infected leaf tissue. In the present work it was shown that eight or more days at 31 C for 10 hours each day killed mycelium within infected leaves (Table 20). Therefore, one might expect that as temperatures begin to exceed 24 C, development of the fungus would be hindered. When the number of days that temperatures exceeded 24.2 C (75 F) are compared with the magnitude of r after deflection, it is seen that the number of such days in May is inversely related to the value of r (Table 36).

From the results of this and other studies control of stripe rust can be considered. Evidently the level of inoculum that must survive the summer is low so that any attempts to reduce it further would

probably be unsuccessful. This is because the level of oversummering inoculum is such a low percentage of the level during the spring (10^{-6} or 10^{-7} percent) that a control measure that reduced the level by ten-fold would probably not alter the pattern of disease development by the following spring. Furthermore, the relative importance of post harvest tillers and grasses in oversummering is not clear. Nothing can be done about stripe rust on grasses, especially in the mountains. Spores can survive on stubble but this method of survival is only effective in oversummering if the wheat ripens late, as in the case of post harvest tillers, or if new wheat emerges early, because spores cannot survive the interval from the time the normal crop matures until the time the fall-sown wheat emerges. Therefore no advantage would be obtained by plowing stubble under, especially when compared to the disadvantages with respect to erosion control. Another step in the disease cycle, though not always an obligate one, is the fall- and early winter multiplication of inoculum on early-sown wheat. The use of rye or resistant wheat and barley varieties in the orchards and other areas where wheat is now sown early as an erosion control measure would remove this intermediate step of inoculum increase and would pose no serious economic problems because grain yields would not be a consideration. Because the practice would be directed at the fungus closer in time to the epidemic stage of the disease the control would not have to be so thorough as

some sanitation measure practiced in the summer. The removal of these early-sown hosts would prevent a fall increase of inoculum which in turn would reduce the level of infection in wheat fields in the spring.

Table 36. The number of days that temperatures exceeded 24.2 C at Hyslop Farm and the late season apparent infection rates for Omar wheat.

Month	Time interval	1964	1965	1966	1967
April	92-121	0	1	1	0
May	122-152	2	4	9	7
June	153-183	6	14	14	19
r^a		0.122	0.036	0.015	0.030

^aLate season r -values from Figure 16.

Another useful control measure can be to prevent fall infection of the fall-sown wheat. This, in conjunction with eradication of early-sown hosts should significantly reduce the level of overwintering fungus. Late sowing of wheat in the fall would reduce the likelihood of infection or at least delay the first sporulation period. Some new systemic fungicides show promise for stripe rust control (Hardison and Anderson, 1965; Powelson and Shaner, 1966 and unpublished), but require more testing before they can be used commercially. The application of a fungicide at the time of 2,4-D application in the

spring might offer sufficient protection to new foliage to prevent an early buildup of inoculum. For any fungicide treatment to be effective it would need to be applied to all wheat in an area since its function would be to prevent inoculum production rather than to protect foliage from outside inoculum.

At the present time the most effective control is resistance in the host. None of the measures already discussed will be very effective if the wheat varieties grown are susceptible to the disease. But they will enhance the effect of resistance. Some resistant varieties are available for use in Oregon, although the most popular variety, Gaines, is not highly resistant. It may show a reduced RT at about the time of heading, but in younger stages is quite susceptible (RT 3 or 4). Its popularity lies in the fact that it far out-yields other varieties available in the state, so that even with a 10 to 15 bushel per acre reduction in yield from stripe rust, the yield will be greater than could be obtained with other varieties. Another recent variety, Moro, is apparently immune to stripe rust but its resistance is presumably vertical (Appendix I-Glossary). Horizontal resistance would be desirable for wheat varieties in Oregon. It has already been suggested that the extension of the latent period by itself would not be an effective type of horizontal resistance. This is because r is usually too low to be greatly influenced by a change in p , unless the change were great (10 days or more), and so far there is

no evidence for this much difference in latent periods between varieties. But combined with other factors of horizontal resistance, an extended latent period would be desirable. Other factors of r such as the number of spores produced at a given level of severity and the number of spores per unit area of leaf required to achieve a given level of infection should also be altered to the detriment of the fungus.

In summary, the buildup of stripe rust in a field or county appears to be mostly a function of local inoculum. Heavy spore loads do not descend on fields from distance sources as occurs in the Midwest with stem rust. Therefore, measures designed to delay the appearance of stripe rust in an area should have significant effect in retarding the epidemic.

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APPENDIX

APPENDIX I

Glossary

A number of terms are used throughout this thesis which do not have any one meaning accepted by all workers. Therefore, these terms are defined here in the way in which they are used in this work.

Focus: A focus is an isolated concentration of disease within a field.

It may involve from one to many plants.

Horizontal resistance: Resistance which is expressed equally against all races of a pathogen is called horizontal resistance (van der Plank, 1963). The effect of horizontal resistance is to reduce the apparent infection rate (r).

Incubation period: The time from the penetration of the host by the pathogen until symptoms become visually evident.

Infectivity: The ability of the spore to infect, as measured by the response of an inoculated host plant.

Isolate: This term is used to identify a collection of stripe rust from a single plant or group of identical plants. There is no intended correspondance between race and isolate.

Latent period: The time interval from penetration of the host by the pathogen until the infected tissue becomes infectious. In the case of stripe rust this is the time from penetration until the

opening of pustules.

Prevalence: The percentage of leaves, plants or fields under consideration that develop symptoms of stripe rust.

Vertical resistance: Resistance which is expressed against some races of a pathogen, but not against others is called vertical resistance (van der Plank, 1963).