# Response of Susceptible and Slow Leaf-Rusting Wheats to Infection by Puccinia recondita

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ABSTRACT

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Flag leaves of slow leaf-rusting winter wheat cultivars Suwon 85 and P6028 and susceptible cultivars Monon and Suwon 92 were inoculated uniformly with urediospores of *Puccinia recondita* in the greenhouse to measure components of slow-rusting resistance. Uredia first appeared on Monon and Suwon 92 on day 6 after inoculation and all uredia had appeared by day 9 or 10. Uredia first appeared on Suwon 85 and P6028 on day 7 but all uredia did not appear until day 12 or 13. Throughout most of the period of opening of uredia, development lagged 2-4 days on Suwon 85 and P6028. The final numbers of uredia per square centimeter on Suwon 85 and P6028 were less than on Monon and Suwon 92, but the difference was not statistically significant. For all cultivars, approximately 12% of the spores applied to the leaf gave rise to uredia. Uredium size was inversely related to the density of uredia, but uredia were consistently larger on Monon and Suwon 92 than on Suwon 85 and P6028. The production of more urediospores per day per uredium on Monon and Suwon 92, compared to Suwon 85, was the result of larger uredia on these two cultivars. Low production of urediospores on P6028 was due to less production per square millimeter of uredium and to smaller uredia. The effects of the resistance mechanisms in Suwon 85 and P6028 would be cumulative over the several infection cycles that occur during epidemic development in the field and should result in a much lower leaf rust severity on them compared to susceptible cultivars.

*Additional key words*: general resistance, horizontal resistance, nonspecific resistance, epidemiology, *Triticum aestivum*, breeding for resistance.

The rapid loss of race-specific resistance to cereal rusts has encouraged plant breeders to seek more stable forms of resistance, such as "slow-rusting" (3, 4, 5, 19). Slow-rusting cereals possess characteristics that interfere with the pathogen's reproduction so that its rate of spread is retarded. These characteristics may include a lower infection efficiency, a longer latent period, or production of fewer spores by each uredium. Slow-rusting resistance was largely ignored until Van der Plank (22) suggested, on epidemiological evidence, that such resistance could give effective control of the rusts. Romig (18) had described and measured slow-rusting resistance to *Puccinia recondita* 6 yr earlier, however. Slow-rusting resistance against several *Puccinia* spp. is now recognized (4, 6, 8, 9, 13, 17, 21, 23).

Because of the ephemeral nature of the hypersensitive-type of resistance to wheat leaf rust, even of genetically complex forms (4), we investigated slow leaf-rusting resistance, particularly as found in the cultivar Suwon 85 and in Purdue breeding line P6028A2-5-9-6-1 (P6028), which is a backcross derivative of Knox with improved resistance to Hessian fly (12, 14, 15, 16). In studying the inheritance of slow-rusting in crosses of Suwon 85 and P6028 with the susceptible cultivars Monon and Suwon 92, we identified three components of resistance: longer latent period, smaller uredia, and fewer uredia per square centimeter of leaf (16). The large populations used in these studies necessitated measuring these parameters by visual estimate. Such estimates were sufficiently accurate to demonstrate significant differences among parents for these components (15). However, they were not sufficiently accurate to estimate the contribution of each component to the slow rate of disease development observed in the field. The objective of the present research was to quantify the components of slow leaf-rusting found in Suwon 85 and P6028, under various inoculum levels.

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## MATERIALS AND METHODS

*Triticum aestivum* L. em. Thell 'Monon' (C.I. 13278), 'Suwon 92' (C.I. 12666), 'Suwon 85' (P.I. 157600), and 'P6028' were grown in the greenhouse following vernalization for 70 days. Plants received natural daylight supplemented with illumination from cool-white fluorescent tubes and incandescent bulbs which supplied $2 \times 10^4$ ergs $cm^{-1}$ $sec^{-1}$ for 16 hr each day. Day temperatures were 22 to 27 C and night temperatures were 17 to 22 C.

The adaxial surfaces of flag leaves of the cultivars were inoculated in a settling tower (7) with urediospores of *Puccinia recondita* Rob. ex. Desm. culture P659-1 (race 76) when plants were in the booting growth stage. Cultivars were arranged in a randomized block design with four replications in the settling tower. Three

inoculum levels were compared in each experiment. Inoculum levels were estimated by counting spores per square centimeter on microscope slides placed in the settling tower during the inoculation; a close linear relation was found between weight of spores discharged into the tower and spores per square centimeter. Estimates of the three inoculum levels in each experiment were as follows: experiment 1: 77, 182, 288 spores/$cm^2$; experiment 2: 77, 498, and 1,023 spores/$cm^2$; experiment 3: 182, 498, and 815 spores/$cm^2$; and experiment 4: 182, 288, and 393 spores/$cm^2$.

Following inoculation at 1600-1800 hours, the plants were placed in a polyethylene enclosure in the greenhouse and misted with deionized water. Moisture remained on the leaves until the following morning when plants were placed on a lighted greenhouse bench. In the first experiment, the latent period was determined by visually estimating the percentage of uredia that had erupted each day (16). In subsequent experiments, to measure the latent period more accurately, the number of uredia per square centimeter were counted at the same hour each day beginning 6 days after inoculation. On each leaf the number of uredia in each of nine, 30.2-$mm^2$ circular areas were counted. The same areas on the leaf were examined each day. When all uredia had erupted, the leaves were detached and photographed. The areas of 40 randomly selected uredia were measured on the enlarged images by matching the uredium to an ellipse of known area. The mean area of projected uredia was adjusted for magnification to derive the actual mean uredium area expressed in square millimeters.

To estimate daily spore production per uredium, spores were collected with a cyclone collector from the four leaves from each cultivar/inoculum level combination each day between 1300-1400 hours, just before the uredia were counted. The collector was tapped repeatedly on a hard surface to cause spores adhering to its inner walls to fall into the vial. The number of spores that could not be dislodged in this way appeared to be minimal in relation to the number collected in the vial. Water with Tween-20 (four drops/100 ml) was added to each vial of spores. After agitating the vial for 30 sec on a Vortex mixer, two aliquots were placed in a haemacytometer to determine the total number of spores in the vial. The area of each leaf was calculated from length and width measurements using the relation:

$$\text{area } (mm^2) = 0.8573\ (L \times W) - 6.7154$$

in which L = mm leaf length and W = mm leaf width at mid-length. This relation was derived from regression of true area of 38 leaves, measured with a planimeter, on L × W. The coefficient of determination for this relation was 0.74. Using data on total spores collected, total leaf area, and uredium number in the sample areas, we calculated the number of spores produced per uredium per day for each genotype.

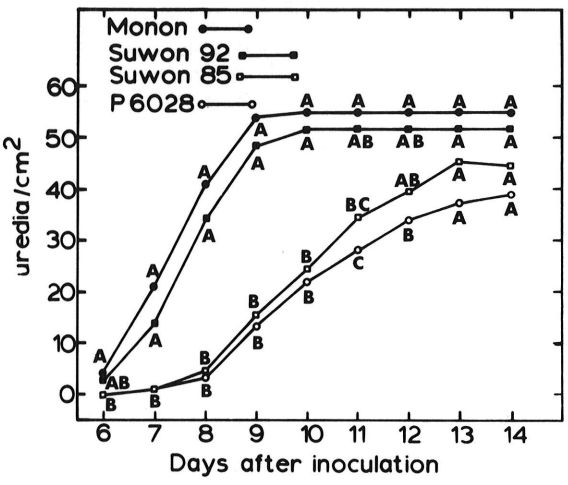


**Fig. 1.** Latent period of *Puccinia recondita* on flag leaves of four winter wheat cultivars, as indicated by the course of appearance of uredia following a single inoculation at day 0. Each point is an average for 24 leaves from two experiments (no. 3 and 4 identified in text). Within each day, points marked by a common letter do not differ at $P = 0.05$ (Duncan's multiple range test).

## RESULTS

**Latent period.**—Although more uredia were present on plants that had received higher inoculum levels, the percentage of uredia (relative to the final number of uredia) present each day within each cultivar was essentially the same regardless of inoculum level. For this reason we pooled data of experiments 3 and 4, each of which included four cultivars. Six days after inoculation uredia appeared on the susceptible cultivars Monon and Suwon 92 and by 9 or 10 days the maximum number had developed (Fig. 1). The appearance of uredia on the slow-rusting cultivars Suwon 85 and P6028 extended from 7 to 12 or 13 days after inoculation.

To reduce each curve of the type in Fig. 1 to a single value, we converted the number of uredia present each day to a proportion of the final number of uredia and calculated a mean latent period (16) using the equation:

$$LP = \sum_{i=0}^{n} P_i\, t_i$$

where $P_i$ is the proportion of uredia (in relation to the final number of uredia) that appear on the $i^{th}$ day after inoculation, $t_i$ is the $i^{th}$ day after inoculation, and n is the number of days after inoculation when all uredia have appeared. Values for LP were: Monon, 7.8 days; Suwon 92, 8.1 days; and Suwon 85 and P6028, 10.4 days. At the LP for Monon, 67% of the uredia had appeared. Corresponding values for Suwon 92, Suwon 85, and P6028 were 68%, 72%, and 63%, respectively.

**Infection efficiency.**—The final number of uredia per square centimeter is the product of the number of spores per square centimeter which are deposited on the leaf, the penetration frequency, and the frequency of successful penetrations that give rise to uredia. Final number of uredia is therefore a measure of infection efficiency. At the highest level of inoculum in the third experiment (815 spores/$cm^2$) both Suwon 85 and P6028 bore significantly fewer uredia per square centimeter than did Monon. No significant cultivar effects occurred at other levels of inoculum or in other experiments. When the data were pooled (Fig. 1), there was no significant difference in final

density of uredia among the four cultivars, although there were 55 and 52 uredia/cm$^2$ on Monon and Suwon 92 compared to 45 and 39 uredia/cm$^2$ on Suwon 85 and P6028, respectively.

Within the range of inoculum there was a clear linear relation between inoculum level and number of uredia that developed. Using the mean density of uredia for each inoculation we calculated the regression of uredia per square centimeter (Y) on urediospores applied per square centimeter (X). A test for homogeneity of regression coefficients revealed no significant difference among the four cultivars (20). The regression line for each cultivar intercepted the Y-axis slightly above zero, suggesting that some uredia would develop when no spores were applied. Because this is impossible, the regression coefficients were recalculated so the line passed through the origin. These recalculated coefficients did not significantly differ from the original regression coefficients. Regression coefficients of the lines which passed through the origin were: Monon, 0.14; Suwon 92, 0.13; Suwon 85, 0.12; and P6028, 0.10 uredia per urediospore. Thus, only ~12% of the inoculum applied infected and gave rise to uredia.

**Size of uredia.**—Uredia on Monon and Suwon 92 were always larger than uredia on Suwon 85 and P6028 (Table 1). On all cultivars, the size of uredia decreased as uredia became more crowded (Table 2). Moreover, the decrease in size of uredia as a function of density of uredia was significantly greater on Monon and Suwon 92 than on the slow-rusting cultivars. Because uredia on Monon and Suwon 92 were more numerous than uredia on Suwon 85 and P6028, the differences in uredium size between the fast-rusting and slow-rusting cultivars in Table 1 are underestimated. A more accurate estimate of uredium size as a component of resistance is obtained by using the regression equations to estimate uredium size for each cultivar at a common number of uredia per square centimeter. In experiments 3 and 4 the mean final number was 47.6 uredia/cm$^2$. Values for expected uredium size on each cultivar (next to last column of Table 2) at this number of uredia are similar to the means for actual numbers in experiments 3 and 4 (Table 1). However, the expected sizes for Monon, Suwon 85, and P6028 are slightly larger relative to Suwon 92 than are the actual sizes.

**Urediospore production.**—Urediospores were collected daily in experiments 3 and 4 to estimate the productivity of uredia on the four cultivars. In experiment 3, collection was not begun until 12 days after inoculation; in experiment 4, however, spores were collected from the day uredia first appeared (Table 3).

By day 13, all four genotypes had borne nearly the maximum number of uredia and the uredia had reached nearly full size. We used the data from days 13 through 15, for the six inoculation levels of experiments 3 and 4, to characterize the spore production capacity of each cultivar (Table 4). Within each cultivar and inoculum level, the spores from the four replications were collected in a single vial. Therefore the data from each inoculation level within each experiment were used as a replication for the analysis of variance.

Monon and Suwon 92 produced considerably more spores per uredium per day than did Suwon 85 and P6028. When spore production was expressed as spores per square millimeter of uredium, uredia on Suwon 85 were as productive as uredia on Suwon 92 and Monon but those on P6028 were less productive.

Spore production expressed as spores per square centimeter of leaf per day is the combined effect of uredium size, spores produced per unit area of uredium, and number of uredia per square centimeter of leaf. According to our estimates, *P. recondita* produces two to three times more inoculum on Monon and Suwon 92 than on Suwon 85 and P6028.

TABLE 1. Size of uredia of *Puccinia recondita* on flag leaves of four winter wheat cultivars

| Cultivar | Experiment 1 (mm$^2$) | 2 (mm$^2$) | 3 (mm$^2$) | 4 (mm$^2$) | Mean[x] (mm$^2$) |
|---|---|---|---|---|---|
| Monon | 0.36 a | ... | 0.21 b | 0.22 a | 0.22 |
| Suwon 92 | ... | 0.21 a | 0.30 a | 0.25 a | 0.27 |
| Suwon 85 | 0.18 b | 0.14 b | 0.15 c | 0.13 b | 0.14 |
| P6028 | 0.19 b | 0.13 b | 0.13 c | 0.15 b | 0.14 |

[x]Based only on data of experiments 3 and 4 because of missing values in experiments 1 and 2. Plants of Suwon 92 or Monon at the proper growth stage were not available for experiments 1 and 2, respectively. Within each experiment, means followed by the same letter do not differ at $P = 0.05$ (Duncan's multiple range test).

TABLE 2. Relation between uredium size in square millimeters (Y) and number of uredia per square centimeter (X) for *Puccinia recondita* on flag leaves of four winter wheat cultivars

| Cultivar | Linear regression coefficient, b[x] | Coefficient of determination, r$^2$ | Y when[y] X = 47.6 uredia/cm$^2$ | Y when[y] X = uredium/cm$^2$ |
|---|---|---|---|---|
| Suwon 92 | −0.001509 a | 0.629 | 0.266 | 0.337 |
| Monon | −0.001336 a | 0.314 | 0.258 | 0.320 |
| P6028 | −0.000628 b | 0.286 | 0.141 | 0.170 |
| Suwon 85 | −0.000508 b | 0.205 | 0.149 | 0.173 |

[x]Values followed by the same letter do not differ significantly at $P = 0.05$ (Duncan's multiple range test).

[y]The mean number of uredia in experiments 3 and 4 was 47.6/cm$^2$. Values for one uredium per square centimeter are included to illustrate size difference at a moderate level of disease.

## DISCUSSION

These results show that the slow leaf-rusting wheats interfere with pathogenesis by *P. recondita* by lengthening the latent period, restricting uredium size, and reducing the number of spores produced.

The prolonged latent period of *P. recondita*, as measured on Suwon 85 and P6028, is a particularly important part of the slow-rusting phenomenon. Although uredia appeared on Suwon 85 and P6028 only 1 day later than they appeared on Monon and Suwon 92, they erupted at a slower rate so that from 7 to 10 days after inoculation there were far fewer uredia on Suwon 85 and P6028 than on Monon and Suwon 92.

Fewer penetrations or a postinfection host response that prevents some infection sites from producing uredia decrease infection efficiency in other cereal rusts and therefore contribute to slow-rusting (1, 2, 5, 6, 8, 10, 11, 18). Because uredia of *P. recondita* were ultimately nearly as numerous on slow- as on fast-rusting wheats in our study, reduced number of penetrations is apparently not important in the resistance of Suwon 85 and P6028.

When Idaed 59 is infected with a virulent culture of *Puccinia graminis*, host cells at some infection sites die and fungus development ceases (1). At other infection sites the host cells do not die and a normal uredium develops. Possibly Suwon 85 and P6028 have a similar, but less violent, reaction to *P. recondita*. The host reaction at some infection sites could slow down the pathogen without completely inhibiting it. Uredia at such infection sites would be those that form later than uredia at more compatible sites. This explanation would account for the long latent period on Suwon 85 and P6028. The reaction of these wheats to *P. recondita* and of Idaed 59 to *P. graminis* may differ only quantitatively and the apparently different mechanisms of slow-rusting could be fundamentally the same.

Another significant component of slow-rusting of Suwon 85 and P6028 is smaller uredia. On the average, uredia on Suwon 92 and Monon were 2.0 and 1.7 times larger than uredia on the slow-rusting wheats. Unlike latent period, which was insensitive to inoculum level, uredia tended to be smaller when they were crowded. Even on the most heavily infected leaves, however, uredia on Monon and Suwon 92 were larger than uredia on Suwon 85 and P6028. On the other hand, some uredia on the slow-rusting wheats were as large as the largest uredia on the fast-rusting wheats. Like latent period, uredium size depends on the response of host cells at the infection site; this response varies from site to site, but on the average it is more adverse to *P. recondita* in the slow-rusting wheats. Both of these components of

TABLE 3. Urediospores produced per uredium of *Puccinia recondita* on flag leaves of four winter wheat cultivars

| Time after inoculation | Cultivar and experiment | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Monon | | Suwon 92 | | Suwon 85 | | P6028 | |
| (days) | 3 | 4 | 3 | 4 | 3 | 4 | 3 | 4 |
| 7 | | 27 | | 25 | | | | |
| 8 | | 87 | | 76 | | | | |
| 9 | | 406 | | 263 | | 92 | | 66 |
| 10 | | 142 | | 87 | | 52 | | 79 |
| 11 | | 439 | | 731 | | 106 | | 142 |
| 12 | 521 | 376 | 763 | 747 | 297 | 152 | 266 | 201 |
| 13 | 275 | 467 | 210 | 634 | 224 | 207 | 36 | 278 |
| 14 | 405 | 508 | 601 | 613 | 446 | 186 | 157 | 210 |
| 15 | 396 | 592 | 495 | 674 | 307 | 423 | 161 | 403 |

TABLE 4. Urediospore production by *Puccinia recondita* on flag leaves of four wheat cultivars

| Cultivar | Spores per uredium per day[x] | Spores produced per unit uredium area per day[y] (no./mm$^2$) | Spores produced per unit leaf area per day[z] (no./cm$^2$) |
|---|---|---|---|
| Monon | 411 a | 2,133 a | 19,590 a |
| Suwon 92 | 538 a | 2,114 a | 23,886 a |
| Suwon 85 | 299 b | 2,134 a | 11,757 b |
| P6028 | 208 b | 1,470 b | 7,847 b |

[x]Average production during days 13 to 15 in experiments 3 and 4 (see Table 3).

[y]Spores per uredium per day divided by mean uredium area, in square millimeters, as measured on day 15 in experiments 3 and 4. The mean uredium area used was a weighted mean, using the number of uredia per square centimeter in each replicate as the weights.

[z]Spores per uredium per day multiplied by the number of uredia per square centimeter on day 14 (see Fig. 1). Beneath each heading, means followed by the same letter do not differ at $P = 0.05$ (Duncan's multiple range test).

resistance–long latent period and small uredia–can be interpreted as an interference with the rate of growth of the fungus at an infection site. If long latent periods and smaller uredia are manifestations of the same resistance response, then one would expect the same host genes to affect both. Correlation of these components of resistance in segregating populations (15) supports this hypothesis.

Uredia of a common size on Monon, Suwon 92, and Suwon 85 produced essentially equal numbers of spores. Thus, the lower productivity of uredia on Suwon 85 was due entirely to their smaller size (Table 4). Uredia on P6028 were not only smaller than uredia on Monon and Suwon 92, which reduced their productivity, but also produced fewer spores per square millimeter of uredium. Wheat line P6028 evidently has greater slow-rusting resistance than Suwon 85. There are several reports (6, 8, 11, 21) of diminished spore production by slow-rusting cereals, but whether this is because uredia are smaller or inherently less productive is not known.

The effects of a longer latent period and smaller uredia on the pathogen would accumulate during the course of the epidemic and the difference in number of infections between the slow- and fast-rusting wheats would increase with each successive generation of *P. recondita*. We did not observe the latent period to shorten with increasing inoculum so that heavy exogenous spore showers on a field of slow-rusting wheat would not cause a diminution in expression of resistance. The latent period becomes shorter for infections that occur after anthesis (16), but the decline of resistance at this stage would probably be too late to permit a destructive buildup of the fungus.

To select for the hypersensitive type of resistance to leaf rust, only a few infections on each plant are necessary. By contrast, to select effectively for slow-rusting resistance in the field, at least a moderately severe epidemic is necessary to distinguish susceptible lines from slow-rusting lines. Weather is not always conducive to such an epidemic so it may be desirable to evaluate breeding material in the greenhouse. The methods used in our study to measure slow-rusting are too time-consuming for screening large numbers of lines. We used visual estimates of percent uredia erupted to estimate latent periods (16), but even this requires daily inspection of plants. A simpler but adequate technique would be to examine plants 8 or 9 days after inoculation. At this time the difference in density of uredia is greatest between the slow- and fast-rusting genotypes. One more inspection at 14 days after inoculation would reveal differences in infection efficiency and uredium size.

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