Slow Leaf-Rusting Resistance in Wheat Against Twenty-Two Isolates of Puccinia recondita

R. C. Kuhn, H. W. Ohm, and G. E. Shaner

Graduate Research Assistant and Associate Professor, Department of Agronomy, and Associate Professor, Department of Botany and Plant Pathology, Purdue University, West Lafayette, IN 47907.
Purdue University Agricultural Experiment Station Journal Series Article No. 6821.
Accepted for Publication 14 October 1977.

ABSTRACT

KUHN, R. C., H. W. OHM, and G. E. SHANER. 1978. Slow leaf-rusting resistance in wheat against twenty-two isolates of Puccinia recondita. Phytopathology 68: 651-656.

In previous studies, a single isolate of *Puccinia recondita* developed more slowly on winter wheat cultivars Purdue 6028A2-5-9-6-1 (P6028) and Suwon 85 than on Suwon 92 and Monon. In this study, we measured the development of 22 isolates of *P. recondita* on these four cultivars in a growth chamber to test the race nonspecificity of the slow leaf-rusting resistances of P6028 and Suwon 85. For a given isolate of the pathogen, only cultivars that developed a susceptible reaction type were compared. Thus, the development of five isolates on P6028 and 21 isolates on Suwon 85 was compared to their development on Monon and Suwon 92. For all five isolates on P6028, and for 17 isolates on Suwon 85, the latent period was longer, a lower percentage of infection sites developed into pustules, there were fewer pustules per unit area of leaf, and pustules were smaller at 10-14 days after inoculation than on Monon or Suwon 92. The other four isolates were exceptions to these trends because of greater resistance to them by Monon and Suwon 92. The development of these four isolates on Suwon 85 was similar to the development of the other 17 isolates on this cultivar. Final pustule size was similar on all cultivars, although pustules reached this size on P6028 and Suwon 85 later than on Monon and Suwon 92. As measured in this study, slow leaf-rusting is race-nonspecific and should be long lasting.

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

Increased awareness of the short-lived nature of most immune-type resistance to plant disease has led to greater interest in other forms of resistance. Resistance expressed as a slow development of disease caused by the rust fungi has been found in the cereals (2, 6, 7, 11, 13, 14, 16) and it has been called slow-rusting (2).

Slow-rusting involves one or more of the following restrictions on the pathogen: (i) decreased frequency of penetration, (ii) slower invasion of host tissue, (iii) longer latent period, (iv) smaller pustules, (v) fewer pustules, (vi) lower sporulation rate, and (vii) shorter infectious period (3, 5, 6, 7, 8, 11, 13, 16, 17, 20).

Winter wheat cultivar Suwon 85 and breeding line P6028 exhibit slow leaf-rusting resistance against *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* (13). We expect that this resistance will delay development of the rust in the field long enough so that yield loss will not be significant. To remain useful for many years, this resistance must be effective against all races of *P. recondita*. Therefore, we investigated the slow leaf-rusting resistances in P6028 and Suwon 85 to determine if they are race-nonspecific, that is, general resistance.

MATERIALS AND METHODS

Twenty-two isolates of *P. recondita* were used (Table 1). Eleven of these were single-pustule isolates from cultures collected in Indiana between 1952 and 1974. The other eleven isolates were obtained from L. E. Browder (U.S. Department of Agriculture, Kansas State University, Manhattan). The development of these isolates on the slow leaf-rusting wheat (*Triticum aestivum* L. em. Thell) cultivars Suwon 85 (P.I. 157600) and Purdue 6028A2-5-9-6-1 (P6028) was compared with their development on Monon (C.I. 13278) and Suwon 92 (C.I. 12666), which do not exhibit slow leaf-rusting resistance. Plants of each of the four cultivars were vernalized for 70 days at 2.5 C and then grown in pots in the greenhouse. Planting was staggered to insure that all cultivars would be in about the same growth stage for inoculation. Plants were inoculated on the adaxial surface of the flag leaf in the early boot stage with 3 mg of spores in a settling tower (4). The tower shutter was left closed for 10 sec to collect spore clumps and then left open 3 min to allow spores to settle on the leaves. Each inoculation included four plants of each cultivar. Plants were placed around the tower in groups of four, with one plant of each cultivar in each group. Two inoculations were made for each of the 22 isolates. Inoculum of each isolate was stored at −80 C and heat-shocked for 5 min at 42 C prior to use. After inoculation, the plants were sprayed with a mist of water and placed in a plastic enclosure in the greenhouse for about 16 hr (overnight), then were transferred to a growth chamber and maintained at 18-21 C with light supplied at about 250 microeinsteins cm^{-2} sec^{-1} in 12-hr photoperiods. Experiments were carried out in four sets. The time period from transplanting into pots until all data were collected for each set was: September-December 1975; January-April 1976; August-November 1976; and January-April 1977. Not all isolates of *P. recondita* were

00032-949X/78/000 107$03.00/0

included in each set of experiments.

Each day from the 6th to the 18th day after inoculation, the percentage of visible infection sites (flecks) that had developed into pustules on each leaf was estimated by holding the leaf at an angle to the light so that both flecks and pustules could be seen. Pustules were counted only if the infection was light or a low percentage of infection sites developed into pustules. For each day, the percentage of flecks that had erupted into pustules on a leaf in the preceding 24 hr was multiplied by the number of days after inoculation. These were summed over all days and the resulting weighted sum was the latent period. The percentage of flecks that had developed into pustules by the 18th day was used as 100% for latent period calculations, and percentages on previous days were adjusted accordingly.

Average pustule size was estimated with a scale (Fig. 1) that was held next to the leaf. In the first set of experiments, pustule size was estimated only after most of the pustules had erupted on a leaf. In the other three sets of experiments, pustule size was estimated every 2nd day, starting on the 7th to 9th day after inoculation. These data were converted to average area per pustule. Average area per pustule was then regressed on days after inoculation to obtain the average rate of increase in pustule size per day. One linear regression coefficient was calculated from the pooled data of the four plants of a cultivar inoculated at the same time. These regression coefficients were analyzed to determine if average area per pustule increased at different rates on the four cultivars.

Six days after the maximum percentage of pustules had erupted, a grid with 10 equidistant openings was placed over the leaf and the number of pustules in each opening (30.2 mm^2) was counted. The total count for the leaf was converted to pustules/cm^2. Then the leaves were detached and taped to graph paper; color slide photographs were taken, and the leaves were dried and preserved. To obtain a more accurate estimate of average final pustule size, we projected the color slides to a known magnification, placed an enlarged version of the pustule size scale under the projected image, and compared 20 pustules per leaf with the ellipses on this scale. The areas of the 20 pustules were averaged for each leaf.

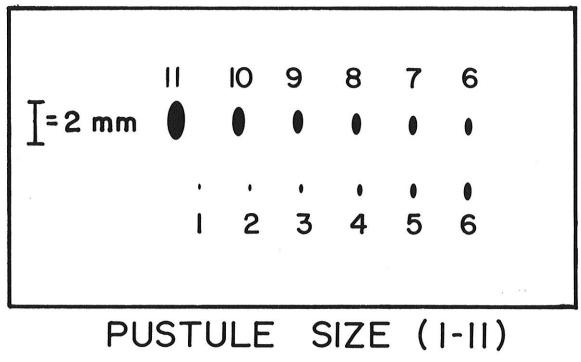

Fig. 1. Scale for estimation of wheat leaf-rust (*Puccinia recondita*) pustule size. Size 1 = 0.03 mm^2 and size 11 = 1.14 mm^2.

TABLE 1. Isolates of *Puccinia recondita* and their avirulence/virulence formulae[a]

Isolate identification number	Purdue culture number	Formula[a]
1[b]	659-1	1, 2a, 2b, 9, 11, 19 / 2c, 2d, 3
2	672-1	2b, 2c, 9, 11, 19 / 1, 2a, 2d, 3
3	7434-1-1T	1, 2a, 11, 19 / 2b, 2c, 2d, 3, 9, 10
4	5228-4-4-1-1-2	9, 19 / 1, 2a, 2b, 2c, 2d, 3, 11
5	534-1-1-1	2b, 2c, 9, 11, 19 / 1, 2a, 2d, 3
6	746	2a, 9, 11, 19 / 1, 2b, 2c, 2d, 3
7	682	1, 2a, 2b, 2c, 2d, 9, 19 / 3, 11
8	691	2b, 2c, 3, 9, 11, 19 / 1, 2a, 2d
9	673-2	2b, 2c, 9, 11, 19 / 1, 2a, 2d, 3
10	662-1-1	1, 2a, 2b, 2c, 2d, 9, 19 / 3, 11
11	672-3	2b, 2c, 9, 19 / 1, 2a, 2d, 3, 11
12	6718	9, 19 / 1, 2a, 2b, 2c, 2d, 3, 11
13	751	2a, 2b, 2c, 2d, 9, 11 / 1, 3
14	752	3, 9, 11 / 1, 2a, 2b, 2c, 2d
15	753	3, 9, 11 / 1, 2a, 2b, 2c, 2d
16	754	9 / 1, 2a, 2b, 2c, 2d, 3, 11
17	755	1, 2a, 2b, 2c, 2d, 9, 11 / 3
18	757	1, 2a, 2b, 2c, 2d, 3, 9, 11 /
19	758	2a, 2b, 2c, 2d, 9, 11 / 1, 3
20	759	9, 11 / 1, 2a, 2b, 2c, 2d, 3
21	7510	1, 2a, 2c, 2d, 9, 11 / 2b, 3
22	7511	1, 2a, 2b, 2c, 2d, 3, 9, 11 /

[a]Numbers to the left of the slash are host resistance genes (12) effective against the *P. recondita* isolate; numbers to the right of the slash are ineffective resistance genes (9). Gene 19 was not tested against isolates 12-24. Gene 2d is not included in the Gene Catalogue (12) but refers to the resistance in cultivar Loros.

[b]Isolates 1-7 and 9-12 were collected in Indiana. Isolates 13-22 and 8 were provided by L. E. Browder, U.S. Department of Agriculture, Kansas State University, Manhattan.

For a given isolate of *P. recondita,* only cultivars that developed a susceptible reaction type were compared, because a hypersensitive reaction precludes measurement of slow-rusting resistance. Cultivars P6028 and Monon expressed a hypersensitive reaction to isolate 8, and Suwon 92 and Suwon 85 expressed a mixed reaction type to this isolate. Thus, isolate 8 was not included in the comparisons. Cultivar P6028 showed a susceptible reaction type only to isolates 1, 3, 6, 9, and 12.

Data were analyzed in a split-plot design. The linear model for the analysis of variance was:

$$Y_{jklm} = \mu + B_j + I_k + \delta_{(jk)} + C_l + (IC)_{kl} + \theta_{(jkl)} + S_{(jk)m} + (SC)_{(jk)lm} + \epsilon_{(jklm)}$$

With j = 1, 2 blocks (sets of experiments); k = 1,2,..., i isolates of *P. recondita*; l = 1, 2, ..., c wheat cultivars; and m = 1, 2, 3, 4 sectors (the four groups of four plants in the settling tower). A whole plot in the analysis was one inoculation (the 16 plants that were inoculated at one time). There were two inoculations for each isolate and these served as replications. The subplots were the individual plants. Sectors were nested within each whole plot. The purpose of including sectors as a factor in the analysis was to remove possible variation due to nonuniform deposition of spores on different sectors of the settling tower.

RESULTS

It was not possible to use sets as blocks in a combined analysis of variance of the data for all isolates, because not all isolates of *P. recondita* were included in each of the four sets of experiments. The data for all isolates could be combined in a single analysis of variance if isolates reacted the same no matter which set of experiments they were in. Analyses of the data for isolates that were common to different sets of experiments, using sets as blocks, showed that sets were not a significant source of variation ($P = 0.25$) for latent period, for pustules per unit area of leaf, or for percentage of infection sites that developed into pustules. Thus, sets were ignored as a source of variation, and the data for all isolates were included in a combined analysis of variance for each of these variables. In some of the analyses, sets were a significant source of variation for pustule size at 10-14 days after inoculation and for final pustule size. However, the conclusions from analyses of groups of isolates with sets as blocks were the same as the conclusions from a single analysis of the combined data of all isolates for each of these two variables. Therefore, the combined analyses

TABLE 2. Leaf-rust development on slow- (P6028 and Suwon 85) and fast- (Monon and Suwon 92) rusting winter wheat cultivars averaged for the indicated isolates of *Puccinia recondita*

P. recondita isolate numbers	Cultivar	Latent period (days)	Pustules (%)[a]	Pustules (no./cm²)	Pustule size 10-14 Days (1-11)[b]	Pustule size Final[c] (mm²)
A. 1, 3, 6, 9, 12	Monon	6.8[d] A	100 A	55 A	7.0 A	0.36 A
	Suwon 92	7.3 A	100 A	52 AB	7.0 A	0.34 A
	Suwon 85	11.0 B	92 B	42 BC	5.0 B	0.41 A
	P6028	11.0 B	86 B	37 C	4.4 B	0.34 A
	S.E.	0.2		4	0.4	0.04
B. 1-7, 9-22	Monon	7.6 A	94 A	36 A	6.5 A	0.34 A
	Suwon 92	8.0 B	86 B	32 AB	6.6 A	0.33 A
	Suwon 85	10.1 C	77 C	30 B	5.6 B	0.39 A
	S.E.	0.1		2	0.1	0.02
C. 1-7, 9-13, 16, 17, 19, 20, 21	Monon	7.3 A	97 A	38 A	6.7 A	0.36 A
	Suwon 92	7.7 B	99 A	37 A	6.5 A	0.33 A
	Suwon 85	10.0 C	80 B	30 B	5.6 B	0.40 A
	S.E.	0.1		2	0.1	0.02
D. 14, 15, 18, 22	Monon	8.5 A	81 A	27 A	5.8 AB	0.27 A
	Suwon 92	9.2 A	34 C	5 B	6.7 A	0.34 A
	Suwon 85	10.3 B	64 B	28 A	5.5 B	0.34 A
	S.E.	0.2		3	0.3	0.04
Probability level		0.01	0.01	0.05	0.01	0.01

[a] Percentage of visible infection sites developed into pustules up to 18 days after inoculation. Arcsin transformation was made before analysis and mean separation but values shown are means of nontransformed data. Since the standard errors are not applicable to the nontransformed data they are not presented.

[b] Average pustule size at 10-14 days after inoculation. Scale numbers represent ellipses ranging in area from 0.03 mm² for size 1 to 1.14 mm² for size 11.

[c] Final average pustule size reached on each cultivar.

[d] Means in the same column of a comparison followed by the same letter are not significantly different by Duncan's new multiple-range test at the probability level indicated.

are presented here for simplicity. In the combined analyses whole plots were in a completely random design; thus, B_j and $\delta_{(jk)}$ in the above model would be combined into a new $\delta_{j(k)}$.

Except where stated otherwise, cultivars were a significant source of variation in the analyses of variance, and isolates and the interaction of isolates and cultivars were not significant sources of variation.

Latent period.—On the average, the latent period for P6028 was about 1.5 times as long (Table 2, Part A) and for Suwon 85 about 1.3 times as long (Table 2, Part B) as the latent period for Monon and Suwon 92. There was a significant interaction between cultivars and isolates in the analysis for latent period of the 21 isolates of *P. recondita* on Monon, Suwon 92, and Suwon 85. Therefore, the latent periods of each isolate on these three cultivars were compared (Fig. 2). The latent period was shorter on Monon and Suwon 92 than on Suwon 85 for each of the 21 isolates for which these cultivars could be compared. However, the latent periods of isolates 14 and 15 on Monon and isolates 15, 18, and 22 on Suwon 92 were not significantly shorter than their latent periods on Suwon 85. This is because these isolates had a longer latent period than other isolates on Suwon 92 and Monon, and not because they had a shorter latent period than other isolates on Suwon 85 (Fig. 2). Readings of latent period were difficult to make for isolates 14, 15, 18, and 22, because there were so few pustules per leaf, particularly on Suwon 92.

Percentage of infection sites that developed into pustules.—With most isolates, more than 90% of the visible infection sites developed into pustules on Monon and Suwon 92. In contrast, less than 90% of the visible infection sites developed into pustules on Suwon 85 and P6028. Exceptions to this were that only 65% of the visible infection sites developed into pustules on Monon when it was inoculated with isolate 14 or 15, and only 20-40% of the infection sites developed into pustules on Suwon 92 when it was inoculated with isolate 14, 15, or 22. Also, more than 90% of the infection sites developed into pustules when P6028 was inoculated with isolate 3 and when Suwon 85 was inoculated with isolate 3, 6, 12, 18, or 19.

On the average, a significantly lower percentage of visible infection sites developed into pustules on P6028 (Table 2, Part A) and Suwon 85 (Table 2, Part B) than on Monon or Suwon 92. However, isolates and the isolate by cultivar interaction were significant sources of variation in the comparison of Suwon 85 with Monon and Suwon 92 that involves 21 isolates. This interaction was largely caused by isolates 14, 15, 18, and 22 for which a low percentage of infection sites developed into pustules on Monon or Suwon 92 (Table 2, Part D). When these isolates were removed from the analysis (Table 2, Part C) the isolate by cultivar interaction was not significant.

Pustules per unit area of leaf.—The isolates of *P. recondita* produced fewer pustules per unit area of leaf on P6028 than they produced on Monon or Suwon 92 (Table 2, Part A). In the analysis involving 21 isolates (Table 2, Part B), fewer pustules per unit area of leaf were produced on Suwon 85 than on Monon, but the difference between Suwon 85 and Suwon 92 was not significant. In this analysis, isolates and the isolate × cultivar interaction were significant sources of variation. Therefore, cultivar means for each isolate were compared. Only isolates 15 and 18 produced significantly fewer pustules per unit area of leaf on Suwon 92 than on Suwon 85. Isolates 14 and 22 produced few pustules per unit area of leaf on Monon, Suwon 92, and Suwon 85. When isolates 14, 15, 18, and 22 were removed from the analysis (Table 2, Part C) the isolate by cultivar interaction was not significant, and there were significantly fewer pustules per unit area of leaf on Suwon 85 than on Monon or Suwon 92.

Pustule size.—Pustules on Monon and Suwon 92

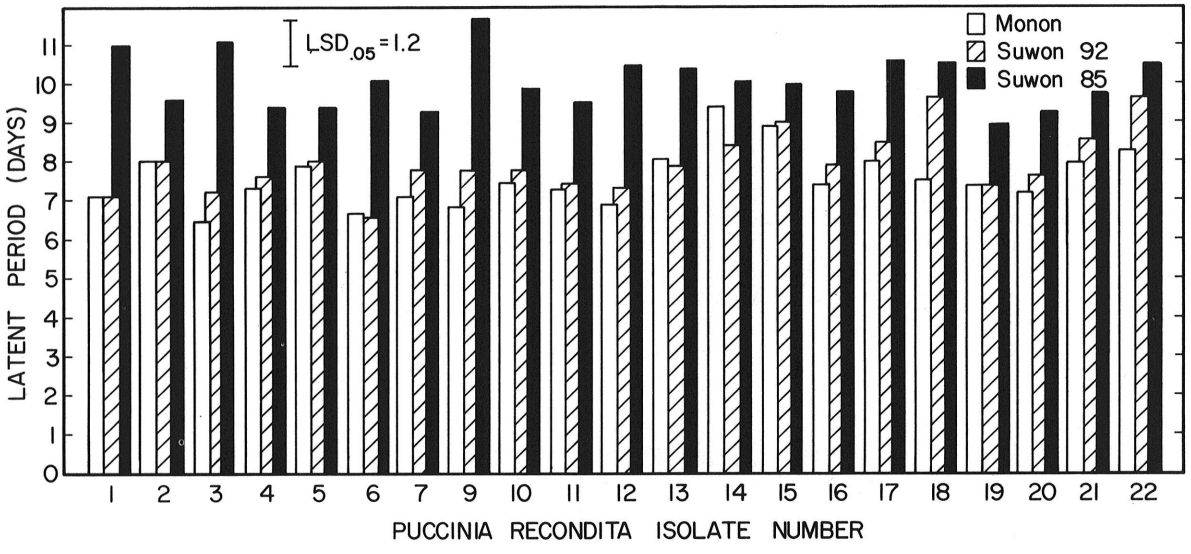

Fig. 2. Latent period of 21 isolates of *Puccinia recondita* on slow leaf-rusting cultivar Suwon 85 compared with fast leaf-rusting cultivars Monon and Suwon 92. Each bar is the average of seven or eight plants except that there were only six observations for Suwon 92 with isolates 1 and 6.

reached maximum size 10-14 days after inoculation. At this time, pustules were larger on Monon and Suwon 92 than on P6028 (Table 2, Part A) or on Suwon 85 (Table 2, Part B). After this time, pustules on P6028 and Suwon 85 continued to increase in size until the final size of pustules on these cultivars was not significantly different from the final size of pustules on Monon or Suwon 92 (Table 2, Parts A and B).

When pustule size was not measured until the 9th day after inoculation, the calculated rates of increase in pustule size on Monon and Suwon 92 were not significantly different from zero. These rates were not included in comparisons since they were underestimated compared to measurements which were started on the 7th or 8th day. Thus, the average rate of increase in pustule size could be compared on all four cultivars for only three isolates and on Monon, Suwon 92, and Suwon 85 for 12 isolates. Pustules increased in size at an average rate of 0.026, 0.029, 0.026, and 0.017 mm^2 per day on Monon, Suwon 92, Suwon 85, and P6028, respectively. The rates were not significantly different for the four cultivars.

DISCUSSION

To be long-lasting, disease resistance must be effective against all variants of a pathogen; i.e., it must be general rather than specific resistance (1). In an analysis of variance to compare the resistance of several host cultivars against several races of a pathogen, a significant mean square for cultivars implies that the cultivars differ in general resistance and a significant mean square for the interaction between cultivars and races implies that the cultivars differ in specific resistance (21). This interaction either can be caused by variation in the magnitude of the differences between cultivars or by reversals in the ranking of the cultivars with different races.

Cultivars were a significant source of variation in all analyses except for the analyses of final pustule size and rate of increase in pustule size. Significant interactions between cultivars and isolates of *P. recondita* occurred only in the comparisons of Suwon 85 with Suwon 92 and Monon. These interactions were caused largely by the unusual reaction of Monon or Suwon 92 to isolates 14, 15, 18, and 22. The resistance of Suwon 85 to these isolates was the same as its resistance to other isolates, but Monon or Suwon 92 showed greater resistance to these four isolates than to other isolates. Thus, the slow leaf-rusting resistances of Suwon 85 and P6028 were effective against all isolates tested, but Monon and Suwon 92 showed specific resistance to some isolates. This agrees with other studies that have shown slow stem-rusting resistance in *Avena sterilis* and wheat and slow leaf-rusting resistance in barley to be effective against all isolates of their respective pathogens that were tested (15, 19, 20, 22).

The rate of increase in pustule size was similar on all four cultivars. Therefore, differences between cultivars for average pustule size 10-14 days after inoculation were probably caused by differences in latent period between cultivars. That is, pustules on the fast-rusting cultivars were probably larger at 10-14 days after inoculation because they erupted sooner than pustules on the slow-rusting cultivars.

A lower percentage of infection sites that develop into pustules would lead to a lower number of pustules per unit area of leaf. For some isolates, the differences between cultivars for pustules per unit area of leaf were greater than could be explained by differences in the percentage of visible infection sites that developed into pustules. This implies that some mechanism in the slow-rusting cultivars interfered with the fungus before it could form visible infection sites. This could be caused by differences in penetration, which was shown by Romig (17) to be a mechanism of resistance in some slow sleaf-rusting wheats.

This study provides evidence that the slow leaf-rusting resistances in P6028 and Suwon 85 are general resistances. The final test of any resistance, however, is whether it will remain effective when it is spread over large geographical areas for many years (1). Cultivar P6028 obtained its slow-rusting resistance from Knox. Knox was released in 1953 with hypersensitive resistance to leaf-rust derived from cultivar Chinese Spring (13). From 1961 to 1965 this hypersensitive resistance was gradually overcome by new races of *P. recondita* (1). Knox, however, continued to show good resistance to leaf rust because of its slow-rusting, and this protected it in commercial fields over millions of hectares until Knox was replaced by cultivars with higher yields in the early 1970's. The slow-rusting resistance of Red Rustproof oats has maintained its effectiveness for more than 20 years (10, 11). Resistance expressed as slow development of late blight on the potato also has been shown to be long lasting (1, 18). The evidence to date justifies breeding more cultivars with slow-rusting resistance. If the results of this study are upheld by further experience, then slow leaf-rusting resistance should play an important role in protecting future wheat crops from losses due to leaf rust.

LITERATURE CITED

1. CALDWELL, R. M. 1968. Breeding for general and/or specific plant disease resistance. Pages 263-272 *in* K. W. Shepherd, ed. Proc. 3rd Int. Wheat Genet. Symp., Canberra, Australia. 479 p.
2. CALDWELL, R. M., J. J. ROBERTS, and Z. EYAL. 1970. General resistance ("slow rusting") to Puccinia recondita f. sp. tritici in winter and spring wheats. Phytopathology 60:1287 (Abstr.).
3. CLIFFORD, B. C. 1972. The histology of race non-specific resistance to Puccinia hordei Otth. in barley. Proc. Eur. Mediterr. Cereal Rusts Conf., Prague, Czechoslavakia 1:75-79.
4. EYAL, Z., B. C. CLIFFORD, and R. M. CALDWELL. 1968. A settling tower for quantitative inoculation of leaf blades of mature small grain plants with urediospores. Phytopathology 58:530-531.
5. HAYDEN, E. B. 1956. Differences in infectability among spring wheat varieties exposed to spore showers of race 15B of Puccinia graminis var. tritici. Phytopathology 46:14 (Abstr.).
6. HEAGLE, A. S., and M. B. MOORE. 1970. Some effects of moderate adult resistance to crown rust of oats. Phytopathology 60:461-466.
7. KOCHMAN, J. K., and J. F. BROWN. 1975. Development of the stem and crown rust fungi on leaves, sheaths, and peduncles of oats. Phytopathology 65:1404-1409.
8. KOCHMAN, J. K., and J. F. BROWN. 1975. Host and

environmental effects on post-penetration development of Puccinia graminis avenae and P. coronata avenae. Ann. Appl. Biol. 81:33-41.
9. LOEGERING, W. Q., and BROWDER, L. E. 1971. A system of nomenclature for physiologic races of Puccinia recondita tritici. Plant Dis. Rep. 55:718-722.
10. LUKE, H. H., R. D. BARNETT, and P. L. PFAHLER. 1975. Inheritance of horizontal resistance to crown rust in oats. Phytopathology 65:631-632.
11. LUKE, H. H., W. H. CHAMPMAN, and R. D. BARNETT. 1972. Horizontal resistance of Red Rustproof oats to crown rust. Phytopathology 62:414-417.
12. MC INTOSH, R. A. 1973. A catalogue of gene symbols for wheat. Pages 893-937 *in* E. R. Sears and L. M. S. Sears, eds. Proc. 4th Int. Wheat Genet. Symp., Columbia, Missouri. 955 p.
13. OHM, H. W., and G. E. SHANER. 1976. Three components of slow leaf-rusting at different growth stages in wheat. Phytopathology 66:1356-1360.
14. PARLEVLIET, J. E. 1975. Partial resistance of barley to leaf rust, Puccinia hordei. I. Effect of cultivar and development stage on latent period. Euphytica 24:21-27.
15. PARLEVLIET, J. E. 1976. Evaluation of the concept of horizontal resistance in the barley/Puccinia hordei host-pathogen relationship. Phytopathology 66:494-497.
16. PARLEVLIET, J. E., and A. VAN OMMEREN. 1975. Partial resistance of barley to leaf rust, Puccinia hordei. II. Relationship between field trials, micro plot tests and latent period. Euphytica 24:293-303.
17. ROMIG, R. W. 1957. Stomatal exclusion of leaf rust of wheat, Ph.D. Thesis. Purdue University, Lafayette, IN. 106 p.
18. SIMONS, M. D. 1972. Polygenic resistance to plant disease and its use in breeding resistant cultivars. J. Environ. Qual. 1:232-240.
19. SOUTHERN, J. W., and R. D. WILCOXSON. 1976. The stability of the slow rusting character of nine spring wheat cultivars. Proc. Am. Phytopathol. Soc. 3:205 (Abstr.).
20. SZTEJNBERG, A., and I. WAHL. 1976. Mechanisms and stability of slow stem rusting resistance in Avena sterilis. Phytopathology 66:74-80.
21. VAN DER PLANK, J. E. 1968. Disease resistance in plants. Academic Press, New York and London. 206 p.
22. WILCOXSON, R. D., B. SKOVMAND and A. H. ATIF. 1975. Evaluation of wheat cultivars for ability to retard development of stem rust. Ann. Appl. Biol. 80:275-281.