Growth of Uredinia of *Puccinia recondita* in Leaves of Slow- and Fast-Rusting Wheat Cultivars

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ABSTRACT

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Rates of expansion of the surface areas of uredinia of *Puccinia recondita* in flag leaves of slow- and fast-rusting wheat cultivars (as judged by latent period and final uredinium size) were studied. Uredinia grew linearly with time and at a significantly faster rate in fast-rusting cultivars than in slow-rusting cultivars. Average rates for the fast-rusting cultivars Morocco, Monon, and Suwon 92 were 0.07, 0.05, and 0.04 mm^2/day, respectively. Average rates for the slow-rusting cultivars CI 13227 and Suwon 85 were 0.03 and 0.02 mm^2/day, respectively. Uredinia reached maximum size 8–10 days after first becoming visible. The more densely uredinia were packed on a leaf, the slower they grew. Simulations of leaf rust epidemics suggested that a slow growth rate of uredinia would be a significant factor in retarding disease development in the field.

Additional key words: durable resistance, general resistance, pustule growth, SLORUS, *Triticum aestivum*.

For many years, wheat breeders have used hypersensitive resistance to develop cultivars resistant to rust fungi. The often ephemeral protection given by this type of resistance has prompted work in recent years on slow-rusting resistance, which may prove to be more durable. When *Puccinia recondita* Rob. ex. Desm. infects a slow-rusting wheat plant (*Triticum aestivum* L. em. Thell), it takes longer to produce uredinia than on a fast-rusting plant (8). Additionally, many infected slow-rusting wheat plants develop smaller uredinia that produce fewer urediniospores able to initiate the next infection cycle, compared to fast-rusting wheats (8,10). *P. recondita* infects slow-rusting wheats less efficiently than fast-rusting wheats (8,10).

Although these components of slow-rusting can be regarded as epidemiologically independent, their effects are correlated, suggesting that they may be under common genetic control (4).

When uredinia first erupt they are small; during the first few days they increase greatly in size. In several studies (4,7,8,10) that report uredinia to be smaller on slow-leaf-rusting wheats than on fast-leaf-rusting wheats, uredinia were measured at one time only, when they were judged to have reached full size. In one study, however, it was suggested that because the latent period was shorter on fast-rusting wheats, uredinia would reach maximum size earlier on these wheats than on slow-rusting wheats, but that given enough time, uredinia would become as large on slow-rusting wheats as on fast-rusting wheats (4). Clifford (2) reported that uredinia of *Puccinia hordei* expanded more rapidly on the susceptible barley cultivar Midas than on the slow-rusting cultivar Vada.

The present study was undertaken with an improved measuring method to examine more critically the growth rate of uredinia on slow- and fast-rusting wheats and to determine whether the growth rates differed on these two types of cultivars or whether they were the same, but out of phase.

MATERIALS AND METHODS

Several of the wheat cultivars used in this study were the subject of previous investigations (4,7,8,10). The susceptible (fast-rusting) cultivars were Morocco, Suwon 92 (CI 12666), Monon (CI 13278), and Purdue breeding line 72482G4-76 (P72482). The slow-rusting cultivars were Suwon 85 (PI 157600), CI 13227, L574-1 (a line derived from Wakeland/Blueboy and that we selected from the 1976 International Winter Wheat Rust Nursery), Purdue breeding line 6028A2-5-9-6-1 (P6028), and SW 72469-6, a line obtained from the Barley and Wheat Research Institute, Suweon, South Korea. The pedigree of SW 72469-6 is Strampelli/69D-3607//Chokwang (M. S. Chin, *personal communication*). Except for Morocco, these cultivars are winter wheats.

Seed was sown in flats of soil. When the coleoptiles emerged, the flats were placed in a room at 3 C for 65–70 days to vernalize. Fluorescent light was supplied for 12 hr/day during vernalization. After vernalization, seedlings were transplanted individually to 10-cm-diameter pots of soil and reared in a greenhouse. Natural daylight was supplemented with cool-white fluorescent and incandescent light (~167 $\mu E \cdot m^{-2} \cdot sec^{-1}$) for 16 hr/day.

Plants at the late boot stage of growth (8) were inoculated in a settling tower with freshly collected urediniospores of *P. recondita* culture 7434-1-1T. This culture is virulent toward all of these cultivars and has been described previously (4). After inoculation in the late afternoon, plants were held overnight in a moist chamber (10). In experiments 1–7, 3 mg of urediniospores were used in each inoculation. In experiments 8–10, 1 mg of urediniospores were used in each inoculation.

When uredinia began to appear, 10 of them on the adaxial surface of each flag leaf were selected for measurement. A small black mark made with a Sharpie® wick pen (Seikert & Baum, Inc., Wauwatosa, WI 53213) was placed about 3 mm from the selected

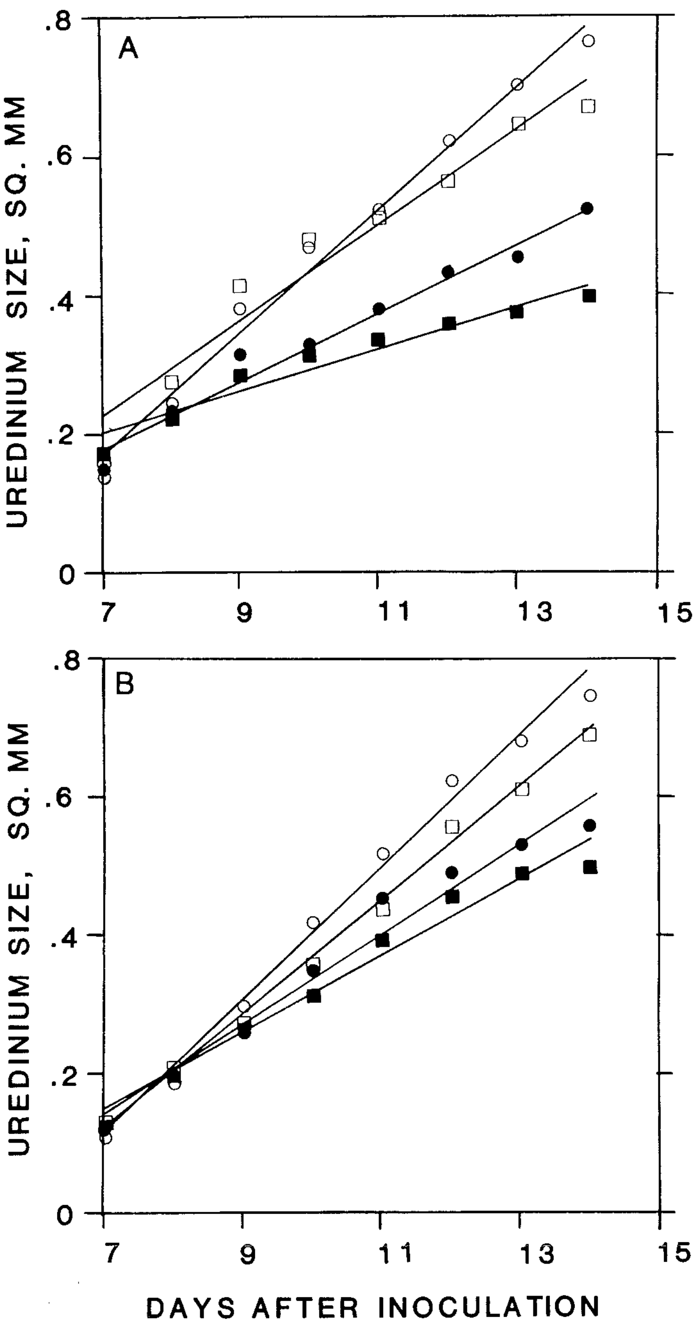

Fig. 1. Effect of density of uredinia of *Puccinia recondita* on their rate of growth in wheat cultivar Morocco. **A,** Experiment 1. Each point is the mean for uredinia in which there was one (o), four to five (□), nine to 10 (•), or >11 (■) uredinia within a circular 16-mm² area centered on the measured uredinium. **B,** Experiment 2. Each point is the mean for uredinia in which there was one (o), three (□), four to five (•), or six to eight (■) uredinia within a circular 16-mm² area centered on the measured uredinium.

uredinium so that repeated measurements could be made on the same uredinia. Preliminary trials showed that the ink was not inhibitory to uredinial development. Before uredinia were measured, excess urediniospores were gently removed from the leaf with a cyclone spore collector to reveal clearly the edges of the uredinia. The length and width of each marked uredinium were measured to the nearest 0.05 mm with an ocular micrometer, and the elliptical area was calculated. There were four replicate plants for a total of 40 measured uredinia per cultivar in each experiment. Six experiments were conducted during the autumn of 1978 and four were conducted during March 1981. Not all cultivars were included in all experiments.

The first two experiments involved only cultivar Morocco and were intended to provide information on the pattern of expansion of uredinium area (referred to, henceforth, as uredinium growth). Uredinia were measured every day until they ceased expanding. Subsequent experiments involved two or more cultivars, and uredinia were measured every 2 or 3 days.

On fast-rusting cultivars, eruption of uredinia extended from about the sixth through the ninth day after infection and it followed a sigmoidal pattern. On slow-rusting cultivars this corresponding period extended from the seventh through 15th days (8,10). To avoid measuring only the first uredinia to appear, selection of uredinia for measurement was deferred until 2–3 days after the first of them appeared. Then, isolated uredinia scattered from the tip to the base of the adaxial surface of the leaf lamina were selected for measurement.

RESULTS

To compare growth of uredinia of *P. recondita* on slow- and fast-rusting wheats, it was necessary to characterize a uredinium growth curve by a rate constant. In the first two experiments, the areas of uredinia on leaves of cultivar Morocco plants were measured daily, beginning 7 days after inoculation. Because the growth of some uredinia on Morocco plants diminished slightly with time, we calculated exponential growth rates by using the logit (12) or Gompertz (1) transformations of uredinium size. To employ these transformations, the uredinium area at each day of measurement was expressed in relative terms by dividing it by the final uredinium area. As an alternative, uredinium area was regressed directly on days after inoculation to calculate a linear growth rate. The logit and Gompertz transformations gave highly similar results, as judged by coefficients of determination. Although these transformations were superior for some sets of data, considering all the data, the simple linear regression was superior. In subsequent experiments, involving several cultivars and, therefore, many more uredinia, measurements were made only every 2 or 3 days. As with the first two experiments, simple regression of size on time was usually superior to regression of transformed data.

Of the 80 uredinia measured on leaves of cultivar Morocco in the first two experiments, the regressions of area on time had coefficients of determination >0.95 for 53 of them, and >0.90 for 70 of them. The lowest coefficient of determination for any uredinium was 0.82. Altogether, growth rates of about 1,350 uredinia were calculated during this study. The coefficient of determination associated with the linear regression of area on time was >0.85 for most of these.

The inoculum levels used in the experiments reported here were lower than in most of our previous studies of slow rusting to avoid densely packed uredinia and consequent interuredinial competition that might affect growth rate. Nonetheless, the number of uredinia in a 16-mm² circular zone around the measured uredinium ranged from 1 to 18 in the first experiment, and 1 to 8 in the second. There was a significant negative correlation between uredinium growth rate and the number of uredinia per 16 mm² ($r = -0.79$ and $r = -0.59$ for experiments 1 and 2, respectively). Growth curves based on mean data for uredinia pooled by density class illustrate this (Fig. 1). The growth rates for pooled uredinia were nonhomogenous (11) (Table 1). The coefficients of determination associated with these growth rates were all >0.94.

In experiments 3–7, each of which involved two or more cultivars, uredinia spacings were too dense to find 10 isolated uredinia per leaf for measurement. The correlation between the density of uredinia and uredinial growth rate was calculated for each cultivar. Correlation coefficients were negative and significantly different from zero at $\alpha = 0.05$ for the fast-rusting cultivars Morocco, Monon, P72482, and Suwon 92. Correlation coefficients were not significantly different from zero for the slow-rusting cultivars. In experiments 8–10, uredinia were widely dispersed so that nearly all uredinia were alone in a 16-mm^2 circular area.

Uredinia consistently grew more slowly in slow-rusting cultivars than in fast-rusting cultivars (Table 2). Although mean uredinium density varied among experiments, differences in density among cultivars within an experiment were significant in only two cases (experiments 6 and 7). These differences in density were not related to level of slow-rusting resistance. For example, in experiment 7, the slow-rusting cultivar SW 72469 had a significantly greater density of uredinia than all other cultivars except Suwon 85 and Suwon 92. Comparison of the uredinium growth rate in SW 72469 with the rate in the fast-rusting Suwon 92 revealed a much lower growth rate in the former (Table 2). In experiment 6, uredinia were more dense in L574-1 than in P6028, but they nonetheless grew faster in L574-1. Whenever cultivar Morocco was in an experiment, uredinia grew faster in it than in any other cultivar. Uredinia grew significantly slower in Suwon 85 than in any fast-rusting cultivar except Monon in experiment 6. Even though the difference was not significant in this one case, uredinia grew only half as fast in Suwon 85 as in Monon. Uredinia grew slower in CI 13227, which is a very slow-rusting cultivar (8), than in any fast-rusting cultivar, but the difference was not always significant. Uredinia grew consistently faster in CI 13227 than in Suwon 85, but the difference was significant in only one experiment.

Because measurements of uredinia were not begun until 1–2 days after the first uredinia erupted, in order to sample from a larger proportion of the uredinial population, measurements were not necessarily begun on each cultivar in an experiment on the same day. Measurements on fast-rusting cultivars commenced 7–9 days after inoculation; measurements on slow-rusting cultivars commenced 7–14 days after inoculation. Measurements were begun later on CI 13227 than on any other cultivar, because CI 13227 had the longest latent period of the cultivars used in these experiments (8). Mean uredinium areas on the first day of measurement were usually less on slow-rusting cultivars than on fast-rusting cultivars (Table 3).

A uredinium was measured every 2 or 3 days until its area did not change from the previous measurement. The maximum size of uredinia was greater on the fast-rusting cultivars than on the slow-rusting cultivars (Table 4). Within each experiment and cultivar there was a significant positive correlation between growth rate and final uredinium size. For the means in Tables 2 and 4, the correlation coefficient between growth rate and final uredinium size was 0.95.

TABLE 1. Effect of density of uredinia of *Puccinia recondita* on their growth rate in leaves of wheat cultivar Morocco

Experiment 1			Experiment 2		
Density[a]	Growth rate (10^{-3} mm^2/day)	Uredinia measured (no.)	Density[a]	Growth rate (10^{-3} mm^2/day)	Uredinia measured (no.)
1	89	6	1	95	8
2–3	73	6	2	95	10
4–5	70	4	3	82	10
6–7	52	8	4–5	65	7
9–10	49	8	6–8	56	5
>11	30	8			

[a]Number of uredinia in a circular area of 16 mm^2 on the leaf surface. The measured uredinium was in the center of this circle.

TABLE 2. Growth rates (10^{-3} mm^2/day) of *Puccinia recondita* uredinia in leaves of several wheat cultivars[a]

Cultivar	Experiment no. 3	4	5	6	7	8	9	10
Fast-rusting								
Morocco	70.5 A	39.2 A			49.8 A	96.1 A	50.6 A	63.4 A
Monon					32.0 BC	46.3 BC	34.5 B	57.1 A
P72482					35.3 B		30.8 B	
Suwon 92			29.4 A		33.5 B	60.8 B	27.6 B	36.1 B
Slow-rusting								
L574-1		26.0 B		34.7 A				
CI 13227					22.4 CD	41.2 BC	28.3 B	29.2 B
Suwon 85	22.8 B		13.5 B	20.3 B	18.2 D	22.8 C	15.4 C	18.1 B
P6028		21.2 B		12.7 C				
SW 72469					13.6 D			

[a]Within each column, means followed by a common letter are not significantly different (Duncan's new multiple range test, $\alpha = 0.05$).

TABLE 3. Initial sizes (10^{-3} mm^2) of *Puccinia recondita* uredinia on leaves of several wheat cultivars[a]

Cultivar	Experiment no. 3	4	5	6	7	8	9	10
Fast-rusting								
Morocco	88 A (7)[b]	94 A (7)			91 A (7)	213 A (7)	197 A (9)	197 A (8)
Monon					88 A (7)	221 A (10)	142 B (9)	46 D (8)
P72482					43 BC (7)		111 C (9)	
Suwon 92			117 A (8)		50 B (7)	113 B (7)	114 BC (9)	148 B (8)
Slow-rusting								
L574-1		57 B (8)		51 AB (7)				
CI 13227					40 BC (12)	100 B (10,13)	56 D (14)	62 CD (12)
Suwon 85	51 B (9,10)		53 B (8)	41 B (7)	44 BC (8)	70 B (7,10)	83 CD (11)	90 C (10)
P6028		51 B (8)		70 A (9)				
'SW 72409					29 C (8)			

[a]Within each column, means followed by a common letter are not significantly different (Duncan's new multiple range test, $\alpha = 0.05$).
[b]Day on which measurement commenced is in parenthesis.

DISCUSSION

Generally, the areas of most uredinia increased linearly with time. In some cases there was a 2- to 3-day period of decreasing growth rate at the end of this linear phase, but this was not consistent enough to warrant calculation of exponential growth rates. A linear growth rate for the first 8–10 days after a uredinium erupted was the most satisfactory statistic for cultivar comparisons. Ogle and Brown (6) found that uredinia of *Puccinia graminis* f. sp. *tritici* increased in area linearly with time in wheat cultivar Yalta.

Not unexpectedly, the growth rate of uredinia tended to be slower when they were crowded in the leaf. This tendency was more pronounced in cultivars in which uredinia had the potential to grow fastest. Therefore, the data for growth rates and final uredinium sizes obtained from experiments 8–10 give the clearest indication of potential differences among cultivars because uredinial crowding was not a factor.

The wheat cultivars and lines investigated in this study were previously classified as to degree of slow-rusting resistance on the basis of length of latent period and final uredinium size (8, 10, and *unpublished*). In this study, uredinia proved to grow slower in slow-rusting cultivars than in fast-rusting cultivars. In an earlier study in our laboratory, Kuhn et al (4) estimated uredinium area 10–14 days after inoculation on four of the cultivars (Monon, Suwon 92, Suwon 85, and P6028) included in the present study. Uredinia were smaller on the slow-rusting cultivars Suwon 85 and P6028. However, when uredinia were measured 6 days after all uredinia had erupted, which would be on about day 15 and day 19 after inoculation for the fast- and slow-rusting cultivars, respectively (10), there was no difference among cultivars (4). Uredinial growth rates in that study were calculated to be 0.016, 0.029, 0.026, and 0.017 mm^2 per day for Monon, Suwon 92, Suwon 85, and P6028, respectively, and were not significantly different for the four cultivars. Thus, in that study we concluded that the smaller uredinia seen on slow-rusting cultivars at 10–14 days after inoculation simply reflected later eruption as compared with uredinia on fast-rusting wheats, and that the uredinia on the slow-rusting wheats were therefore "younger." However, the techniques used to measure uredinium area were not as precise as the technique used in the present study. Uredinium size was estimated in the earlier study by comparison with standard drawings (4). Growth rates were based on estimates of average uredinium size for entire leaves. Moreover, numbers of uredinia per square centimeter were greater in that study, which would have inhibited uredinium growth, especially in the fast-rusting cultivars. The growth rates of uredinia in Suwon 85 and P6028 in the present study were similar to those reported by Kuhn et al (4), but the growth rates in Suwon 92 and Monon were greater. Evidently, growth rate of uredinia can be a component of slow-rusting resistance. As yet, there is no physiological explanation for a longer latent period in some cultivars, but it would appear that the factors responsible continue to exert an inhibitory effect as the erupted uredinium expands. A common underlying mechanism that extends latent period and reduces uredinium size would explain the observed correlation between these components of slow-rusting (5,7,8,10). Although latent period and uredinium size were negatively correlated in the study of Kuhn et al (5), the correlation was not complete, indicating that latent period and uredinium size are not controlled solely by the same set of genes. Kuhn et al (5) estimated uredinium size by visual comparison to standard drawings because of the large plant populations that had to be studied. Further work is underway with progeny of slow- by fast-rusting crosses to investigate this correlation more closely.

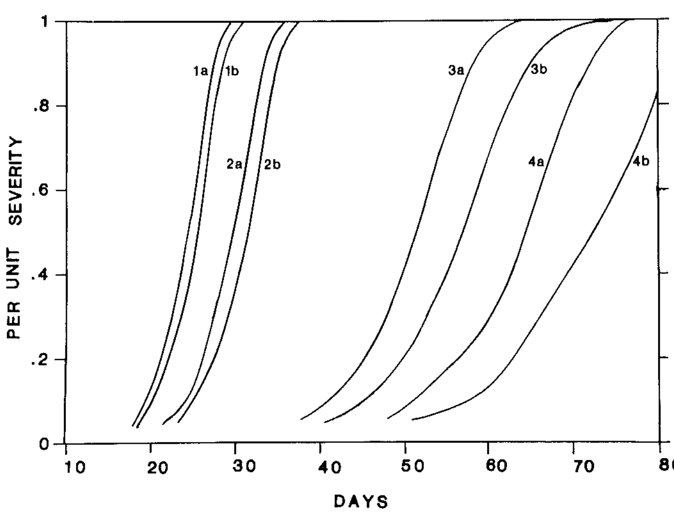

Fig. 2. Simulated leaf rust epidemics on wheat cultivars Monon (curves 1), Suwon 92 (curves 2), Suwon 85 (curves 3), and CI 13227 (curves 4) in which uredinia were assumed either to erupt at full size (a) or to grow at a rate characteristic of each cultivar (b). See text and Shaner and Hess (9) for details of the model.

We have shown previously that differences among cultivars in urediniospore production per uredinium were directly related to differences in mean uredinium area (8,10). A linear relationship has also been shown between uredinium area and spore production for *Puccinia coronata* and *Puccinia graminis* f. sp. *avenae* on oats (3). In a mathematical model of slow rusting, Shaner and Hess (9) treated urediniospore production per uredinium per day as a constant for each cultivar-pathogen isolate combination. From the present study it is evident that the model would be more realistic if the constant S (see equations 2 and 3 in Shaner and Hess [9]) were replaced with a uredinium growth function. Thus, equation 3 of Shaner and Hess (9):

$$I_i = S\lambda\,(1 - A_{i-1})\, v \sum_{j=i}^{n} N_{i-(j-1)} \qquad (1)$$

can be rewritten as:

TABLE 4. Maximum sizes (10^{-3} mm^2) of *Puccinia recondita* uredinia on several wheat cultivars[a]

	Experiment no.							
Cultivar	3	4	5	6	7	8	9	10
Fast-rusting								
Morocco	467 A	374 A			468 A	955 A	514 A	525 A
Monon					367 AB	436 B	408 B	461 AB
P72482					345 B		344 BC	
Suwon 92			274 A		340 B	534 B	293 CD	351 BC
Slow-rusting								
L574-1		228 B		313 A				
CI 13227					220 C	316 B	222 DE	220 C
Suwon 85	158 B		141 B	200 B	213 C	242 B	177 E	212 C
P6028		190 B		146 B				
SW 72469					148 C			

[a] Within each column, means followed by a common letter are not significantly different (Duncan's new multiple range test, $\alpha = 0.05$).

$$I_i = \lambda\,(1 - A_{i-1})\,\upsilon \sum_{j=1}^{j=n} \sum_{t=0}^{t=9} (u_0 + rt)\,U\,N_{i-(j-1)} \qquad (2)$$

In both of these equations, I_i is the number of infections that occur on the ith day, λ is the proportion of daily inoculum produced each day that lands on leaves, A_{i-1} is the proportion of diseased (preempted) leaf tissue on the $(i-1)$th day, ν is the proportion of spores on leaves that infect (disregarding preempted tissue), n is the infectious period, and $N_{i-(j-1)}$ is the number of spore-producing uredinia on the ith day. In equation 1, S is the number of spores produced per uredinium per day. This is replaced in equation 2 by the expression $(u_0 + rt)\,U$, in which u_0 is the area of the uredinium (mm^2) when it first erupts, r is the uredinium growth rate (mm^2/day), t is the uredinium age (days from eruption of the uredinium), and U is the number of urediniospores produced per square millimeter of uredinium per day. In equation 2, a uredinium reaches its maximum size when it is 9 days old. This was a typical period of expansion of a uredinium on both slow- and fast-rusting cultivars. For values of $n > 10$ days, $t = 9$.

The Basic-Plus computer program "SLORUS" (8,9) was modified by substituting equation 2 for equation 1. Then, epidemics of leaf rust were simulated for Monon, Suwon 92, Suwon 85, and CI 13227. These simulations, in addition to the parameters previously described (9), required values of u_0 and r for each cultivar. Representative values of u_0 and r were obtained from the data of experiments 8–10, in which crowding of uredinia was not a factor. With average values for the slopes and y-intercepts for each of the uredinia measured in these experiments for each cultivar, uredinium size was calculated for the day uredinia first appeared. Typically, the first uredinia appeared 6 days after inoculation of Monon, and Suwon 92 (10), 7 days after inoculation of Suwon 85 (10), and 11 days after inoculation of CI 13227 (8 and *unpublished*). Thus, values of u_0 are: Suwon 92, 0.067; Monon, 0.037; CI 13227, 0.035; and Suwon 85, 0.034 mm^2. Values of r are: Suwon 92, 0.0399; Monon, 0.0474; CI 13227, 0.0330; and Suwon 85, 0.0192 mm^2/day. In this model, a uredinium grows for 10 days, which is also the infectious period. If a longer infectious period were to be used, the uredinium would only be allowed to grow for 10 days, and then would remain at a constant size.

Paired simulations were then run for each of the four cultivars, one in which uredinia grew and one in which uredinia were at their maximum size from the first day they erupted (the original model). Within each cultivar, all other parameters were the same in the two simulations. Not unexpectedly, the epidemic progressed slower when uredinia grew compared to when they were assumed to erupt fully grown (Fig. 2). This difference was more pronounced for Suwon 85 and CI 13227, which had slower uredinium growth rates compared to Monon and Suwon 92. Apparent infection rates (12) calculated for percent severity data in the range 5–95% were 0.573, 0.464, 0.250, and 0.195 per unit per day for Monon, Suwon 92, Suwon 85, and CI 13227, respectively, when a constant uredinium size was used in the simulation; corresponding infection rates for simulations in which uredinia grew were 0.516, 0.402, 0.187, and 0.147 per unit per day, respectively. These simulations suggest that the significantly slower rate of uredinium growth on slow-rusting cultivars contributes, along with previously described components of slow-rusting resistance, to the slower rate of disease progress in the field compared with fast-rusting cultivars.

LITERATURE CITED

1. Berger, R. D. 1981. Comparison of the Gompertz and logistic equations to describe plant disease progress. Phytopathology 71:716-719.
2. Clifford, B. C. 1972. The histology of race non-specific resistance to *Puccinia hordei* Otth in barley. Proc. 5th Eur. Mediterr. Cereal Rusts Conf., Prague, Czechoslovakia 1:75-79.
3. Kochman, J. K., and Brown, J. F. 1975. Host and environmental effects on post-penetration development of *Puccinia graminis avenae* and *P. coronata avenae*. Ann. Appl. Biol. 81:33-41.
4. Kuhn, R. C., Ohm, H. W., and Shaner, G. E. 1978. Slow leaf-rusting resistance in wheat against twenty-two isolates of *Puccinia recondita*. Phytopathology 68:651-656.
5. Kuhn, R. C., Ohm, H. W., and Shaner, G. E. 1980. Inheritance of slow leaf-rusting resistance in Suwon 85 wheat. Crop Sci. 20:655-659.
6. Ogle, H. J., and Brown, J. F. 1971. Quantitative studies of the post-penetration phase of infection by *Puccinia graminis tritici*. Ann. Appl. Biol. 67:309-319.
7. Ohm, H. W., and Shaner, G. E. 1976. Three components of slow leaf-rusting at different growth stages in wheat. Phytopathology 66:1356-1360.
8. Shaner, G., and Finney, R. E. 1980. New sources of slow leaf-rusting resistance in wheat. Phytopathology 70:1183-1186.
9. Shaner, G., and Hess, F. D. 1978. Equations for integrating components of slow leaf-rusting resistance in wheat. Phytopathology 68:1464-1469.
10. Shaner, G., Ohm, H. W., and Finney, R. E. 1978. Response of susceptible and slow leaf-rusting wheats to infection by *Puccinia recondita*. Phytopathology 68:471-475.
11. Steel, R. G. D., and Torrie, J. H. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Co., Inc., New York. 481 pp.
12. Vanderplank, J. E. 1963. Plant Diseases: Epidemics and Control. Academic Press, New York. 349 pp.