The Oversummering and Dispersal of Inoculum of Puccinia striiformis in Oregon

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ABSTRACT

Stripe rust (Puccinia striiformis) was found on grasses in wheat-growing regions and in adjacent mountains of Oregon during late spring only after the disease was well established on the wheat crop. Disease incidence on these grasses diminished during summer, and approached zero in wheat fields near the traps. Throughout northeastern Oregon, urediospores moved predominantly from west to east.

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

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

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

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

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

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

Fig. 1. Wheat-growing areas of Oregon and location of the Mountain plots: 1 = Mary's Peak, 975 m; 2 = Tupper, 1,311 m; 3 = Dale, 1,615 m; 4 = Meachum, 1,219 m; and 5 = Tollgate, 1,524 m.
near ground level, completely enclosed each plot to prevent damage by animals.

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

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

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

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

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

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

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

b Where rust was observed more than once on the species at the given location, the number of observations is given in parentheses.
TABLE 2. Development of stripe rust on the wheat cultivars grown at the mountain plots

<table>
<thead>
<tr>
<th>Wheat cultivars</th>
<th>Tollgate 1965</th>
<th>Meachum 1965</th>
<th>Dale 1965</th>
<th>Tupper 1965</th>
<th>Mary's Peak 1966</th>
</tr>
</thead>
<tbody>
<tr>
<td>Suwon/2*Omar</td>
<td>0a</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Gaines</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Moro</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Druchamp</td>
<td>0</td>
<td>NSb</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Heines VII</td>
<td>+</td>
<td>+</td>
<td>0</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Capelle Desprez</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nord Desprez</td>
<td>+</td>
<td>NS</td>
<td>0</td>
<td>+</td>
<td>0</td>
</tr>
<tr>
<td>Omar</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Hymar/Orfed</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Golden</td>
<td>0</td>
<td>+</td>
<td>0</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>P.I. 173438/Elgin</td>
<td>0</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

Month first observed

<table>
<thead>
<tr>
<th>Sep.</th>
<th>Sep</th>
<th>June</th>
<th>Sep</th>
<th>June</th>
<th>July</th>
<th>July</th>
<th>June</th>
<th>Aug</th>
<th>June</th>
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</thead>
<tbody>
<tr>
<td>66</td>
<td>66</td>
<td>68</td>
<td>66</td>
<td>68</td>
<td>67</td>
<td>68</td>
<td>66</td>
<td>67</td>
<td>68</td>
</tr>
</tbody>
</table>

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

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

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

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

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

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

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

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

*Spore trapping studies.*—The average number of spores caught per trap per 24-hr exposure for each...
TABLE 3. Spore trapping summary for northeastern Oregon

<table>
<thead>
<tr>
<th>Month</th>
<th>1964</th>
<th>1965</th>
<th>1966</th>
<th>1967</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Feb.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Mar.</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Apr.</td>
<td>92</td>
<td>1</td>
<td>1</td>
<td>31(1)</td>
</tr>
<tr>
<td>May</td>
<td>34</td>
<td>20</td>
<td>16</td>
<td>125(17)</td>
</tr>
<tr>
<td>June</td>
<td>23</td>
<td>1</td>
<td>210</td>
<td>23(20)</td>
</tr>
<tr>
<td>July</td>
<td>1</td>
<td>0</td>
<td>349</td>
<td></td>
</tr>
<tr>
<td>Aug.</td>
<td>1</td>
<td>0</td>
<td>349</td>
<td></td>
</tr>
<tr>
<td>Sep.</td>
<td>1</td>
<td>0</td>
<td>349</td>
<td></td>
</tr>
<tr>
<td>Oct.</td>
<td>2</td>
<td>0</td>
<td>349</td>
<td></td>
</tr>
<tr>
<td>Nov.</td>
<td>0</td>
<td>0</td>
<td>349</td>
<td></td>
</tr>
<tr>
<td>Dec.</td>
<td>0</td>
<td>0</td>
<td>349</td>
<td></td>
</tr>
</tbody>
</table>

*Number in parentheses excludes data from one severely rusted field in Gilliam County.

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

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

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

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

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

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

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

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

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