Spatial and Temporal Spread of Oat Crown Rust

R. D. Berger and H. H. Luke

Professor, Department of Plant Pathology, University of Florida, and Research Plant Pathologist, Science and Education Administration, Agricultural Research, U.S. Department of Agriculture, Gainesville, FL 32611.
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ABSTRACT

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The spread of oat crown rust (caused by *Puccinia coronata*) in time and space was measured equally well by disease severity assessed on whole plants or on the leaf below the flag leaf (F−1) for cultivars Fulghum (susceptible) and Burt (intermediate). The assessment of leaf F−1 on cultivar Red Rustproof-14 (resistant) underestimated the total proportion of disease (x). The average apparent infection rates (r) for rust on whole plants of Fulghum and Burt were 0.4, and 0.35 units per day, respectively. These rates were significantly faster than that for Red Rustproof-14 (r = 0.2). Rust isopaths spread outward from plot centers at rates that averaged 0.9, 0.4, and 0.35 m/day for cultivars Fulghum, Burt, and Red Rustproof-14, respectively. The rate of isopath movement also was used to measure interplot interference. On Red Rustproof-14, isopath movement increased from 0.2 to 1.2 m/day when secondary foci enlarged. Rust increased equally fast (as measured by r) at centers and peripheries of foci. There was no flattening of disease gradients for Burt or Fulghum when logit x was plotted against $\log_{10} d$ (distance). The $\log_{10} x$ versus $\log_{10} d$ transformation for disease gradients provided an aberration of true gradients.

Additional key words: Avena byzantina, disease gradients, epidemiology, isopaths, *Puccinia coronata,* slow rusting resistance.

Disease progress is generally measured as rate of change over time (12). Variation in levels of disease from a source is usually expressed as a gradient in space (3). In the time function, Van der Plank (12) used $r = (1/t)$ [logit (x_2) − logit (x_1)] in which r is the average apparent infection rate, t is time in the interval between x_1 and x_2 (disease proportions), and logit $x = \log_e (x/[1-x])$. Growth functions other than the logistic transformation may be more suitable to express epidemic rates for certain epidemics (1,2). For the spread of disease in space, Gregory (3) advised that $\log_{10} x$ be plotted against $\log_{10} d$ (d = distance unit) to define the gradients. MacKenzie (10) suggested that both infection rate and gradient be used to characterize slow rusting components. However, MacKenzie found no significant differences among gradients for susceptible and slow rusting wheat cultivars, even though there were significant differences in infection rates of the causative fungus, *Puccinia graminis* f. sp. *tritici.*

The objective of this study was to characterize the spread of crown rust (*Puccinia coronata* Cda. f. sp. *avenae* Fraser & Led.) on oats (*Avena byzantina* K.) in time and space.

MATERIALS AND METHODS

Three oat cultivars with different degrees of horizontal resistance (slow rusting) to crown rust (8,9) were planted. Red Rustproof-14 (CI 4876) is a resistant, late-maturing cultivar that was selected from Red Rustproof around 1865. Burt (CI 824) is an intermediately resistant, early maturing cultivar selected from Red Rustproof around 1878. Fulghum (CI 708) is a susceptible, early maturing cultivar selected from Red Rustproof around 1897 (11). None of the cultivars has vertical resistance (8) against known races of *P. coronata* f. sp. *avenae.*

Seed of the three cultivars were planted at 3.3 g/m with a funnel seeder in rows 30.5 cm apart. Red Rustproof-14 was planted 1 mo earlier (25 October 1977) than Burt and Fulghum (29 November 1977) to synchronize maturities. The plots were square, and measured 7.6 m on a side. The plot design was 3 × 3 Latin square with a 1.2-m cultivated strip between rows (of plots) and a 0.9-m strip between columns. A single plot of each cultivar also was grown 5 km away. These latter three plots were separated from each other by a 15.2-m cultivated strip. They were considered to be "partially isolated reference plots" and data from them were used to assess interplot interference in the Latin square plots. Stakes were placed in all plots in transects oriented in four compass directions (NE, NW, SE, and SW) to mark data collection points. The points were 1.22, 2.44, and 4.88 m from the plot center; each plot therefore had a total of 12 data collection points.

To initiate the epidemics, 1-mo-old, infected Fulghum plants were transplanted in the center of each plot on 6 March 1978 (considered day 0). The last leaf (flag) was just visible but still rolled up in the whorl for plants in the plots. The source plants had been grown in the greenhouse in 15.2-cm diameter clay pots, three to four plants per pot. The plants were uniformly inoculated in a settling tower and provided with a 14-hr moisture period in a dew chamber. Numerous sporulating pustules were present on these source plants when the plants were positioned in the plots on day 0. The amount of disease on all source plants on day 0 was approximately equal. These source plants remained in the plots for the duration of the experiment.

Disease severity was assessed independently by two individuals on each sampling date. One person estimated disease severity on whole plants at each data collection point, the other individual estimated disease severity on the leaf immediately below the flag leaf (leaf F−1) on each of three plants from each collection point. In early epidemic stages, both persons estimated the number of pustules (per plant or per F−1 leaf). In later epidemic stages, both persons used the Horsfall-Barratt rating scale (4), modified by within-class integration to obtain more accurate intraclass ratings (R.D. Berger, *unpublished*). The ratings included all chlorosis and necrosis associated with the disease. Disease ratings were begun on 30 March (day 24) and continued at 3- or 4-day intervals until 25 April (day 50).

The average apparent infection rates were calculated as described by Van der Plank (12). Disease gradients were obtained by plotting logit x vs. $\log_{10} d$ (d=meters). The rate of disease spread in space was calculated from plotted logit lines for disease observed at 1.22 and 4.88 m from the plot centers for four time periods. The interlinear distance (3.66 m) was divided by the number of days needed for disease at 1.22 m to reach the same severity at 4.88 m.

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RESULTS

Comparison of disease assessment methods. Estimates of disease severity on leaf F−1 were not significantly different ($P = 0.05$) from independent estimates of disease on whole plants for Fulghum and Burt. However, the disease estimates on leaf F−1 of Red Rustproof-14 always were significantly lower ($P = 0.05$) than disease estimates for whole plants of this cultivar (Fig. 1A, B).

The average apparent infection rates for rust calculated from disease estimates on whole plants and on leaf F−1 were, respectively, $r = 0.40$ and 0.35 units per day for Fulghum and $r =$ 0.35 and 0.33 for Burt. The difference in rates measured by either of the assessment methods was not significant ($P = 0.05$) for both cultivars. On Red Rustproof-14, the apparent infection rate for disease estimated on leaf F−1 ($r = 0.08$) was significantly lower ($P =$ 0.05) than that estimated on whole plants ($r = 0.20$).

For Fulghum and Burt, the amount of disease assessed on leaf F−1 was proportional and representative of the total disease on the whole plant, so either method of estimation validly assessed disease severity at each sampling site. On Red Rustproof-14, rust proceeded more slowly from basal leaves to the upper leaves. Therefore, the assessment of disease on leaf F−1 on Red Rustproof-14 significantly underestimated disease for the whole plant and for the plot.

Cultivars and disease severity. Fulghum (susceptible) always had the highest disease severity of the three cultivars, but severity on Fulghum was not always significantly greater than that on Burt. Red Rustproof-14 (resistant) always had the lowest disease severity. Both Fulghum and Burt had significantly more ($P = 0.05$) disease than Red Rustproof-14 on all sampling dates.

Cultivar differences in susceptibility also could be detected by comparing the respective infection rates (Fig. 1A, B). The infection rate was highest for the susceptible Fulghum, intermediate for Burt, and lowest for the resistant Red Rustproof-14. The infection rate was significantly lower ($P = 0.05$) for Red Rustproof-14 than for Burt and Fulghum; the rates for Burt and Fulghum were not significantly different. The significance of these differences in disease severity and infection rates among cultivars was similar for both assessment methods.

Directional gradient. Rust developed more rapidly northeast of the initial focus in all plots and more slowly to the southwest. This directional gradient was most noticeable on the intermediately susceptible cultivar, Burt. The directional gradient on the susceptible Fulghum was largely obliterated toward the season's end by the rapid development of rust. The slower development of rust on Red Rustproof-14 did not exhibit much directional effect. The directional gradient was measured equally by either assessment method. Wind direction information for the plot area was not available to allow correlation of specific wind conditions with disease spread.

Disease gradients. Crown rust developed at approximately the same infection rate at all sampled distances from the initial focus in Fulghum and Burt; ie, the logistically transformed disease progress curves for whole plants at each distance were essentially parallel for the respective cultivars (Fig. 2A, B). Therefore, the disease gradient observed for any date on Fulghum or Burt was representative of the gradient at most other dates (Fig. 3A, B). For Red Rustproof-14 in the later stages of the epidemic, disease development in secondary foci intensified, which caused some flattening of the gradient (Figs. 2-C and 3-C). These secondary foci were distinct in the Red Rustproof-14 plots. The foci were presumed to have arisen from the airborne influx or mechanical dispersal of inoculum from the neighboring plots of the more susceptible oats.

Spatial spread of rust. The outward spread of disease from infection foci can be considered moving annuli of disease of equal intensity (isopaths). The outward movement of rust isopaths was calculated to give a measure of rust movement over distance in time. Because the proximity of plots increased the likelihood of interplot interference, these plots were compared to the partially isolated reference plot of each cultivar 5 km away. The rate of movement of the isopaths would be assumed to be nearly constant if environmental conditions were stable and favorable, and if no spurious disease spread occurred. Correspondingly, any deviation of rate in the replicated plots from the rate observed for the

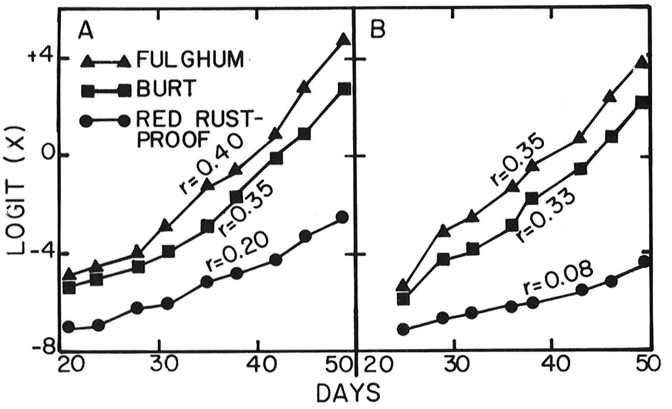

Fig. 1. Progress of *Puccinia coronata* f. sp. *avenae* on three cultivars of oats assessed by two methods. The *r* values are apparent infection rates averaged for 36 ratings (three distances × four directions × three replications) over each time entered. **A,** Crown rust assessed on whole plants. **B,** Crown rust assessed on leaf F−1 (first leaf below the flag leaf).

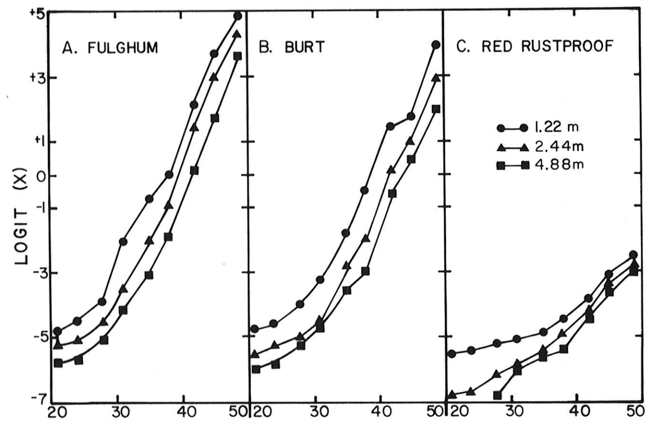

Fig. 2. Progress of *Puccinia coronata* f. sp. *avenae* assessed on whole plants of three oat cultivars at three distances from plot center. Each point is the average of 12 ratings (four directions × three replications).

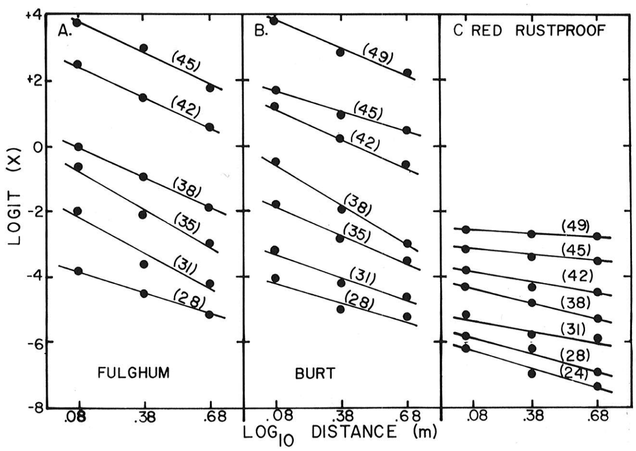

Fig. 3. Disease gradients for *Puccinia coronata* f. sp. *avenae* on three cultivars of oats. Each point is the average of 12 ratings on whole plants (four directions × three replications). Numbers in parentheses are days after epidemic initiation.

reference plots should represent interplot interference. Because the plots were large, the observers had to move through them to make the disease estimates. This movement of personnel may have spread inoculum that showed as an inordinate amount of disease one incubation period (about 12 days) later.

Rust isopaths spread outward in the Red Rustproof-14 reference plot at mildly fluctuating rates (0.3–0.4 m/day). In the Red Rustproof-14 plots in the Latin square experiment, the rust isopaths increased in rate with each observation; ie, the rate was 0.2 m/day for the isopath beginning on day 21 to 1.2 m/day for the isopath beginning on day 42. This increase in rate reflected the interplot interference that occurred as the season advanced. The rust isopaths averaged 0.4 and 0.9 m/day for Burt and Fulghum, respectively, in the reference plots. In the Latin square experiment, the isopath rates were 0.6 and 0.7 m/day for Burt and Fulghum, respectively. All differences in isopath movement between locations of each cultivar were significant ($P < 0.05$).

DISCUSSION

Epidemiology is the study of disease in populations (12). The course of an epidemic may be charted by monitoring the severity of disease (x) on all or a few individuals, or on representative portions of individuals. The entire epidemic is a summation of the progress of disease on each component subgroup. The assessment unit (leaf, whole plant, groups of plants, etc.) is a choice left to the experimenter. For oat crown rust, assessment of leaf F−1 and of whole plants provided comparable information on epidemic progress with about the same amounts of labor and requisite skill. The leaf assessment method was somewhat more variable in determining x. Cultivar responses, disease increase in time, and disease gradients were readily detected and were similar with both methods.

In our experiment, a Latin-square design was used to gain experimental precision; variation partitioned to rows and columns was not significant for either grouping on any observation date. Disease also was assessed on whole plants at the infection focus. These assessments had no replication for direction and were more variable than those made at sites away from the focus. In all cases, the disease estimates for the plants at the focus were greater than the estimates for the disease at the other observed sites for each experimental plot.

Gregory (3) recommended plotting disease gradients as $\log_{10} x$ versus $\log_{10} d$, where x and d are proportion of disease and distance units, respectively. Disease gradients plotted with this function frequently flatten over time. Various workers (3,10,12) have interpreted this flattening to mean that disease was proceeding faster at the focal periphery than at the center. However, the $\log_{10} x$ transformation does not adequately straighten disease progress curves and therefore it would not be expected to sufficiently define the gradient when $x > 0.5$. We used logit x rather than $\log_{10} x$ to determine our gradients. Only in plots with very noticeable secondary foci did the disease gradients flatten over time. We found that crown rust generally progressed as fast at the focal periphery as at the center over a very broad range of disease severities. The flattening of disease gradients when the $\log_{10} x$ transformation is used may be more an aberration of the transformation than it is an actual change in epidemic rate.

The spatial spread of crown rust in our plots was measured as the average rate of isopath movement. This rate is another parameter to compare epidemics in addition to those described by Kranz (7). We used isopath movement to rank cultivar resistance. In the more resistant cultivar, Red Rustproof-14, not only was disease severity lower, but the isopaths moved outward from the focal centers more slowly than did those of the more susceptible cultivars, Burt and Fulghum. This rate can also be used to compare environmental conditions; ie, a higher average rate would mean that weather more favorable for disease prevailed. The isopath rate was not as sensitive as the apparent infection rate in assessing the effects of environment on disease development.

The horizontal resistance of Burt to crown rust is influenced greatly by environment. In our experiment, Burt was intermediate in resistance, but was not significantly different from the susceptible Fulghum for most epidemic parameters that were calculated. In other seasons, the resistance to rust expressed by Burt has been truly intermediate between that of Fulghum and Red Rustproof-14 or has even approached the high resistance of Red Rustproof-14 (8,9; and H. H. Luke, *unpublished*). The "late rusting" phenomenon (9) exhibited by Red Rustproof-14 was not clearly detected because our disease estimates were begun too late for critical definition of this effect.

The probable inadvertent spread of disease when experimenters enter plots (eg, to estimate disease) is of major epidemiological concern. Careful consideration must be given to reduce this effect. The inadvertent spread and interplot interference (5,6,12) most likely cannot be fully eliminated from experiments. However, their contribution to the epidemic may be partially characterized, as reported by James et al (5, 6) and by isopath differences, as we did here.

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