Control of Wheat Stem Rust by Low Receptivity to Infection Conditioned by a Single Dominant Gene

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Cooperative investigations, Agricultural Research Service, USDA, and the University of Minnesota. Scientific Journal Series Paper 11,525, Minnesota Agricultural Experiment Station.

Accepted for publication 8 June 1981.

ABSTRACT

Rowell, J. B. 1982. Control of wheat stem rust by low receptivity to infection conditioned by a single dominant gene. Phytopathology 72:297-299.

The effectiveness of a single dominant gene for low receptivity to infection by *Puccinia graminis* f. sp. *tritici* in wheat (*Triticum aestivum*) cultivars Idaed 59 and W2691SrTt-1 was assessed for control of a moderately severe natural stem rust epidemic. This gene for low receptivity is either very closely linked to or identical to the gene *Sr*Tt-1 for specific resistance, for which the prevalent races in the epidemic were virulent. In the early stages of the epidemic, disease incidence and rate of disease increase were markedly less than those of the highly receptive Purdue 5481C1 and the intermediately receptive Baart and W2691. In the late stages of plant maturity, receptivity in leaf blades of Idaed 59 and W2691SrTt-1 increased, resulting in a rate of disease increase similar to that of the other cultivars, but terminal disease severities remained less. Rust caused significant losses in yield of W2691SrTt-1 and in kernel weight of Idaed 59 and W2691SrTt-1, but the percentage of loss was significantly less than that for the more receptive cultivars. Thus, the low receptivity of wheats with *Sr*Tt-1 to infection by races virulent to *Sr*Tt-1 offers useful protection against stem rust in areas of the United States where epidemics are light to moderate and infrequent.

Additional key words: general resistance.

A single dominant gene for low receptivity to infection by *Puccinia graminis* Pers. f. sp. *tritici* Eriks. and E. Henn. apparently is linked or identical to the gene *Sr*Tt-1 for specific resistance in Idaed 59 and W2691SrTt-1 wheat (7). The resistance of *Sr*Tt-1, infection type 0;, is effective against many races in the United States (eg, 151-QSH) but ineffective against prevalent races such as 15-TNM, 15-TDM, 15-TLM, and 113 RKQ (5). These races, considered virulent for the resistance of gene *Sr*Tt-1 (5), produce a seedling reaction of W2691SrTt-1 and Idaed 59 in which about 30% fewer visible infections occur than occur on a susceptible cultivar; the infections are a mixture of uredia, predominantly type 4, with an occasional fleck present. This mesothetic reaction, infection type 40;, on seedlings apparently is conditioned by the gene for low receptivity evident in adult plants (6). Among the race groups virulent for the resistance of *Sr*Tt-1, no isolates have been found in the United States that have the pathogenic capability to overcome the low receptivity in these cultivars (1). Thus, the combination of the specific resistance of *Sr*Tt-1 and the associated low receptivity appears to offer useful protection against stem rust. In this study, the development of natural stem rust epidemics caused by races virulent for *Sr*Tt-1 and the associated crop losses were compared on wheat cultivars with and without the dominant gene for low receptivity to assess the effectiveness of this dominant gene for stem rust control.

MATERIALS AND METHODS

The resistant wheats (*Triticum aestivum* L.) were Idaed 59 (CI 13631) and W2691SrTt-1 (CI 17385), in which the dominant trait of low receptivity is associated with the resistance conditioned by *Sr*Tt-1 (1,8). Idaed 59 matures early and W2691SrTt-1 matures late in Minnesota. The susceptible wheats, genotype *Sr*Tt-1, were Purdue 5481C1 (P5481C1), Baart (CI 1697), and W2691, a parent of W2691SrTt-1. P5481C1 has high receptivity in all adult stages of maturity (8), but Baart and W2691 have intermediate receptivity in the adult stages preceding anthesis (*unpublished results*). Under the test conditions, P5481C1 ripened at the same time as Idaed 59; Baart and W2691SrTt-1 ripened 1 wk later; and W2691 ripened 2 wk later.

The wheats were planted in a randomized, split-plot design of two replicates at Rosemount, MN, in 1975. In addition to the wheat plots, a vacant plot was included in each replicate to determine the background of exogenous spores in the experimental area. The

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plots were separated from each other by a 30.5-m border of Era wheat, which is resistant to leaf and stem rusts. The split plots were divided into a 6.1×4.6-m plot of rusted wheat and a 6.1×2.1-m plot of rust-free wheat separated by a 1.8-m alley. The rust-free wheat was protected against stem rust during the rust season by nine sprays of zinc ion-maneb complex, a coordination product of zinc ion and manganous ethylenebis (dithiocarbamate), at 1.8 kg (active)/ha. All plots were sprayed 2 days after planting with triazbutil, 4-butyl-4*H*-1,2,4-triazole, at 0.84 kg (active)/ha for control of leaf rust. All spray treatments were applied by a power sprayer at a rate of 281 L/ha with a pressure of 21 kg/cm^2.

The wheat epidemics resulted from natural infection. Races 15-TNM, 15-TDM, and 15-TLM, which are virulent for *Sr*Tt-1, comprised 83% of the rust isolates identified in region 5 (4) where the experimental plots were located. Primary infection appeared on 1 July. On 8 July and weekly thereafter, a culm was collected from each of 20 plants at 25-cm intervals in the next to last row on each side of the rusted wheat plots. The number of uredia on each culm was determined by counting or by estimating percent disease severity when the number exceeded about 200 uredia per culm. Percent severity was converted to the number of uredia per culm according to the relationship: 10 uredia per culm equals 1% severity. The mean number of uredia per culm for each side of a plot was treated as a replicate in statistical analysis. Exposure of rod spore traps (3) 10 cm above the crop canopy in the center of each rusted wheat and vacant plot commenced on 1 July. Traps were changed daily except during weekends. The number of spores trapped over the vacant plots established the background of exogenous spores, and the mean background number per square centimeter was subtracted from the total number per square centimeter trapped over each rusted wheat plot to assess the number of endogenous spores that originated from the infections present.

Samples for yield and kernel weight determinations were taken from the third row from each side of the plots. The inner 5 m of the row was cut and loosely bundled; 100 culms were withdrawn individually from the bundle by the cut end; and all seed was threshed from this sample. The weight per culm and weight per 1,000 kernels from each sample were treated as a replicate in statistical analysis. The percentage losses in yield and kernel weight caused by rust were calculated from the differences between the corresponding samples from the rusted and rust-free plots and were converted to arc sines for analysis.

RESULTS AND DISCUSSION

The 1975 growing season was near normal in temperature but wetter than normal in May and June. Natural primary infection appeared later than normal and was found on P5481C1 in the early heading stage on 1 July at a frequency of about one uredium per 100 culms. No infection was found on any of the remaining cultivars until 8 July when uredial counts commenced. On that date, the uredial counts indicated that receptivity was high for P5481C1, intermediate for Baart and W2691, and low for Idaed 59 and W2691SrTt-1. The uredial frequencies confirmed previous observations (1,8) on the receptivity of these wheats to infection by races of *P. graminis* f. sp. *tritici* virulent for the resistance conditioned by *Sr*Tt-1.

The data for trapped spores indicated that the subsequent progress of the stem rust epidemics in each wheat plot was dependent principally on endogenous inoculum. Thus, the mean cumulative number of trapped spores per square centimeter by 5 August was 41,460 for P5481C1, 33,307 for Baart, 27,105 for W2691, 8,787 for Idaed 59, 7,011 for W2691SrTt-1, and 1,330 for the vacant plot.

The disease progress curve, plotted as the common log of the uredial number per culm, illustrates the effect of differences in the receptivity to infection among the cultivars (Fig. 1). Disease increased rapidly at first on the highly receptive P5481C1 and then slowed markedly as the proportion of uninfected host tissue declined. The rate of disease increase on Baart and W2691 from 8 to 21 July indicated that the receptivity of these cultivars was lower than that for P5481C1, but thereafter, disease increased at a faster rate and indicated that their receptivity increased in the later stages of maturity. Hence, the final severities observed on Baart and W2691 were similar to that on P5481C1. The low receptivity of Idaed 59 and W2691SrTt-1 was evident in the low initial infection and in the rate of disease increase, which was markedly slower than that of P5481C1 until 21 July. The faster rate of disease increase from 21 to 28 July on these cultivars was mostly due to the occurrence of large numbers of infections on the leaf blades. This shift in the receptivity of leaf blades of Idaed 59 after anthesis has been observed previously. I have observed that in wheat cultivars possessing *Sr*Tt-1, the leaf blades die prematurely when plants are stressed by drought or heat. When leaf blades die prematurely, the shift in receptivity cannot be observed (8). In this experiment, however, both wheats retained normal-appearing leaves late in their maturation because of favorable conditions of temperature and moisture. Senescence in seedling leaves increases the susceptibility to avirulent rust cultures (9), and probably the changes of senescence increase the receptivity of blades on adult plants of Idaed 59 and W2691SrTt-1.

The slopes of the regression equation for the logs of the number of uredia per culm and the cumulative number of trapped endogenous spores per square centimeter were compared for each of the wheats for the periods of 8–21 and 8–28 July (Table 1). The correlation coefficients exceeded 0.9 in all comparisons and the data for trapped spores confirmed the effects of the different receptivities of the test wheats observed on the disease progress curve. Thus, the low receptivity of Idaed 59 and W2691SrTt-1 markedly decreased the slope of the disease progress curve from 8 to 21 July on these cultivars, but the overall slope from 8 to 28 July approached that of the more receptive wheats, owing to the

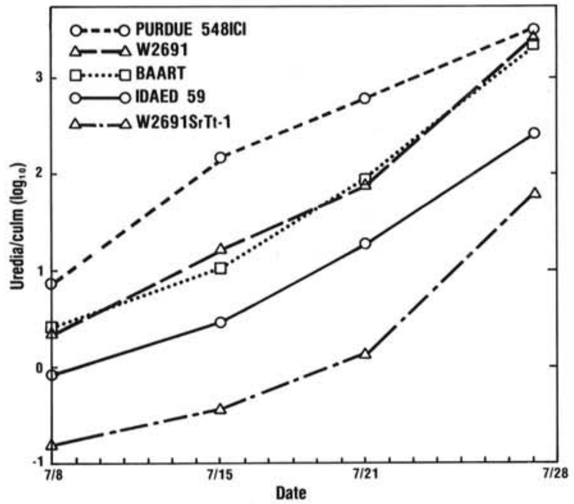

Fig. 1. Disease progress curves for stem rust epidemics on wheats with high and low receptivity to infection at Rosemount, MN, 1975.

TABLE 1. Slopes of the regression equation[a] and correlation coefficients (r) for the disease progress curves, determined by log uredia per culm and log cumulative trapped spores per square centimeter for wheat cultivars with high and low receptivity to infection by *Puccinia graminis* f. sp. *tritici*

	July 8–21			July 8–28		
	Slope			Slope		
Cultivar	Uredia	Spores	r	Uredia	Spores	r
Idaed 59	0.086	0.076	0.966	0.116	0.152	0.966
W2691SrTt-1	0.066	0.038	0.909	0.123	0.111	0.920
Purdue 5481C1	0.138	0.143	0.999	0.106	0.104	0.998
Baart	0.110	0.136	0.993	0.124	0.156	0.990
W2691	0.111	0.105	0.970	0.125	0.139	0.984

[a] For the equation $\log \hat{y} = a + bx$, where $\hat{y}$ = number of uredia per culm or cumulative number of trapped spores per square centimeter and x = number of days after initial occurrence of disease.

TABLE 2. Effect of receptivity on losses in yield and kernel weight due to wheat stem rust at Rosemount, MN, 1975

Wheat cultivar	Receptivity	Disease status	Yield			1,000 Kernels	
			Weight[a] (g/100 heads)	Loss[b] (%)	Estimated loss[c] (%)	Weight[a] (g)	Loss[b] (%)
Idaed 59	Low	Rust-free	52.20 bc			32.34 ab	
		Rusted	46.85 bc	10.3 d	20	24.91 c	23.0 c
W2691SrTt-1	Low	Rust-free	56.54 b			23.57 c	
		Rusted	44.22 c	21.8 c	18	19.02 d	19.3 c
Purdue 5481C1	High	Rust-free	41.40 c			30.29 ab	
		Rusted	22.82 d	44.9 b	62	16.74 d	44.7 b
Baart	Intermediate	Rust-free	95.53 a			34.60 a	
		Rusted	44.12 c	53.8 b	54	19.01 d	45.1 b
W2691	Intermediate	Rust-free	41.88 c			18.95 d	
		Rusted	10.84 e	74.1 a	83	7.82 e	58.7 a

[a] Values followed by the same letter are not significantly different according to Duncan's multiple range test at $P = 0.05$.
[b] Loss calculated by difference. Values followed by the same letter are not significantly different according to Duncan's multiple range test at $P = 0.01$.
[c] Estimates using the generalized model of Calpouzos et al (2).

increased receptivity of leaf blades in the late stages of maturity.

The infection rates, for Idaed 59 and P5481C1 were 0.21 and 0.42 per unit per day, respectively. Previous field trials (1,8) have shown that the low receptivity of Idaed 59 at the heading stage reduced infection about 92–98% in comparison to that on P5481C1. The effect of the low receptivity of Idaed 59 on the infection rate approaches that predicted by Vanderplank (10) for wheat stem rust. His calculations show that resistances reducing infection 90 and 95% would lower the infection rate to 0.2 and 0.15, respectively, when the rate was 0.4 on a susceptible cultivar. The increase in receptivity of leaf blades of Idaed 59 in the late stage of maturity, however, subsequently increased the infection rate to 0.42 from 21 to 28 July.

The potential production in yield and kernel weight was determined for rust-free wheat protected by frequent fungicidal sprays (Table 2). Yield weight per 100 culms was significantly better for rust-free Baart and 1,000-kernel weight was significantly less for rust-free W2691 than for the other cultivars. Yields of the rust-free wheat did not differ between the early-maturing cultivars Idaed 59 and P5481C1 but were significantly different among the late-maturing cultivars W2691SrTt-1, Baart, and W2691. Rust caused significant losses in kernel weights in all cultivars and significant losses in yield in all cultivars except Idaed 59. The effect of low receptivity in retarding the rust epidemics on Idaed 59 and W2691SrTt-1 significantly reduced the percentage of loss in yield and kernel weight below that of cultivars with high receptivities. Rate of maturation also affected the extent of yield losses caused by rust, as indicated by the significantly greater percentage of loss in W2691SrTt-1 than in Idaed 59 and in W2691 than in P5481C1.

Data from the late stages of the epidemics in these wheats were entered into the generalized model of Calpouzos et al (2) for measuring yield losses caused by stem rust to determine whether the differences in the disease progress curves due to differences in receptivity to infection altered the relations between rust development and crop loss (Table 2). The estimated losses from their model were similar to the observed losses for the late-maturing cultivars Baart, W2691, and W2691SrTt-1 but overestimated the losses for the early-maturing cultivars Idaed 59 and P5481C1. No effect of the low receptivity of Idaed 59 and W2691SrTt-1 was evident in the estimates of loss from the model because the model's procedures required the use of disease observations on these cultivars in the late stages of the epidemic, when the rate of disease development resembled that of the more receptive cultivars.

These results indicate that the low receptivity associated with gene *Sr*Tt-1 provides partial protection in moderate epidemics by races of *P. graminis* f. sp. *tritici* that have virulence for the specific resistance conditioned by *Sr*Tt-1. The shift from low to high receptivity of leaf blades in Idaed 59 and W2691SrTt-1 in the late stages of crop maturation reduces the effectiveness of this protection. This combination of resistances is effective against all races presently known to be present in the United States (1). Thus, the combined resistances should be useful protection against stem rust in areas where epidemics are light to moderate and infrequent.

All wheat cultivars and breeding lines with the specific resistance conditioned by *Sr*Tt-1 that have been tested have the trait for low receptivity (7). In addition to Idaed 59 and W2691SrTt-1, this combination of resistances was found in the germ plasm lines CI 12632 and CI 12633 derived from ILL*1/Chinese*2//*Triticum timopheevi*, Ramona 64 (CI 17581), Arthur (CI 14425), Abe (CI 15375), and the Australian cultivar Mengavi. Thus, the protection against stem rust offered by the specific resistance of *Sr*Tt-1 and the trait of low receptivity is presently in use.

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