New Sources of Slow Leaf Rusting Resistance in Wheat

Gregory Shaner and Robert E. Finney

Associate professor and research associate, Department of Botany and Plant Pathology, Purdue University, West Lafayette, IN 47907.
The authors thank Wayne Austin for technical assistance and the Indiana Crop Improvement Association for partial support of this work.
Purdue University Agricultural Experiment Station Journal Series Article 7914.
Accepted for publication 3 June 1980.

ABSTRACT

SHANER, G., and R. E. FINNEY. 1980. New sources of slow leaf rusting resistance in wheat. Phytopathology 70:1183-1186.

Three wheat cultivars were selected from the 1976 International Winter Wheat Rust Nursery because they had a low severity of leaf rust coupled with a compatible infection type. In subsequent inoculations with *Puccinia recondita* in the greenhouse, the latent period was longer, and uredinia were smaller and fewer compared to susceptible cultivars. The mean latent period on CI 13227 was twice as long as that on Monon. In hill plots in the field, leaf rust developed more slowly on cultivars that showed longer latent periods and smaller and fewer uredinia in greenhouse inoculation experiments. The area under the disease progress curve in the field was correlated with that mathematically predicted from the levels of components of slow rusting measured in the greenhouse. CI 13227 has the highest level of slow leaf rusting resistance we have yet found.

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

There are only a few wheat cultivars reported to have slow leaf rusting resistance (1,3,9,14–16). These cultivars were first suspected of having slow rusting resistance because they had low severities of rust in field plots or breeding nurseries but had compatible infection types. Their slow rusting was confirmed in experiments conducted in the field or greenhouse. In none of these cases were the slow rusting wheats selected by screening extensive germplasm collections specifically for slow rusting. It is quite likely that many wheats among various germ plasm collections may have slow rusting resistance that has remained undetected.

In an attempt to find additional cultivars with slow leaf rusting resistance for use in our breeding program we selected five lines from the 1976 International Winter Wheat Rust Nursery (IWWRN) that had a low severity of leaf rust at the end of the season but a compatible infection type and that were adapted in other respects. From each line showing these traits we selected three heads for evaluation in the greenhouse. We report here the degree of slow leaf rusting in three of these lines, which is greater than any we have previously found.

MATERIALS AND METHODS

Greenhouse. All plants used in these experiments were vernalized in a dimly lighted cold room (3 C) for 65 days and then transplanted individually into 10-cm-diameter plastic pots containing a standard greenhouse soil mix. Natural daylight was supplemented with fluorescent light (2×10^4 ergs $\cdot$ cm^{-2} $\cdot$ sec^{-1}) for 16 hr per day. When plants were in the boot stage of development, the adaxial surface of the flag leaves was inoculated in a settling tower (2) with 3 mg of urediniospores of *Puccinia recondita* Rob. ex. Desm. This quantity of deposited inoculum is equivalent to ~340 urediniospores per square centimeter of leaf. In some experiments *P. recondita* culture 659-1 was used and in others 7434-1-1T was used. These single-uredinial cultures have been previously described (6). Both cultures were virulent toward the wheat cultivars used in these experiments. Inoculated plants were incubated overnight in a moist chamber, which maintained a fine film of moisture on the leaves, and then placed on greenhouse benches. Temperatures in the greenhouse ranged 20–26 C. Within each experiment the cultivars were arranged in the settling tower and subsequently in the greenhouse in a randomized block design, with four replications.

Erupted uredinia on each leaf were counted beginning 6 days after inoculation, as previously described (13). Size of uredinium was measured either by direct comparison with a series of ellipses of known size or by measurement of length and width with an ocular micrometer. In some experiments urediniospore production was measured by harvesting spores directly into a 0.1% Tween-80 solution with cyclone spore collectors. Spore density in the suspension was calculated from counts made with a hemacytometer. Using this value, the total volume of suspension, and the total number of uredinia from which the spores were collected, we calculated the number of spores produced per uredinium per day (13).

We calculated latent periods differently than reported previously (9,13). The probit of the proportion of uredinia erupted is a linear function of days after inoculation (11). From the slope and intercept of this line one can calculate T_{50}, the day by which 50% of the uredinia have erupted. T_{50} is analogous to ED_{50} or LD_{50} of toxicology. T_{50} was calculated for each inoculated plant, and genotype means were compared by analysis of variance.

Altogether, eight experiments were conducted during a 3-yr period. All of the experiments included Monon, the fast-rusting control cultivar. The known slow rusting wheats Suwon 85 and Purdue breeding line P6028A2-5-9-6-1 (P6028) and lines selected from the IWWRN that appeared to have slow rusting potential were included in various experiments. Each experiment was analyzed independently and data from all experiments involving common genotypes were pooled and analyzed as well.

Field experiment. Ten cultivars and breeding lines were sown in hill plots of five seeds per hill and with the hills spaced 60 cm apart in a randomized design at the Purdue Agronomy Farm on 2 October 1978. On 2 May 1979 three tillers in each hill were inoculated by injecting an aqueous suspension of urediniospores of *P. recondita* culture 7434-1-1T into leaf whorls with a hypodermic syringe. The hills were observed daily after inoculation to determine the time required for uredinia to appear on inoculated leaves. Beginning 30 May 1979 mean rust severity (modified Cobb scale) on the flag leaf (F) and the leaf just below (F−1) were recorded each week for five culms per hill with the aid of standard drawings (Plant Pathology Laboratory, Herpenden, Herts, U.K., Lab Key No. 1-3-1). Apparent infection rates for plants in each hill were calculated as the regression coefficient of ln [Y/100−Y], where Y is modified Cobb percent rust severity, plotted against time in days. Using the slope and intercept of this regression line, a smooth disease progress curve (percent severity vs time) was generated. The area under this curve was calculated for the period from 10 days prior to 20 days after the beginning of anthesis.

0031-949X/80/12118304/$03.00/0

RESULTS

Greenhouse experiments. In the initial greenhouse experiment, the suspected slow rusting wheats were inoculated at the four- or five-leaf stage by shaking urediniospores over them. Only the infection type was recorded following this inoculation. There was variation in infection type among progeny of single selected heads from some lines. Only plants with compatible infection types were used in subsequent slow rusting studies.

During a 3-yr period eight experiments were conducted involving three of the suspected slow leaf rusting lines from the 1976 IWWRN. Not every line was included in every experiment, so the experiments were pooled in various combinations to give the maximum number of comparisons for each line (Table 1). In four of the five pooled analyses Monon had significantly more uredinia per square centimeter of leaf than did any other cultivar (Table 1). In the other pooled analysis Monon had significantly more uredinia than did CI 10745 and CI 13227, but not significantly more than Suwon 85 and P6028. Among the wheats selected for slow rusting there were no significant differences in number of uredinia. The rather large variation in uredinium numbers on both Monon and CI 13227 among comparisons reflects the large error variance in this component of slow rusting, despite carefully controlled inoculation. The frequencies of successful infection (final number of uredinia per urediniospore applied as inoculum) were as follows: Monon, 0.19; Suwon 85, 0.14; P6028, L574, and CI 13227, 0.13; CI 10745, 0.12.

The error variance associated with T_{50} was much lower than that for numbers of uredinia. Consequently, more significant differences among cultivars were revealed for this component of slow rusting. T_{50} for CI 13227 was more than twice T_{50} for Monon and was significantly greater than T_{50} for all other cultivars. L574 had a significantly greater T_{50} than did Suwon 85 and P6028, and CI 10745 had a significantly greater T_{50} than did P6028.

Uredinia were larger on Monon than on all other wheats except L574. This component of slow rusting showed more variation among replications than did T_{50} or uredinium number; consequently cultivar means for this parameter were not as clearly separated.

In four experiments, spore production was measured from 9 to 17 days after inoculation. Within an experiment, cultivar, and sampling day, spores from all replications were harvested into a single vacuum collector. Each day's collection per cultivar was treated as a replication for a pooled analysis of spore production data. Only uredinia that actually erupted on each day of spore collection were used in calculating spores produced per uredinium. Thus, differences in latent period did not influence the calculation of spore production capacity. *P. recondita* produced slightly (but nonsignificantly) fewer spores per uredinium on Suwon 85 and P6028 compared to the fast rusting wheat Monon (Table 2). It produced considerably fewer spores on CI 10745 and CI 13227. Spore production on L574, a wheat with a long latent period, was as great as on Monon.

Field experiment. There were some cultivars in the field experiment that were not included in the greenhouse studies. Vigo (CI 12220) and Fairfield (CI 12013) are later maturing cultivars of soft red winter wheat of a type grown ~25 yr ago. The late R. M. Caldwell considered them to be slow rusting (1). Selection 45 is a fast rusting line of this later maturity class. Purdue 65113, a breeding line with cultivar Bulgaria 88 in its pedigree, has shown an intermediate level of slow rusting in previous field studies (5). Suwon 92 is a fast rusting cultivar described previously (9).

With the hypodermic injection method of inoculation, the primary infection site on a leaf may be a small zone no more than 2 cm long or it may cover much of a leaf. Despite this variation, we inspected inoculated leaves at 8, 9, 12, and 13 days after inoculation and estimated the percent uredinia erupted. From these data we calculated T_{50} in the way described for the greenhouse experiments. The cultivars that had high T_{50} values in the greenhouse had similar T_{50}s in the field (Table 3). As in the greenhouse, CI 13227 had the longest T_{50}. The inoculated leaves were the third or fourth leaves below the flag leaf. At the time of inoculation the leaf below the flag leaf was one-third to one-fourth emerged. Inoculum for the flag leaves came from spores produced on lower leaves within the plot area.

Uredinia were found on flag leaves of Suwon 92, Monon, and Suwon 85 on 30 May. At the next observation time, 6 June, they were found on flag leaves of P6028, Vigo, Fairfield, Selection 45, and P65113. Uredinia were not found on flag leaves of CI 10745 and CI 13227 until the third observation time, 14 June. By 28 June disease severities were 98–100% on Suwon 92, Monon, Selection 45, P65113, and P6028.

Logit severity was regressed on time for each hill plot to calculate apparent infection rates. Of the 99 disease progress curves analyzed

TABLE 1. Pooled analyses of slow leaf rusting resistance components in six wheat cultivars

		Component of resistance[a]					
		Infection efficiency		Latent period		Uredinium size	
Comparison	Cultivar	No. of experiments	Uredinia per square centimeter of leaf	No. of experiments	T_{50} (days)	No. of experiments	Area (mm^2)
1	Monon	8	63 a	7	6.2 a	5	0.165 b
	CI 13227	8	45 b	7	12.8 b	5	0.112 a
2	Monon	6	57 a	5	6.4 a	3	0.166 b
	CI 10745	6	35 b	5	10.4 b	3	0.097 a
	CI 13227	6	40 b	5	12.5 c	3	0.109 ab
3	Monon	6	70 a	6	6.1 a	4	0.170 b
	L574	6	41 b	6	11.1 b	4	0.138 ab
	CI 13227	6	53 b	6	12.9 c	4	0.106 a
4	Monon	4	56 a	3	6.5 a	2	0.211 b
	P6028	4	42 ab	3	9.4 b	2	0.101 a
	Suwon 85	4	42 ab	3	10.3 bc	2	0.135 a
	CI 10745	4	33 b	3	10.6 c	2	0.122 a
	CI 13227	4	40 b	3	13.9 d	2	0.111 a
5	Monon	3	75 a	3	6.2 a	2	0.211 b
	P6028	3	53 b	3	9.1 b	2	0.101 a
	Suwon 85	3	51 b	3	9.9 c	2	0.135 a
	L574	3	50 b	3	11.3 d	2	0.174 ab
	CI 13227	3	57 b	3	13.6 e	2	0.111 a

[a] Within each comparison and component of resistance, means followed by a common letter do not differ significantly, $P = 0.05$ according to Duncan's New Multiple Range Test.

(there were only nine replications for CI 10745), only four regressions had coefficients of determination less than 0.9.

Because there was a range of 9 days in commencement of anthesis among cultivars, area under the disease progress curve (percent severity vs time) was calculated for a 30-day period of comparable plant development. Using any fixed calendar period for calculating area under the disease progress curve (AUDPC) would underestimate disease development on the later-maturing wheats. The 30-day period used to calculate AUDPC began at 10 days before commencement of anthesis, about the time flag leaves were fully emerged, and terminated when the grain was in the early dough stage of development.

There was a 14-fold difference in AUDPC between CI 13227 and Suwon 92 (Table 3). P65113 rusted no slower than did Monon, but Vigo and Fairfield did reveal an intermediate level of slow rusting. The slowest rusting cultivars were CI 10745 and CI 13227. The AUDPCs for these cultivars were not significantly different from those for Suwon 85 and P6028, because of the large contribution to error variance made by the fast rusting cultivars. A separate analysis of variance for these four slow rusting cultivars indicated that AUDPCs for CI 10745 and CI 13227 were significantly lower than those for the other two slow rusting cultivars.

High values of AUDPC were associated with high apparent infection rates, but the converse was not always true. For example, the apparent infection rate on P6028 was greater than that on Monon, nevertheless its AUDPC was less than one-third that for Monon. The two wheats with lowest AUDPC had the lowest apparent infection rates as well.

The correlation coefficient relating AUDPC to T_{50} measured in the greenhouse was −0.71 for the five cultivars in comparison 4 (Table 1). The plot of AUDPC vs T_{50} was actually more hyperbolic than linear.

Mean percent disease severities on flag leaves on 6 and 24 June reveal significant differences among cultivars but the rankings are not the same as for AUDPC (Table 3). The correlation coefficients between AUDPC and severity at days 45 and 51 are 0.72 and 0.84, respectively. The correlation between AUDPC and the sum of severities at these two dates is 0.85. All of these are statistically significant at $P = 0.05$.

Comparison of the field epidemics with simulated epidemics. The equations for integrating components of slow leaf-rusting resistance in wheat (12) were used to analyze the data from the present experiments. The variable λ in these equations is the proportion of spores produced that land on leaf tissue and cannot be measured in the greenhouse. To obtain a value of λ characteristic of the hill plot experiment, we modeled epidemics for Monon, using data from Tables 1 and 2, and "SLORUS" a computer program in Basic-Plus language that utilizes the equations of Shaner and Hess (12) to simulate an epidemic for some chosen number of days. The model was run using several values of λ until a disease progress curve was generated that approximated Monon's disease progress curve in the field experiment. A value of $\lambda = 0.035$ gave the best fit. This value was then used in simulations for the other cultivars.

AUDPC was calculated for the simulated epidemics over a 30-day period comparable to what was done for the field epidemics (Table 4). The correlation between the AUDPCs for the simulated epidemics and the field epidemics reported in Table 3 is 0.91. The model underestimated the amount of rust development on the four slow rusting cultivars. This underestimation is not surprising because the model does not allow for the intrusion of exogenous inoculum.

DISCUSSION

Three lines selected from the 1976 International Winter Wheat Rust Nursery proved to have higher levels of slow rusting resistance in greenhouse evaluations than we have previously encountered. Overall, CI 13227 possessed the highest level of this resistance. Infection efficiency was reduced, latent period was considerably longer, and uredinia were small and produced fewer spores compared to Monon.

At the time we selected these wheats in the field we had no information on their background. Subsequent investigation revealed that CI 13227 is a wheat developed at Purdue (Purdue 481A6-1-2) and is one of a group of wheats selected some years ago for slow rusting by R. M. Caldwell and submitted to the IWWRN. Its pedigree is Wabash//American Banner/Aniversario. It appears to be reasonably winterhardy under our conditions but requires more evaluation. CI 10745 is a club wheat from mainland China and appears to be not very winterhardy. The pedigree given in the

TABLE 2. Urediniospore production by *Puccinia recondita* on six winter wheat cultivars

Cultivar	Urediniospores produced[a] (no./uredinium/day)
Monon	207 a
L574	203 a
P6028	184 a
Suwon 85	155 ab
CI 10745	90 b
CI 13227	86 b

[a] Means followed by a common letter do not differ significantly, $P = 0.05$, according to Duncan's New Multiple Range Test.

TABLE 3. Leaf rust development on flag leaves of winter wheat in hill plots at Purdue University Agronomy Farm, 1979

Cultivar	Day of flowering[a]	AUDPC[b]	Apparent infection rate (per unit per day)	Severity[c] at day 45 (%)	Severity[c] at day 51 (%)	T_{50}[d] (days)
CI 13227	37	84 a	0.272 b	0.9 a	5.3 a	13.2
CI 10745	38	96 a	0.202 a	1.3 ab	5.2 a	10.7
Suwon 85	28	187 a	0.327 bc	23.1 f	28.3 b	9.4
P6028	28	226 a	0.439 e	24.8 f	87.5 e	10.5
Vigo	36	475 b	0.339 cd	8.0 cd	47.5 c	8.9
Fairfield	37	652 c	0.320 bc	12.5 de	64.9 d	8.3
P65113	35	819 d	0.396 de	19.1 e	87.1 e	9.8
Monon	31	883 d	0.408 e	77.6 g	99.5 f	7.8
Selection 45	36	937 d	0.447 e	22.8 f	91.5 e	7.8
Suwon 92	31	1,171 e	0.452 e	98.5 h	100.0 f	8.6

[a] Day 1 = 1 May.
[b] Area under the disease progress curve from 10 days before through 20 days after the beginning of anthesis.
[c] Mean separation is based on an analysis of data after the arcsin-square root transformation. Transformed means were converted back to percent severity for presentation in the table.
[d] Calculated from rate of eruption of uredinia on leaves inoculated by hypodermic injection. Within each column, means followed by a common letter are not significantly different, $P = 0.05$, according to Duncan's New Multiple Range Test.

TABLE 4. Simulted leaf rust epidemics on eight wheat cultivars differing in degree of slow rusting resistance

Cultivar	AUDPC[a]	Severity at early dough stage from simulation (%)	Severity at early dough stage from field[b] (%)
CI 13227	5	0.4	19
CI 10745	11	3	13
Suwon 85	38	5	43
P6028	55	8	60
Vigo	725	93	80
Fairfield	1,254	100	88
Monon	1,272	100	97
Suwon 92	1,171	100	100

[a] Area under the simulated disease progress curve.
[b] Calculated as Y in the equation $\ln [Y/100-Y] = bX + a$ in which Y = percent severity and X is 20 days after the beginning of anthesis. Values of b and a are from the regression of $\ln [Y/100-Y]$ on time using field data from the hill plot experiment.

IWWRN planting list for L574, a wheat from Louisiana, is Wakeland/Blueboy.

As in our previous studies of slow rusting in Suwon 85 and P6028 (6,13), we found that latent period was the component of resistance measured with least error. Because of this, and the fact that it can be estimated with reasonable accuracy by visual estimate of percent uredinia erupted, in contrast to actually counting uredinia erupted each day (5,9), we believe that this is the component of slow rusting most suited as a selection criterion in large scale greenhouse screening. Others also have reached this conclusion (4,8,9). T_{50} was significantly negatively correlated with AUDPC. Long latent period also was associated with small uredinia and lower infection efficiency. Of the five slow rusting wheats in this study, only L574 had uredinia not significantly smaller than those on Monon.

For analysis of the field hill plot data, we found AUDPC a more sensitive criterion than apparent infection rate. This has been noted previously (10,17). However, care must be used in calculation of AUDPC because the choice of time base can affect the interpretation of data. Because the severity of leaf rust on the flag leaf depends in part on how long that leaf has been exposed, we calculated AUDPC for a 30-day period adjusted for differences in date of anthesis among cultivars. When the coefficient of determination associated with the apparent infection rate is high, it is valid to use this rate to generate a smooth disease progress curve for some chosen time interval from which AUDPC can be calculated.

Despite movement of inoculum between plots, large differences were detected in AUDPC among cultivars, indicating that hill plots would be useful in screening large populations for slow leaf rusting in winter wheat as Wilcoxson and his associates have found for spring cereals (3,4,17). Although percent severities 45 and 51 days after 30 April clearly revealed the slow rusting of CI 13227 and CI 10745, those values gave ambiguous information about some other cultivars. The slow rusting of later-maturing cultivars could be overestimated at the earlier observation whereas the slow rusting of early-maturing cultivars could be overlooked by a late observation. In a large breeding program it is difficult to inspect lines several times during a growing season. However, two rust severity readings separated by about 10 days, in conjunction with a heading date note, could be used to calculate the AUDPC for lines obviously not fully susceptible. No doubt, slow rusting wheats develop more rust in a hill plot experiment than they would in large isolated plots or fields because of interplot movement of inoculum. Kuhn (5) found a greater difference in leaf rust severity between Monon and Suwon 85 when these were grown in isolated 216 m^2 plots than we found in the hill plots. The difference was especially noticeable at distances of 4 m or more from the central point of inoculation. Although hill plots underestimate slow rusting, large differences still were apparent among cultivars. Even lines with a terminal severity of 30–40% may possess a useful level of resistance.

In addition to slow rusting, CI 13227 and CI 10745 displayed late rusting as described by Luke et al (7). First uredinia did not appear on flag leaves of these cultivars until several days later than they did on other cultivars of comparable maturity. Luke et al (7) hypothesized that late rusting oats required a higher level of inoculum before uredinia would form compared to susceptible oats. We have no data from greenhouse inoculations with very low inoculum levels that bear on this question. However, the very long latent perids on these cultivars could explain the delay in eruption of uredinia on the flag leaf in the field. In most experiments, the first uredinia did not erupt on CI 13227 until the 11th day after inoculation and those of CI 10745 until the 8th day.

Based upon the performance of CI 10745 and CI 13227 in the greenhouse and field, and the level of slow leaf rusting of Suwon 85 in large isolated plots (5), we believe that these first two wheats have adequate resistance to provide excellent protection from leaf rust in the northern soft red winter wheat region. L574 was not studied in the field but, based upon its performance in the greenhouse experiments, it also appears to have a useful level of resistance. L574 displayed the low infection efficiency and long latent period characteristic of slow-rusting wheats, but did not have uredinia smaller than those on Monon. CI 13227, CI 10745, and L574 are not closely related nor are they related to the previously described slow leaf rusting wheats Suwon 85 and P6028. This encourages us to think that slow rusting resistance genes will be found in other wheats representing diverse adaptations and market classes. A breeder might profitably screen wheats for slow rusting that are adapted to his own area to find parents for crosses before resorting to slow rusting parents that are completely unadapted to his area. Also, the diversity of plant types exhibiting slow rusting suggests that this resistance is not associated with any other specific undesirable traits such as late maturity, tallness, or weak straw. We did observe in the field that Suwon 85 is highly susceptible to speckled leaf blotch caused by *Mycosphaerella graminicola* (Fuckel) Schröter and to powdery mildew caused by *Erysiphe graminis* DC. However, the other slow-rusting wheats were not nearly as susceptible to these diseases.

LITERATURE CITED

1. 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. (Abstr.) Phytopathology 60:1287.
2. 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.
3. GAVINLERTVATANA, S., and R. D. WILCOXSON. 1978. Inheritance of slow rusting of spring wheat by *Puccinia recondita* f. sp. *tritici* and host parasite relationships. Trans. Br. Mycol. Soc. 71:413-418.
4. JOHNSON, D. A., and R. D. WILCOXSON. 1979. Inheritance of slow rusting of barley infected with *Puccinia hordei* and selection of latent period and number of uredia. Phytopathology 69:145-151.
5. KUHN, R. C. 1979. Genetics and epidemiology of slow leaf-rusting resistance in wheat. Ph.D. thesis, Purdue University, W. Lafayette, IN. 90 pp.
6. 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.
7. LUKE, H. H., R. D. BARNETT, and W. H. CHAPMAN. 1975. Types of horizontal resistance of oats to crown rust. Plant Dis. Rep. 59:332-334.
8. NEERVOORT, W. J., and J. E. PARLEVLIET. 1978. Partial resistance of barley to leaf rust, *Puccinia hordei* V. Analysis of the components of partial resistance in eight barley cultivars. Euphytica 27:33-39.
9. OHM, H. W., and G. E. SHANER. 1976. Three components of slow leaf-rusting at different growth stages of wheat. Phytopathology 66:1356-1360.
10. SHANER, G., and R. E. FINNEY. 1977. The effect of nitrogen fertilization on the expression of slow-mildewing resistance in Knox wheat. Phytopathology 67:1051-1056.
11. SHANER, G. 1980. Probits for analyzing latent period data in studies of slow rusting resistance. Phytopathology 70:000-000 (In press).
12. SHANER, G., and F. D. HESS. 1978. Equations for integrating components of slow leaf-rusting resistance in wheat. Phytopathology 68:1464-1469.
13. SHANER, G., H. W. OHM, and R. E. FINNEY. 1978. Response of susceptible and slow leaf-rusting wheats to infection by *Puccinia recondita*. Phytopathology 68:471-475.
14. STATLER, G. D., J. T. NORDGAARD, and J. E. WATKINS. 1977. Slow leaf rust development on durum wheat. Can. J. Bot. 55:1539-1543.
15. STATLER, G. D., J. E. WATKINS, and J. NORDGAARD. 1977. General resistance displayed by three hard red spring wheat (*Triticum aestivum*) cultivars to leaf rust. Phytopathology 67:759-762.
16. VERMA, M. M., J. KUMAR, and S. KOCHAR. 1975. Variability for horizontal resistance against brown rust (*Puccinia recondita* f. sp. *tritici*) in strains of *Triticum aestivum* L. and their progeny. Cereal Res. Comm. 3:149-162.
17. 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.