Contribution of Adult Plant Resistance Gene *Yr18* in Protecting Wheat from Yellow Rust

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ABSTRACT

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Yellow, or stripe, rust of wheat (caused by *Puccinia striiformis*), an important disease in many wheat growing regions of the world, is best controlled through genetic resistance. The *Yr18* gene is known to confer slow rusting resistance in adult plants. This study was conducted to quantify the effectiveness of *Yr18* in reducing losses in grain yield and other traits under high yellow rust pressure. Fungicide-protected and nonprotected plots of two near-isogenic lines, Jupateco 73R with the *Yr18* gene and Jupateco 73S without it, were sown on two planting dates during two crop seasons. Yellow rust epidemics were initiated by artificial inoculation. The area under the disease progress curve and final rust severity were significantly higher for both plantings of nonprotected plots of Jupateco 73S, confirming that the *Yr18* gene does confer slow rusting in Jupateco 73R. Comparison between protected and nonprotected treatments showed that yellow rust infection caused grain yield losses of 31 to 52% in Jupateco 73R and 74 to 94% in Jupateco 73S. This indicates that the slow rusting resistance conferred by *Yr18* protected grain yield in the range of 36 to 58%, depending on the year and sowing date. Grain yield losses in both cultivars were mainly associated with reductions in kernel weight and kernels per m^2; however, reductions in spikes per m^2 and kernels per spike also contributed to yield loss in Jupateco 73S. A reduction in plant height was observed in late plantings of Jupateco 73S, suggesting that early yellow rust infection may affect stem elongation on susceptible cultivars. Although deployment of *Yr18* alone is not recommended in areas with high yellow rust pressure, previous studies have shown that the *Yr18* pyramided with other slow rusting genes, a combination commonly known as the "*Yr18* complex," should provide effective control of yellow rust.

Yellow, or stripe, rust (caused by *Puccinia striiformis* Westend.) is an important disease of wheat (*Triticum aestivum* L.) in various areas of the world (17). Use of genetic resistance is the most economic and environmentally sound measure to reduce production losses. A number of genes are known to confer resistance to yellow rust (2,3,11), but several of them are now ineffective because of the occurrence of races that overcome their effect. However, some genes that confer adult plant resistance have remained effective. Such adult plant resistances are controlled mostly by temperature-sensitive, minor, or additive genes (1,6,9,10,13,15,16,18–20). In recent studies, Singh (21) and McIntosh (12) attributed the durable resistance of several wheats, including the CIMMYT-derived North American cultivar Anza, to adult plant resistance gene *Yr18*. The *Yr18* gene is closely linked to durable leaf rust (caused by *Puccinia recondita* f. sp. *tritici*) resistance gene *Lr34* (21) and to leaf tip necrosis in adult plants (22). Cultivars with *Yr18* alone show slow rusting, but the level of adult plant resistance can be inadequate under high disease pressure. However, Singh and Rajaram (23) found that the "*Yr18*-complex," based on additive interaction between *Yr18* and two to three additional slow rusting genes, can confer an acceptable level of adult plant resistance even under high disease pressure.

Our objective in the present study was to quantify the effectiveness of slow rusting resistance conferred by *Yr18* in reducing losses in grain yield and other agronomic traits under high yellow rust pressure.

MATERIALS AND METHODS

The host. Bread wheat cultivars used in this study, Jupateco 73R (CIMMYT accession BW17890) and Jupateco 73S (BW17891), are reselections for the presence and absence of the gene *Lr34*, respectively, from the heterogeneous Mexican cultivar Jupateco 73. Singh (21) reported that the *Lr34* gene is closely linked to gene *Yr18* for adult plant resistance to yellow rust and confirmed that Jupateco 73R carries *Yr18*, whereas Jupateco 73S lacks it. Therefore, the two cultivars are considered near-isogenic lines for the *Yr18* gene.

Field layout. The 1993 and 1994 experiments were conducted at the CIMMYT research station near Toluca, Mexico, which has a favorable environment for yellow rust development. During both years, the experiment was planted on two dates (early and late) in a split-plot arrangement with four replicates in 1993 and three in 1994. Fungicide treatments (protected and nonprotected) were the main-plot factors, and the cultivars were

Table 1. Yellow rust severity assessments in nonprotected plots of wheat cultivars Jupateco 73R and Jupateco 73S infected with pathotype 14E14 of *Puccinia striiformis* in 1993 and 1994

Date of assessment	Growth stage[a]		Yellow rust severity (%)[d]			
			Jupateco 73R		Jupateco 73S	
	1st[b]	2nd[c]	1st[b]	2nd[c]	1st[b]	2nd[c]
1993						
28 July	52-54	31-32	1	1	5	1
5 August	56-58	49-52	5	5	15	15
13 August	60-64	56-58	15	15	60	40
24 August	71-75	60-64	50	30	100	80
3 September	77-83	71-75	60	50	100	100
20 September	85-87	77-83	70	60	100	100
1994						
21 July	56-58	31-32	10	5	20	15
27 July	60-64	49-52	15	10	60	60
9 August	69-71	56-58	20	15	100	80
22 August	73-75	64-69	40	30	100	90
1 September	77-83	71-73	50	40	100	100
8 September	83-85	75-77	70	60	100	100

[a] Growth stages based on Zadoks et al. (24).

[b] First planting date.

[c] Second planting date.

[d] Yellow rust severity estimates based on the modified Cobb Scale (14).

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the subplot factors. Seeds were sown on raised 9 × 0.75 m^2 beds with 2 rows and 0.25-m row spacing. Each experimental unit (subplot) consisted of two such beds and was separated from the others by an empty bed and a 1.5-m pathway. Spreader rows of the susceptible cultivar Morocco were sown as hills in the pathways on both sides of the subplots. Plots were planted using a 110 kg/ha seeding rate on 5 and 19 May 1993, and on 12 and 25 May 1994. The crop was fertilized with 150 kg of N (split equally at seeding and stem elongation), 46 kg of P, and 60 kg of K per ha.

Rust inoculation and assessment. Approximately 4 to 5 weeks after the first planting (at tillering), spreader rows were inoculated with pathotype 14E14 of *P. striiformis* (7), which is virulent to yellow rust resistance genes *Yr2, 3, 6, 7,* and *A*, and occurs predominantly in the highlands of Mexico.

The systemic fungicide tebuconazole (Folicur, Bayer de Mexico), at the recommended rate of 0.5 liters/ha, was initially applied to the protected experimental plots 3 weeks after inoculation. Four to five subsequent biweekly applications were necessary to maintain the plots rust free. Disease severity in the nonprotected plots was assessed six times (Table 1) each season using the modified Cobb Scale (14). The area under the disease progress curve (AUDPC) was calculated from these ratings using a computer program developed at CIMMYT.

Assessment of grain yield and other agronomic traits. At physiological maturity, 50 arbitrarily selected reproductive culms from each experimental unit were carefully cut at ground level. The 50 culms were placed in a paper bag, oven-dried for 48 h at 60°C, and weighed to obtain their dry weight, from which culm weight was calculated. All spikes of these culms were subsequently threshed to obtain kernel weight. A 5-m length of each plot was hand-harvested, which gave a harvested area of 7.5 m^2 for each experimental unit. Grain yield was recorded and adjusted to 0% moisture after measuring moisture content. Kernel weight was estimated by counting 400 kernels from each experimental unit. Other agronomic traits were calculated as follows: Harvest index (HI) = kernel weight per spike/culm weight; biomass = grain yield/HI; spikes/m^2 = biomass, g/m^2/culm weight, g; kernels/m^2 = grain yield, g/m^2/kernel weight, g; kernels/spike = (kernels/m^2)/(spikes/m^2). Plant height was measured at maturity.

Statistical analysis. The four experiments, i.e., plantings on 5 and 19 May 1993 and on 12 and 25 May 1994 were combined for the statistical analysis. A mixed model of combined split-plot analysis of variance was performed for AUDPC, final disease rating, grain yield, and other traits. The experimental effect was considered to be random, while the fungicide treatment and cultivar effects were fixed. The analysis was carried out using the SAS computer program (SAS Institute, Cary, NC).

RESULTS AND DISCUSSION

Yellow rust epidemic development. Severe yellow rust epidemics developed during both years (Figs. 1 and 2), but fungicide-protected plots remained rust free, indicating that the fungicide treatment was effective in protecting plants from yellow rust infection. Significant differences in AUDPCs and final disease severities (FDS) for cultivars and cultivar-by-fungicide treatments were also detected (Table 2). Nonprotected plots of Jupateco 73S showed rapid yellow rust development, reaching 100% disease severity at the late flowering–medium milk stage (decimal growth stages 69 to 75) (24) (Table 1). The leaves were prematurely necrotic. Yellow rust progress was much slower on Jupateco 73R, with 60 to 70% FDS. The AUDPC and FDS of Jupateco 73R were significantly lower ($P < 0.05$) than those of Jupateco 73S, confirming that the *Yr18* gene does retard yellow rust progress.

The ANOVA (Table 2) indicated that the mean AUDPC values for experiments varied significantly and ranked in the order of experiment 2 (mean AUDPC 1,199), 1 (1,425), 4 (1,460), and 3 (1,562), respectively. This indicated that the yellow rust epidemic was more severe in 1994. The mean AUDPC of Jupateco 73S was 28% higher ($P < 0.05$) in 1994 than in 1993 (Table 3) in the nonprotected plots; however, no difference was observed for Jupateco 73R. The higher AUDPC of Jupateco 73S in 1994 was due to the fact that the yellow rust epidemic started earlier that year. Late planting consistently resulted in lower AUDPC ($P < 0.05$) for both years (Table 3). During both years, rainfall was less earlier in the season and gradually became greater. Heavy rainfall may retard, or even stop, yellow rust development, especially on the plantings of slow rusting genotypes such as Jupateco 73R. Although interactions between experiment and fungicide treatment, and between experiment and cultivar, were significant, their effects were smaller than the main factors (Table 2).

Grain yield and other agronomic traits. Significant differences ($P < 0.05$–0.001) in grain yield and most other agronomic traits were detected for fungicide treatment, cultivar, and fungicide-by-cultivar interaction (Table 2). Protected Jupateco 73R and Jupateco 73S did not show significant differences in grain yield and other yield traits in either year (Table 3). This was expected because they are reselections of Jupateco 73 and are similar in appearance. Significant differences in grain yield and other traits were common when Jupateco 73R and Jupateco 73S were compared in nonprotected treatments (Table 3). Grain yield loss for Jupateco 73S was greater in 1994 (94 to 89%, for experiments 3 and 4, respectively) than in 1993 (experiments 1 and 2). In contrast, Jupateco 73R showed grain yield losses ranging from 31 to 52% over the four experiments (Table 4). Our results clearly indicate that the slow rusting resistance to yellow rust conferred by *Yr18* can reduce the percentage loss in grain yield to the range of 36 to 58% (Table 4). The degree of protection may vary with the environment, depending on such factors as temperature, rainfall, disease pressure throughout the crop season, and plant growth stage at rust epidemic onset.

Comparison of protected and nonprotected treatments also showed reductions in other agronomic traits for both Jupateco cultivars (Table 4). Except for kernels per spike and harvest index in experiments 1

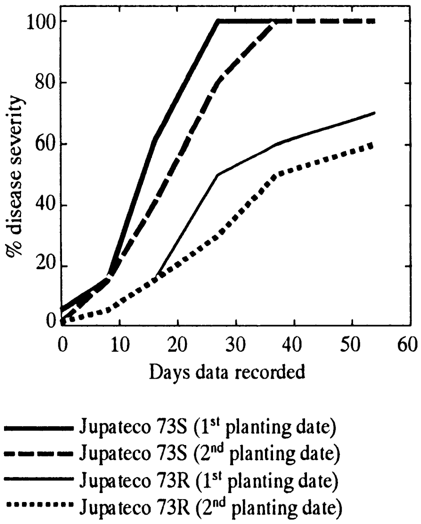

Fig. 1. Progress of wheat yellow rust on wheat cultivars Jupateco 73S and Jupateco 73R during the 1993 season.

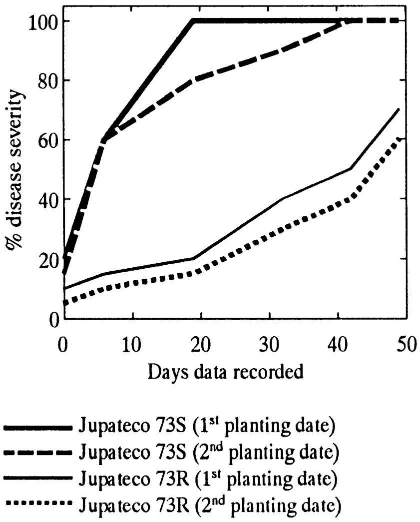

Fig. 2. Progress of wheat yellow rust on wheat cultivars Jupateco 73S and Jupateco 73R during the 1994 season.

Table 2. Summary of combined split-plot analysis of variance (ANOVA) for area under the disease progress curve (AUDPC), final disease severity (FDS), and seven other traits of wheat cultivars Jupateco 73R and Jupateco 73S

		Mean square								
Source of variance	df	AUDPC $(\times 10^3)$	FDS	Grain yield $(\times 10^{-3})$	Harvest index $(\times 10^{-3})$	Biomass $(\times 10^3)$	Spikes/m^2	Kernel weight	Kernels/m^2	Kernels/ spike
Experiments (E)	3	340***[a]	43**	3,546	26***	74**	2,888	127***	64***	715***
Replicates in E	10	12	4	136	0.47	6	2,165	1.3	0.81	31
Treatments (T)	1	109,694***	91,548***	124,938***	239**	427***	92,733**	1,209**	735**	3,151**
T × E	3	340**	43**	543**	7*	5	658	5	9***	86
Pooled error A	10	12*	4	59	0.87	10	3,782	2	0.31	34
Cultivars (CV)	1	19,502**	4,714**	17,719***	81**	689***	44,644***	323**	137***	514**
CV × E	3	304***	43**	22	2.3	1	58	6	0.67	15
CV × T	1	19,502**	4,714**	14,916***	48*	897***	74,915**	163**	172***	411
CV × T × E	3	304***	43***	41	3	3	1,343	5	1*	93
Pooled error B	20	4.1	4	33	0.9	6	2,962	2	0.32	33

[a] ***, **, * Significant F values at $P = 0.001$, 0.01, and 0.05, respectively.

Table 3. Comparison of area under the disease progress curve (AUDPC) and seven traits of wheat cultivars Jupateco 73R (JupR) and Jupateco 73S (JupS) in plots protected or nonprotected from yellow rust and sown on two planting dates in 1993 and 1994

	First planting						Second planting					
	Protected			Nonprotected			Protected			Nonprotected		
Trait	JupR	JupS	Change[a] (%)	JupR	JupS	Change[a] (%)	JupR	JupS	Change[a] (%)	JupR	JupS	Change[a] (%)
1993												
AUDPC	0.0	0.0	0	1,918.0	3,781.2	−97*	0.0	0.0	0	1,460.7	3,335.5	−129*
Grain Yield (t/ha)	5.5	5.3	4	3.4	1.4	59***	5.6	5.3	5	3.6	1.4	61***
Harvest Index (%)	47.0	44.0	6	37.5	32.0	14	45.7	43.5	7	40.7	32.0	22
Biomass (kg/m^2)	1.2	1.2	0	0.9	0.4	55***	1.2	1.2	0	0.9	0.4	55***
Spikes/m^2	323.8	359.1	−11	349.2	188.8	46*	370.4	365.3	1	349.1	242.0	31*
Kernel weight (mg)	38.3	37.1	3	31.4	24.9	19*	31.4	29.9	3	24.1	18.9	21*
Kernels/m^2 $(\times 10^3)$	15.3	14.4	7	10.8	6.0	45***	18.1	16.7	5	14.3	8.0	43***
Kernels/spike	46.1	41.4	11	34.3	30.0	12	49.3	48.3	2	40.5	32.1	22
1994												
AUDPC	0.0	0.0	0	1,674.7	4,780.0	−185**	0.0	0.0	0	1,480.0	4,363.3	−195**
Grain Yield (t/ha)	5.0	4.8	4	2.4	0.3	88***	4.2	4.4	5	2.9	0.5	83***
Harvest Index (%)	46.0	44.6	2	33.7	11.3	68*	38.0	37.3	3	35.3	17.0	51*
Biomass (kg/m^2)	1.1	1.1	0	0.8	0.3	63**	1.1	1.2	−9	0.8	0.3	62**
Spikes/m^2	378.4	390.3	−3	343.9	217.1	37	362.1	383.3	−6	358.7	228.9	36
Kernel weight (mg)	33.1	32.3	3	27.5	14.7	46**	34.3	30.5	9	29.1	20.1	31*
Kernels/m^2 $(\times 10^3)$	15.1	14.9	0	9.1	1.9	78***	12.4	14.5	−17	10.1	3.2	70***
Kernels/spike	40.4	38.7	4	26.3	9.4	65	34.2	38.3	−12	28.3	10.9	61

[a] Change (%) = [(Jupateco 73R − Jupateco 73S)/Jupateco 73R] × 100; ***, **, * denote $P < 0.001$, $P < 0.01$, and $P < 0.05$ significance levels, respectively.

Table 4. Comparison of seven traits of wheat cultivars Jupateco 73R and Jupateco 73S in plots protected or nonprotected from yellow rust and sown on two planting dates in 1993 and 1994

	Percent change[a]					
	Jupateco 73R		Jupateco 73S		Contribution of *Yr18*[d]	
Trait	1st[b]	2nd[c]	1st[b]	2nd[c]	1st[b]	2nd[c]
1993						
Grain yield	38***	36***	74***	74***	36	38
Harvest index	21	11	27	22	6	11
Biomass	21**	30**	63***	55***	42	25
Spikes/m^2	−8	6	47*	31*	55	25
Kernel weight	19*	22*	32**	39**	13	17
Kernels/m^2	23*	20*	62***	43***	39	23
Kernels/spike	24	15	27	33	3	7
1994						
Grain yield	52***	31**	94***	89***	42	58
Harvest index	26	8	76**	54*	50	46
Biomass	31**	22*	78***	75***	47	53
Spikes/m^2	9	1	44*	40*	35	39
Kernel weight	15*	14*	52**	35**	37	21
Kernels/m^2	42**	15	88***	82***	46	67
Kernels/spike	30	15	77*	71*	47	56

[a] Percent change = [(protected − nonprotected)/protected] × 100; ***, **, * denote $P < 0.001$, $P < 0.01$, and $P < 0.05$ significance levels, respectively.

[b] First planting.

[c] Second planting.

[d] Contribution of *Yr18* = percent change in Jupateco 73S - percent change in Jupateco 73R.

and 2, Jupateco 73S showed significant reductions in the values of all other traits. Although an effect on spikes per m^2 was evident, its level of significance ($P < 0.05$) was generally lower than that of the effect on other traits. Variation in harvest index, spikes per m^2 and kernels per spike was not observed for Jupateco 73R. However, significant reductions ($P = 0.05–0.001$) in biomass and kernel weight were found in all experiments and in kernels per m^2 in experiments 1, 2, and 3.

Relationships between grain yield and other agronomic traits were further investigated through multiple regression by combining data of four experiments for both Jupateco 73R and Jupateco 73S. Significant regression coefficients between grain yield and kernel weight (2.8, $P = 0.007$), kernels per m^2 (6.3, $P = 0.001$), spikes per m^2 (−4.6, $P = 0.001$), and kernels per spike (−2.8, $P = 0.006$) were observed. When the grain yields of Jupateco 73R and Jupateco 73S were regressed separately on various traits, only regression coefficients of kernel weight (4.3 for Jupateco 73R and 2.4 for Jupateco 73S) and kernels per m^2 (4.4 for Jupateco 73R and 4.1 for Jupateco 73S) were significant ($P = 0.007–0.001$). Therefore, kernel weight and kernels per m^2 had greater effect on grain yield losses than the other traits. The significant effects of spikes per m^2 and kernels per spike in combined regression were attributed to the large reductions of the two traits for Jupateco 73S. These results agree with the findings of King (8) and Schultz and Line (18), who reported that grain yield loss due to yellow rust could be largely attributed to reductions in kernel number and kernel weight. Reduction in tiller number was observed only on highly susceptible cultivars, especially when an early infection of yellow rust (e.g., at jointing stage) occurred.

Plant height of nonprotected Jupateco 73S measured at maturity was reduced significantly ($P < 0.05$), with a greater reduction observed for the second sowing date of 1994 (16%, experiment 4) than for the first (7%, experiment 3). As illustrated in Table 1, the rust epidemic had started at growth stage 31 to 32, when the culms were just beginning to elongate. Thus, it is reasonable to believe that yellow rust may inhibit culm elongation and reduce plant height when plants are severely infected prior to elongation. Doodson et al. (4) and Hendrix and Lloyd (5) reported that early yellow rust infection can adversely affect root growth. This may also influence plant height and growth.

Although the high yellow rust severity and grain yield losses observed for Jupateco 73R are not acceptable for most breeding purposes, the slow rusting resistance conferred by the *Yr18* gene is nonetheless attractive because it prevents severe grain yield loss by protecting various yield traits. The level of yellow rust resistance could be improved and grain yield losses further reduced by combining *Yr18* with other additive slow rusting genes to form the *Yr18*-complex (23). Breeding cultivars with the *Yr18*-complex should be a useful strategy for controlling yellow rust worldwide.

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