Expression of Adult Resistance to Stripe Rust at Different Growth Stages of Wheat

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ABSTRACT

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Stripe, or yellow, rust (caused by *Puccinia striiformis*) is a common disease of wheat in cool, humid climates. Genes that confer adult resistance to stripe rust are known to be present in high-yielding spring wheats (*Triticum aestivum*). However, it is not known when in the growth of the plant adult resistance is first expressed. The objectives of the study were to evaluate the expression of adult resistances at various growth stages in the greenhouse, and to assess the effect of such resistances on stripe rust development in the field. Eight wheat cultivars known to carry different levels of adult resistance and three susceptible cultivars were evaluated for resistance in the greenhouse at six growth stages (from seedling to anthesis), using a Mexican race of *P. striiformis*. Resistance was measured by infection type (IT) and latent period (LP). The cultivars were also evaluated in the field using the same race to determine disease progress. In all tests, Morocco was the most susceptible cultivar (IT 7 to 9, LP 11 to 13 days), followed by Avocet S (IT 6 to 9, LP 12 to 15 days) and Jupateco 73S (IT 6 to 9, LP 12 to 17 days). Seedling IT and LP for cultivars with adult resistance were similar to those of the susceptible cultivars (IT 6 to 8, LP 12 to 15 days). However, as plants grew, resistance increased and was expressed as lower IT and longer LP. The changes in IT displayed by HD2258 and PBW65 were the greatest; intermediate to low IT (2 to 3) were seen as early as the completion of tillering and changed to immunity (IT 0) at anthesis. Other cultivars with adult resistance, viz., Mexico 82, Pavon 76, Jupateco 73R, Apache 81, Anahuac 75 and Ciano 79, generally showed intermediate to moderately susceptible responses (IT 4 to 6) at growth stages later than tillering. The IT and LP displayed at anthesis by resistant cultivars were lowest and highest, respectively, indicating that adult resistance was best expressed at this growth stage. A strong negative rank correlation ($r = -0.939$, $P < 0.01$) between IT and LP at anthesis suggested that lower ITs of the cultivars were generally associated with longer LP. In the field study, HD2258 and PBW65 were highly resistant (relative AUDPC ≤5% of Morocco). Pavon 76 and Mexico 82 had acceptable resistance levels (relative AUDPC ≤20%), whereas other cultivars displayed moderate resistance levels (relative AUDPC 30 to 52%).

Stripe, or yellow, rust (caused by *Puccinia striiformis* Westend.) is a common disease of wheat in cool, humid climates. Use of genetic resistance is the most economical and environmentally benign method of disease control. Genes conferring seedling and adult resistances are known to occur in wheat (*Triticum aestivum* L.). Seedling resistance is usually race specific and can be recognized by its characteristic low infection type at all plant stages. Adult resistance can be either race specific or race nonspecific and is usually better recognized after the seedling stage (5). Although more than 20 genes for seedling resistance to stripe rust are currently known (3,10), most are ineffective due to the presence of corresponding virulence in the pathogen. Some known adult resistances that have remained durable appear to involve slow rusting mechanisms conferred by minor additive genes that may be temperature sensitive (1,4,7,8,11,14,15,17–20). Singh (19) recently reported that adult resistance gene *Yr18* is involved in durable resistance of several bread wheat cultivars, including the North American cultivar Anza. Utilization of durable resistance for the global control of stripe rust is a major objective of CIMMYT's bread wheat breeding program (16). Genes that confer adult resistance (including *Yr18*) are now known to be present in high-yielding spring wheats (19,20). However, it is not known when in plant development adult resistance is first expressed. The time when adult resistance is initiated could significantly affect grain yield, especially if expression is too late to check an early rust epidemic. Therefore, identifying the plant growth stages at which adult plant resistance is expressed could assist in developing cultivars that provide more effective disease control under various epidemic situations.

The objectives of this study were to evaluate the expression of adult plant resistance of eight bread wheats at various growth stages in the greenhouse, and to assess the effect of such resistance on stripe rust development in the field.

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MATERIALS AND METHODS

The host. Eleven spring bread wheats (Table 1) from Mexico, India, and Australia were selected for the study based on seedling and field reactions to stripe rust in previous studies. Morocco and Avocet S are highly susceptible to stripe rust as seedlings and adult plants in the field. Jupateco 73S is also susceptible at both stages; however, it is less susceptible in the field than Morocco. These three wheats were used as susceptible controls in all tests. The remaining eight cultivars were found to have different degrees of adult resistance to a Mexican race of *P. striiformis*.

Greenhouse studies. Two similar greenhouse experiments (inoculated dur-

Table 1. Wheat cultivars, country of origin, and previous (1992) seedling infection type (IT) and disease severity assessments in the field

Cultivar	Origin	Seedling IT[y]	Disease severity (%)[z]
HD2258	India	7 to 8	1
PBW65	India	7 to 8	1
Anahuac 75	Mexico	7 to 8	15
Pavon 76	Mexico	7 to 8	5
Mexico 82	Mexico	7 to 8	5
Jupateco 73R	Mexico	8	15
Apache 81	Mexico	8	20
Ciano 79	Mexico	7 to 8	20
Jupateco 73S	Mexico	8	60
Avocet S	Australia	8 to 9	100
Morocco	Australia	9	100

[y] ITs are based on a 0 to 9 scale (9) in which 7 = necrotic and/or chlorotic blotches or stripes with abundant sporulation; 8 = chlorosis behind the abundantly sporulating area; and 9 = abundant sporulation with no chlorosis or necrosis.
[z] Disease severities are based on the modified Cobb scale (13).

ing March and November 1994) were conducted to assess the cultivar's reactions to stripe rust at various growth stages. For each experiment, the design was a randomized complete block with three replicates. Each replicate (block) consisted of all the cultivars at six growth stages: (i) seedling, decimal growth stage 11 to 12 (21); (ii) tillering, 21 to 24; (iii) stem elongation, 31 to 32; (iv) booting, 39 to 41; (v) early heading, 49 to 52; and (vi) beginning of anthesis, 59 to 61. Ten seeds per cultivar were sown in 15-cm-diameter pots at 7-day intervals to obtain each growth stage in all cultivars for a single day of inoculation. Two weeks after each planting, plants were thinned to five healthy plants per pot. Before inoculation, unwanted tillers were also removed, with five tillers of similar growth stage retained per pot.

Each plant's fully unfolded uppermost leaf tip was marked with a marker and then uniformly inoculated with an isolate of race 14E14 (6) of *P. striiformis* by spraying urediniospores suspended in a lightweight mineral oil (Soltrol 170) at a concentration of 5 mg/ml. This race is virulent to resistance genes *Yr2, 3, 6, 7*, and A, and predominates in the Mexican highlands. After inoculation, plants were placed in a dew chamber overnight at 12 to 14°C, and then transferred to a greenhouse with temperatures of 15 to 22°C and 15 to 19°C, respectively, for the two experiments. Latent period (LP) and infection type (IT) were recorded for each of the inoculated leaves. LP was defined as the number of days from inoculation to the appearance of the first uredinium. Previous study at CIMMYT (2) has shown that appearance of the first uredinium correlates highly with LP50 (days to the appearance of 50% of the uredinia) and should be used because each infection site of *P. striiformis* can produce a linear series of uredinia, which complicates the estimation of LP50. IT was assessed 30 days after inoculation by means of a 0 to 9 scale (9).

Field studies. Each cultivar's field response to stripe rust was evaluated at CIMMYT's research station near Toluca (State of Mexico) during the 1994 season. Environmental conditions at this site favor the development of stripe rust. A randomized complete block design with three replicates was used. Seeds of each cultivar were sown in a 2-m paired row plot (20 cm between rows) with spacing of 55 cm between plots and a 1-m pathway. Each plot consisted of approximately 40 to 60 plants. The stripe rust epidemic was initiated by inoculating 4-week-old plants of Morocco, planted as hills in the pathway on one side of each plot. Race 14E14 was also used in the field study. Morocco and Avocet S were susceptible checks with the earliest and latest days to heading, respectively. Using the modified Cobb Scale (13), average disease severity on upper three leaves was first recorded 40 days after inoculation when the susceptible control had reached 60 to 80% disease severity. Five additional readings were taken at weekly intervals. The six disease ratings were used to calculate the area under the disease progress curve (AUDPC) using a computer program developed at CIMMYT. The relative AUDPC (percent) for each cultivar was calculated by dividing its actual AUDPC by Morocco's AUDPC.

Statistical analysis. Latent period for each cultivar were estimated by averaging the values of the five inoculated leaves per pot. For two cultivars, latent periods were not found (i.e., no uredinium formation) at certain growth stages. These cultivars were not included in the analysis of variance (ANOVA). A combined ANOVA was conducted using a mixed model in which experiments were random, and cultivars and growth stages were fixed. In the field, disease severities were estimated from the entire plot, and ANOVA was conducted for a randomized complete block design. Rank correlations were calculated for IT and LP at anthesis by using their means over the two experiments, and with the relative AUDPC in the field. Cultivars HD2258 and PBW65 were excluded in these calculations. An SAS computer program (SAS Institute, Cary, NC) was used for all analyses.

Table 2. Infection type (IT) ranges of 11 wheat cultivars inoculated with *Puccinia striiformis* race 14E14 at six growth stages and their comparisons in two experiments

		Post-seedling ITs[y]				
Cultivar	**Seedling IT**	**Tillering**	**Stem elongation**	**Booting**	**Heading**	**Anthesis**
Experiment 1						
HD2258	6 to 8[z]	4 to 5	2 to 3	0	0	0
PBW65	7 to 8	4 to 5	2 to 3	0	0	0
Mexico 82	6 to 8	6 to 7	4 to 5	4 to 6	4 to 5	3 to 4
Anahuac 75	6 to 8	6 to 7	4 to 5	4 to 5	4 to 6	4 to 5
Pavon 76	6 to 8	6 to 7	4 to 6	5 to 6	4 to 5	4 to 5
Apache 81	6 to 8	6 to 7	4	5 to 6	5 to 6	5 to 6
Jupateco 73R	7 to 8	6 to 7	4 to 6	4 to 6	4 to 5	4 to 5
Ciano 79	7 to 8	6 to 7	4 to 5	5 to 6	5 to 6	4 to 5
Jupateco 73S	7 to 9	7 to 8	6 to 7	7 to 8	7 to 8	7 to 8
Avocet S	7 to 9	6 to 8	6 to 7	7 to 8	8	8 to 9
Morocco	8 to 9	8 to 9	7 to 8	9	9	9
Experiment 2						
HD2258	6 to 7	4 to 6	3	3	2 to 3	0
PBW65	7 to 8	4 to 6	2 to 3	2 to 3	2 to 3	0
Mexico 82	6 to 7	6 to 7	4 to 6	5 to 6	4 to 6	4 to 5
Jupateco 73R	6 to 8	6 to 7	5 to 6	4 to 6	4 to 5	4 to 5
Pavon 76	7 to 8	6 to 7	5 to 7	4 to 6	4 to 6	4
Anahuac 75	7	6 to 7	4 to 6	5 to 6	5 to 7	4 to 6
Apache 81	6 to 8	6 to 7	4 to 6	6 to 7	4 to 7	5 to 6
Ciano 79	7 to 8	6 to 8	4 to 7	5 to 7	5 to 7	5
Jupateco 73S	7 to 8	7 to 8	6 to 7	6 to 7	7 to 8	6 to 8
Avocet S	7 to 9	6 to 8	6 to 8	7 to 8	7 to 8	7 to 8
Morocco	8 to 9	7 to 8	7 to 9	9	8 to 9	8 to 9

[y] ITs are based on a 0 to 9 scale (9) in which 0 = no visible symptom; 1 = necrotic and/or chlorotic flecks without sporulation; 2 = necrotic and/or chlorotic blotches or stripes without sporulation; 3 = necrotic and/or chlorotic blotches or stripes with trace sporulation; 4 = necrotic and/or chlorotic blotches or stripes with light sporulation; 5 = necrotic and/or chlorotic blotches or stripes with intermediate sporulation; 6 = necrotic and/or chlorotic blotches or stripes with moderate sporulation; 7 = necrotic and/or chlorotic blotches or stripes with abundant sporulation; 8 = chlorosis behind the abundantly sporulating area; and 9 = abundant sporulation with no chlorosis or necrosis.

[z] The IT range represents the lowest and highest readings for plants of a particular cultivar at a particular growth stage.

RESULTS AND DISCUSSION

Greenhouse studies. *IT.* Reactions ranging from moderately susceptible to susceptible (IT 6 to 9) were recorded for the susceptible controls (Morocco, Avocet S, and Jupateco 73S) at all growth stages, although the level of susceptibility varied slightly at certain growth stages (Table 2). The ITs of Avocet S and Jupateco 73S were generally rated lower than the IT of Morocco in both experiments because these two cultivars had some chlorotic blotches associated with moderate to abundant sporulation. Plants of other cultivars had their highest IT (mostly 6 to 8) at the seedling stage and were indistinguishable from Avocet S and Jupateco 73S. IT became lower as plants grew into post-seedling growth stages, and reductions of different degrees were observed (Table 2). Cultivars HD2258 and PBW65 showed intermediate reactions (mostly IT 4 to 5) at tillering, which changed to resistant reactions after tillering (IT 2 to 3), and reached immunity at anthesis in both experiments. ITs of the remaining six cultivars (Mexico 82, Pavon 76, Jupateco 73R, Apache 81, Anahuac 75, and Ciano 79) at tillering in general were similar to their seedling reactions (mostly IT 6 to 7), which varied within the moderately susceptible range. However, changes in intermediate levels of resistance (IT 4 to 6) were subsequently observed in most plants after tillering (Table 2).

Our results suggest that adult resistance to stripe rust may begin at mid tillering. As plants continue to develop, the change in IT can be slight or large, depending on gene effect and environmental factors. In cultivars that are highly resistant in the field, such as HD2258 and PBW65, expression may start even earlier (beginning of tillering). This agrees with the findings of Qayoum and Line (15) on winter wheat cultivars that carry genes conferring high-temperature, adult-plant resistance to stripe rust. In contrast, in six other cultivars that showed intermediate resistance levels, the expression of resistance as a reduction in IT initiated later, after tillering.

Cultivars Apache 81 and Ciano 79 had lower IT ratings at stem elongation than at subsequent stages. A similar tendency was also observed in the susceptible controls. It is not known why plants are less susceptible to stripe rust infection at stem elongation. A study of slow rusting resistance to wheat leaf rust by Ohm and Shaner (12) also indicated that plants at growth stages 30 to 39 had a longer latent period, smaller pustule size, and fewer pustules/cm^2 than plants at growth stages 40 to 67. In our greenhouse study, plants at the stem elongation stage (GS 31-32) had less stripe rust sporulation that was associated with extensive chlorotic and necrotic blotches. Moreover, the inoculated leaves also showed slight yellowing a few days after inoculation. This may have been due to stem elongation, which can cause plants to reallocate nutrients to fulfill their physiological needs. This translocation of nutrients may cause host and pathogen to compete for the supply of nutrients in green leaf tissues, critical for the survival and growth of obligate parasites such as rusts.

LP. LPs for Morocco were the shortest, averaging from 11 to 13 days at all growth stages in both experiments (Table 3). Compared with those of Morocco, LP variations were slightly larger for Avocet S (12 to 15 days) and Jupateco 73S (12 to 17 days) across all growth stages in both experiments. As plants grew, the LP for Jupateco 73S increased, especially in experiment 1, suggesting that it may carry resistance that slows down the establishment of stripe rust in host tissues. The LPs of the adult plant resistant cultivars at the seedling stage were generally similar to those of Avocet S and Jupateco 73S, but 1 to 3 days longer than that of Morocco. There was a tendency for LP to increase as plants developed. Deviation from the susceptible controls occurred mostly at tillering in experiment 1 and at stem elongation in experiment 2. Because uredinia did not develop on cultivars HD2258 and PBW65 after tillering in both experiments, their LPs at subsequent growth stages could not be estimated. Sporulation occurred in the remaining cultivars. ANOVA was conducted only for cultivars that sporulated at all growth stages. Significant differences were found among cultivars, growth stages, and cultivar × growth stage interaction (Table 4).

LP was also affected by environmental conditions, as evidenced by the significant differences detected for experiments, interactions between experiment and cultivar, and between experiment and growth stage (Table 4). These variations may be due mainly to greenhouse temperatures and day length. The first experiment was conducted in March, when days are longer and greenhouse daytime temperatures reached 22°C for short periods. Because the second experiment was carried out in November, when days are shorter, we were able to maintain greenhouse temperatures at 16 to 19°C.

Comparison of mean LPs among growth stages showed a significant ($P < 0.05$) increase in LP as plant growth advanced (Table 3). However, significant differences in mean LPs between seedling and tillering occurred only in experiment 1. Mean LPs at stem elongation, booting, and heading did not show significant differences. Mean LP was longest at anthesis and significantly different from that at tillering. In experiment 2, average LP did not increase significantly until anthesis. Ranking of post-seedling LP means showed that Jupateco 73R had a longer LP than other cultivars in both experiments. The ranking of the remaining cultivars varied between experiments. The adult plant resistance of Jupateco 73R is known to be conferred by the *Yr18* slow rusting gene (19).

The significant and high negative correlation coefficient ($r = -0.939$, $P < 0.01$) between the ranks of the cultivars for LP and IT suggests that cultivars with shorter latent periods generally had higher ITs. In the wheat-stripe rust pathosystem, genotypes with low ITs are usually associated with less sporulation and extensive chlorotic or necrotic blotches. In a recent study, Broers and Lopez-Atilano (2) found that a long LP was also associated with low infection frequency, short length of stripe, and low disease severity in the field.

Field observation. Stripe rust began developing early in the field and became severe. Differences in relative AUDPC and final disease severity (FDS) among cultivars were highly significant ($P < 0.001$). As expected, Morocco was the most susceptible cultivar in the experiment, displaying an FDS of 100% (Table 5). It was followed by Avocet S and Jupateco 73S, with relative AUDPCs of 88 and 83%, respectively, compared with Morocco's (100%); however, their FDSs were also 100%. HD2258 and PBW65 had the lowest relative AUDPCs (2 and 5%, respectively) and FDSs (8 and 10%, respectively). These two cultivars were also the most resistant in the greenhouse tests

Table 3. Mean latent period (LP) of 11 wheat cultivars inoculated with *Puccinia striiformis* race 14E14 at six growth stages and their mean comparisons in two experiments

		Post-seedling LPs					
Cultivar	**Seedling LP**	**Tillering**	**Stem elongation**	**Booting**	**Heading**	**Anthesis**	**Mean**
Experiment 1							
HD2258	12.7	21.0	...	...	...	...	...
PBW65	12.0	19.0	...	...	...	...	...
Jupateco 73R	12.1	16.3	20.7	17.8	21.9	23.6	20.1 a
Anahuac 75	12.6	17.8	18.7	19.2	19.3	24.3	19.9 a
Ciano 79	12.1	18.0	20.9	18.0	17.9	23.0	19.6 a
Mexico 82	12.0	18.9	19.5	18.2	18.9	21.3	19.4 a
Apache 81	13.2	18.3	22.9	18.8	18.1	18.5	19.3 a
Pavon 76	12.2	16.7	18.7	18.4	18.0	20.6	18.5 a
Jupateco 73S	12.0	15.0	16.7	15.3	16.7	15.9	15.4 b
Avocet S	12.3	14.5	14.9	13.6	14.8	13.4	14.2 bc
Morocco	10.7	13.6	13.0	11.2	11.7	13.2	12.5 c
Mean[y]	12.4 a[z]	17.7 b	20.1 bc	18.4 b	19.0 b	21.9 c	
Experiment 2							
HD2258	15.0	17.1	...	...	...	...	...
PBW65	12.9	16.6	...	...	...	...	...
Jupateco 73R	13.3	13.4	16.2	17.7	18.1	22.2	17.5 a
Pavon 76	13.8	13.4	15.1	15.7	16.0	20.7	16.2 ab
Mexico 82	14.1	15.8	15.3	14.5	15.4	19.1	16.0 abc
Apache 81	14.5	13.8	17.0	15.9	16.3	16.0	15.8 abc
Ciano 79	13.0	13.4	15.0	13.8	15.0	17.8	14.8 bcd
Anahuac 75	14.2	13.6	15.1	15.1	13.9	14.4	14.4 bcd
Jupateco 73S	12.7	12.4	14.9	13.1	13.5	14.4	13.7 bcd
Avocet S	12.9	13.4	14.7	12.3	13.1	12.8	13.3 cd
Morocco	12.0	12.2	12.9	12.1	13.0	12.8	12.6 d
Mean[y]	13.8 a[z]	13.9 a	15.9 ab	15.4 a	15.8 ab	18.4 b	

[y] Mean was calculated by averaging all resistant cultivars readings except for HD2258 and PBW65 (susceptible controls were excluded).

[z] Means within each experiment followed by different letters differ significantly at $P = 0.05$ (least significant difference tests).

(Tables 2 and 3). Pavon 76 and Mexico 82 had similar and acceptable slow rusting responses (relative AUDPCs 18 and 20%, respectively; FDS, 20%). Jupateco 73R also showed slow rusting behavior, but its final disease level was significantly higher ($P < 0.05$) than those of Pavon 76 and Mexico 82, and lower than those of Apache 81, Anahuac 75, and Ciano 79. There was a high positive correlation of the ranks of the cultivars for relative AUDPC with IT at anthesis ($r = 0.966$, $P < 0.01$) and a negative correlation of relative AUDPC with LP ($r = -0.892$, $P < 0.01$). This indicated that IT and LP assessed at the anthesis stage in the greenhouse may reflect rust development in the field, especially in the most resistant and susceptible cultivars. However, predicting field response under polycyclic disease conditions based on monocyclic greenhouse tests may not be valid. For example, although the postseedling IT and LP of Mexico 82, Pavon 76, and Jupateco 73R were not that different (Tables 2 and 3), these cultivars showed notable differences in field tests (Table 5).

Pavon 76 and Mexico 82 displayed adequate levels of slow rusting resistance with relative AUDPCs of 18 and 20%, respectively, and an FDS of 20%, whereas Jupateco 73R had a relative AUDPC of 30% and an FDS of 50%. This clearly indicates that rust development was much faster on Jupateco 73R. It is not known why Jupateco 73R's resistance was less effective than that of Pavon 76 and Mexico 82 under field conditions. The resistance genes that confer slow rusting in Pavon 76 and Mexico 82 are different from the *Yr18* gene present in Jupateco 73R (20). It is likely that different resistance genes affect stripe rust development differently in reducing number of infections, restricting rust colonization, and limiting growth of sporulating areas. These differences are difficult to distinguish by measuring IT or LP under monocyclic greenhouse conditions in cultivars carrying moderate resistance. Broers and Lopez-Atilano (2) have suggested that the resistance component that best reflects stripe rust development under field conditions is infection frequency.

Although race specificity of the resistance genes present in the studied cultivars is not known, the *Yr18* gene present in Jupateco 73R is known to confer durable resistance (19). Similarly, Singh and Rajaram (20) indicated that Pavon 76 may also carry durable yellow rust resistance, given that its moderate adult resistance has remained effective wherever it is grown. Resistances present in Mexico 82, Apache 81, Anahuac 75, and Ciano 79 had characteristics similar to those in Jupateco 73R and Pavon 76. If these resistances are controlled by different additive genes, it may be possible to combine them to achieve higher levels of adult resistance (20). Because only a few additive genes need to be combined to achieve high levels of stripe rust resistance (11,20), the selection methodology needed to generate such combinations in a breeding program should be straightforward. It will, however, be necessary to determine the genetic basis of resistance in the parents of the crosses, and the virulences needed to overcome the presence of any major or race-specific genes they possess. If these measures are taken, selection of low levels of disease in the presence of high inoculum load would ensure the accumulation of the necessary partially effective additive genes. The adult resistances of HD2258 and PBW65 may involve gene(s) of a hypersensitive nature that become effective in the early post-seedling growth stages.

Table 4. Summary of the combined analysis of variance for latent period of the cultivars evaluated at six growth stages in the greenhouse

Source of variance	df	Mean square
Experiments (E)	1	354 ****x
Replicates in E	4	2
Growth stage (GS)	5	171 *y
GS × E	5	31 ***
Cultivar (CV)	8z	121 ***
CV × E	8	17 ***
CV × GS	40	10 ***
CV × GS × E	40	3 ***
Error	212	1

x Significant F values at $P = 0.001$.
y Significant F values at $P = 0.05$.
z Cultivars PBW65 and HD2258 excluded from the analysis.

Table 5. Ranking of mean relative area under the disease progress curve (relative AUDPC) and final disease responses for 11 wheat cultivars evaluated in the field with race 14E14 of *Puccinia striiformis*

Cultivar	Relative AUDPCw	Final disease response: Severityx	Final disease response: Infection type rangey
HD2258	2.3 az	8 a	2 to 3
PBW65	5.2 a	10 a	2 to 3
Pavon 76	17.8 b	20 b	5 to 7
Mexico 82	19.6 b	20 b	5 to 7
Jupateco 73R	29.6 c	50 c	5 to 7
Apache 81	43.2 d	60 d	5 to 8
Anahuac 75	44.0 d	60 d	5 to 8
Ciano 79	51.9 e	60 d	5 to 7
Jupateco 73S	83.4 f	100 e	6 to 9
Avocet S	88.2 f	100 e	8 to 9
Morocco	100.0 g	100 e	8 to 9

w Relative AUDPC is the actual AUDPC of each cultivar divided by the AUDPC of Morocco and multiplied by 100.
x Disease severity is based on the modified Cobb Scale (13).
y Infection types are based on a 0 to 9 scale (9; Table 2 footnote).
z For comparisons within columns, values followed by different letters are significantly different at $P = 0.05$ (least significant difference tests).

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