

Adult Plant Resistance of Thatcher Wheat to Stem Rust

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ABSTRACT

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No relationship was found between the independent *Sr* genes for seedling resistance and the adult plant resistance of Thatcher wheat, as measured by rust severity. Pyramids of seedling resistance genes *Sr5*, *Sr12*, *Sr16*, and *SrTc* did not improve resistance to stem rust. The performance of some progeny lines with both *Sr12* and *SrTc* was similar to Thatcher's, and this suggests that the factor(s) involved in the adult plant resistance of Thatcher

might be related to this *Sr* gene combination. The adult plant resistance of Thatcher was sensitive to inoculum density. Although this character had been selected successfully under heavy inoculum density at the end of the season, the resistance was most apparent at stage 24 (early milk). Under light inoculum density, however, the greatest difference existed in the terminal disease severities.

Additional key words: *Puccinia graminis*, race-specific resistance.

Stem rust of wheat caused by *Puccinia graminis* Pers. f. sp. *tritici*, can be an important disease wherever wheat (*Triticum* sp.) is grown extensively. The wheat cultivar Thatcher was released in 1934, after more than 25 yr of breeding for resistance to stem rust, desirable agronomic type, and milling and baking qualities (4). Thatcher resulted from crosses between Marquis/Kanred, hard red spring and winter wheats, respectively, and Marquis/Iumillo, a red durum (4). Thatcher inherited the milling and baking qualities of Marquis, seedling stem rust resistance from Kanred and Iumillo, and the adult plant resistance from Iumillo. Currently, Thatcher is important in the spring wheat breeding program because it has adult plant resistance. Although the genetics of seedling resistance of Thatcher was generally understood, the genetics of its adult plant resistance was not.

The value of adult plant resistance in protecting wheat cultivars against stem rust has been pointed out by Stakman and Christensen (22). They stated that breeding for resistance against individual races of a pathogen would continue, but every effort should be made to combine all characters in a single cultivar that conferred some degree of generalized resistance against the pathogen. Brennan (1) stated that a breeding program should develop rust resistant cultivars with resistance conditioned by several genes, and since race-specific and race-nonspecific resistance exist in wheat, both should be used.

The objectives of this study were to determine: the relationship, if any, between race-specific seedling resistance genes and adult plant resistance, and the effect of inoculum density (17) on the adult plant response.

MATERIALS AND METHODS

The study was divided into two parts: the first, an investigation of relationship of the adult plant resistance of Thatcher with the race-specific seedling resistance genes *Sr5*, *Sr9g*, *Sr12*, *Sr16*, or *SrTc*, known in Thatcher; and the second, a field evaluation of the sensitivity of Thatcher resistance to inoculum density. Both studies were performed in F_6 - F_8 single-seed-derived generations of Baart/Thatcher (91 sib-lines), and Prelude/Thatcher (95 sib-lines) crosses, and on the parents. Baart and Prelude have been

susceptible in the field to prevalent U.S. stem rust races, whereas Thatcher has been rated from moderately resistant to moderately susceptible under the same conditions.

Relationship between seedling and adult plant resistance of Thatcher. The presence of resistance genes was postulated (7) by inoculation with four races of stem rust. The races were chosen on the basis of avirulence or virulence on lines possessing the stem rust seedling resistance genes of Thatcher (Table 1). Seven-day-old seedlings of the progenies, the parents (Thatcher [CI 10003], Prelude CI 4323, and Baart CI 1697), and of the "single" gene lines ISr5-Ra (CI 14159), 743642ASr9g, ISr16-Ra (CI 14173), and Line R (*Sr12*) or BtSr12Tc (CI 17783) were inoculated independently and evaluated for infection type (16) 10-14 days after inoculation. The lack of a race avirulent on *Sr9g* made the detection of this gene in the progenies impossible. Purity of races was verified by using a set of "single" gene differential lines, and standard inoculation techniques (16). The term "single" gene line is used to refer to a host line that has only the designated gene pair for resistance to the wheat stem rust fungus population that occurred naturally in the United States Great Plains during the past 20 yr.

After inoculation, seedlings were placed in a dew chamber (18 C, darkness, and 100% relative humidity) for approximately 16 hr. The chamber was then illuminated (10,000 lux) for 3 hr, the temperature was gradually increased to 30 C, and the dew dried slowly. Seedlings were then transferred to a greenhouse (approximately 18 C) supplemented with 11,000 lux light when daylength was less than 12 hr.

The Prelude/Thatcher sib-lines were planted side-by-side, in

TABLE 1. Infection types produced on "single" gene lines for the seedling resistance genes known to occur in Thatcher, and on Thatcher, Prelude, and Baart wheats when inoculated with certain races of *Puccinia graminis* f. sp. *tritici*

Races	Infection type produced on "single" <i>Sr</i> gene line or cultivar							
	5	9g	12	16	Tc ^a	Thatcher	Prelude	Baart
HJC	0-0;	4	4	4	23C-X	0	4	4
MBC	4	4	0-0;1	4	23C-X	0-0;1	4	4
RBC	4	4	4	2-2+	23C-X	0;1-2	4	4
TDM	4	4	4	4	23C-X	23C-X	4	4

^aIneffective at >23 C, in seedling tests.

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duplicate field nurseries, at St. Paul and Rosemount in 1978. Each sib-line occurred once per location in a 1.0 m row, 0.3 m apart. There were eight replicates of Prelude, and two each of the "single" gene lines, PdSr5Tc, 743642ASr9g, ISr16-Ra, and BtSr12Tc, among the progeny lines. Thatcher was used to separate the replicates and test lines; there were 24 replicates of Thatcher per location. The Baart/Thatcher sib-lines were planted similarly, but the Prelude was replaced by Baart, and the "single" gene line for Sr5 by BtSr5Tc. At Rosemount, a row of Baart was planted perpendicular to and 0.3 m from, the upwind end of both progenies to provide a more uniform inoculum source.

Disease severity was assessed at 4- to 7-day intervals, beginning before uredia appeared in the plots and continuing to crop maturity. Severity ratings were based on the modified Cobb Scale (14). Disease prevalence was 100% except at the beginning of the season when uredia per row were counted. The Romig growth stage scale (2) was used to record plant development. Data were analyzed by regression and means were compared according to the *t* test (23).

Effect of inoculum density on the adult plant resistance of Thatcher. The 1978 experiment was the same as previously described. The east central Minnesota locations were at St. Paul (heavy inoculum density) and Rosemount (light inoculum density). The heavy inoculum density was obtained when winter wheat nurseries were inoculated weekly (starting at about stage 10) with a mixture of representative U.S. stem rust races. Airborne spores produced on susceptible lines in those nurseries were the source of inoculum in both years at St. Paul. Initial infection at Rosemount resulted from naturally occurring airborne inoculum, and primary infections appeared 1 wk or more later than at St. Paul.

Lines selected in 1978 represented the range of severities and

genotypes for seedling resistance. These 15 lines and the three parents (9) comprised the 1979 experiment. When possible, lines were chosen that were similar in maturity. The experimental design in 1979 was the generalized randomized block with two randomly assigned replicates of treatments within each of three blocks. The two reps/block element was introduced to calculate the block \times treatment interaction in the analysis of variance (24). Each replicate was a 1.5-m row, 0.6 m apart from the next row. A 1.5-m row of oats (cultivar Stout, CI9195) was planted between the rows to reduce block \times treatment interaction.

Each block (18 treatments \times two replicates) was planted in two parallel ranges separated by a 0.5-m alley. The long axis of blocks was planted perpendicular to the prevailing wind direction, to reduce inoculum movement among blocks. Seven 3.5-m rows of Stout oats, 0.3 m apart, separated the blocks. At both locations, a susceptible wheat spreader row (Baart) was planted upwind, 0.5 m from the blocks. Stem rust was assessed at 4-day intervals from the initial infection to crop maturity. Analysis of variance and a test of hypothesis of the data were done (23,24).

Inoculum concentration was estimated through the 1979 season by cumulative spore counts at both locations. Uredospores were collected from wind-oriented rod impaction traps (15,17) located in stem rust resistant blocks, approximately 5.0 m from the experiment. Traps were changed daily at St. Paul and each fourth day at Rosemount.

The planting date at Rosemount was early in the recommended period for the region; at St. Paul it was near the end of the period so that the potential for inoculum buildup was enhanced. Each stem rust race identified from collections made in both years and locations was virulent on Sr5, Sr9g, Sr12, and Sr16.

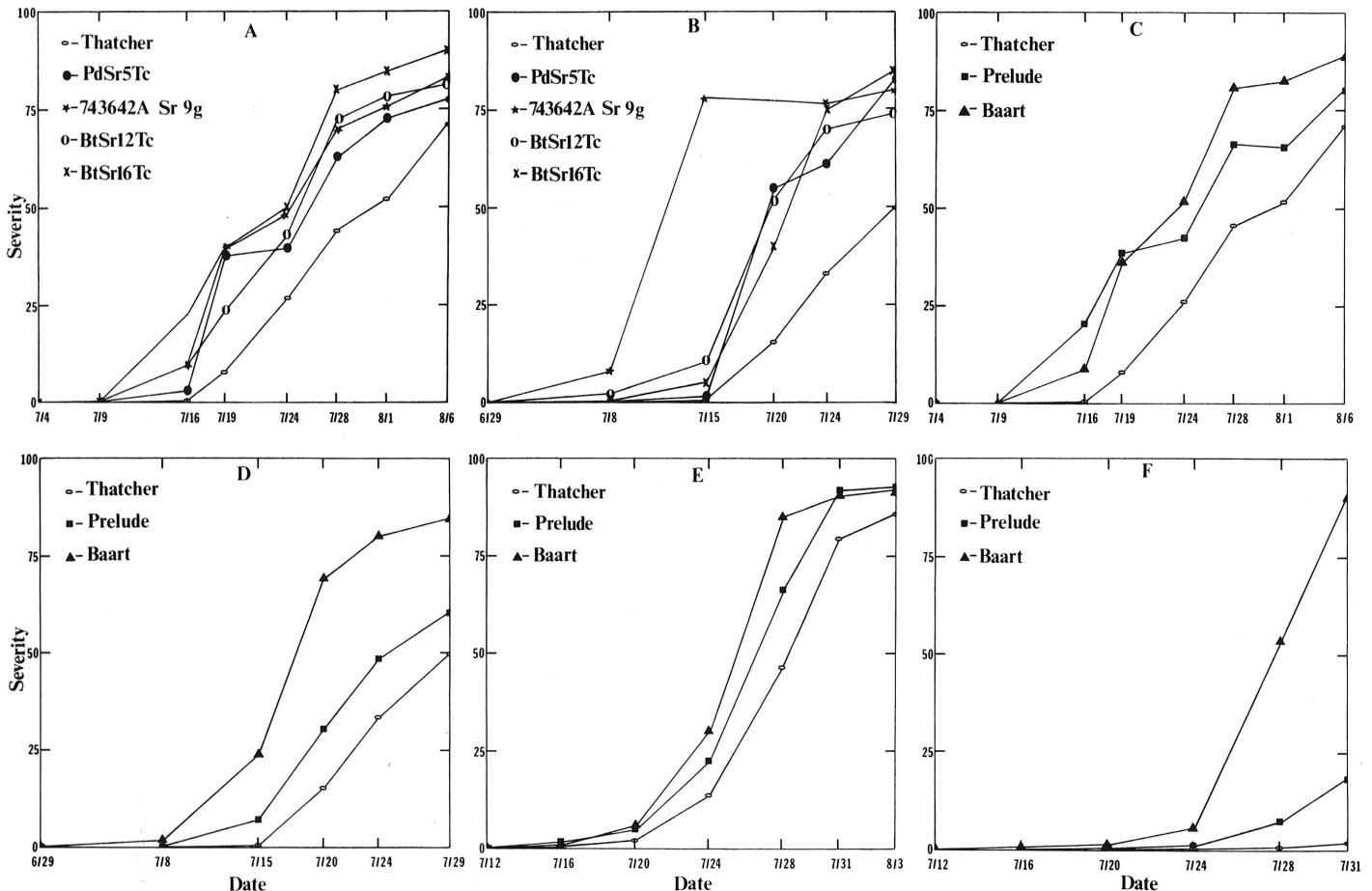


Fig. 1. Wheat stem rust progress curves for: **A,B**, Thatcher, and "single" gene lines PdSr5Tc, 743642ASr9g, BtSr12Tc, and BtSr16Tc, at St. Paul and Rosemount, in 1978, respectively. Data are means of 2, 2, 4, and 4 replicates of the "single" gene lines, respectively, and 48 of Thatcher. **C, D**, Thatcher, Prelude, and Baart, at St. Paul and Rosemount in 1978, respectively. Data are means of 48, 8, and 8 replicates, respectively. **E,F**, Thatcher, Prelude, and Baart, at St. Paul and Rosemount in 1979, respectively. Data are means of 6 replicates.

RESULTS

Relationship of seedling and adult plant resistance of Thatcher.

The stem rust progress curves for the "single" gene lines and Thatcher are shown in Fig. 1A and B for St. Paul and Rosemount, respectively.

The 1978 terminal rust severity of the sib-lines, grouped by seedling resistance genes possessed, are shown in Table 2. Most groups behaved similarly at both locations as indicated by the *t* values; ie, differences in terminal rust severity of the sib-lines were not significantly different ($P > 0.05$) between locations. The susceptible parent Baart responded similarly. Terminal rust severity for the sib-lines that had both *Sr12* and *SrTc*, and for Thatcher and Prelude at St. Paul, differed significantly from those at Rosemount ($P < 0.05$ for the sib-lines, and $P < 0.01$ for the cultivars Thatcher and Prelude).

The field response to stem rust of the "single" gene lines for *Sr5*, *Sr9g*, *Sr12*, and *Sr16* was similar at both locations, in contrast to the response of Thatcher (Table 2). At Rosemount, stem rust developed faster on 743642ASr9g early in the epidemic than on the other "single" gene lines, but terminal severities were similar for all lines. BtSr5Tc, PdSr5Tc, and BtSr16Tc rusted slowly at the beginning, at Rosemount, but reached terminal severities over 70%. Stem rust developed slowly on ISr16-Ra at St. Paul; however, this line had a semiwinter type of growth (it remained at stage 6 while the plot average was stage 25).

Effect of inoculum density on the adult plant resistance of Thatcher. Terminal rust severity of the parents and most "single" gene lines was greater at St. Paul than at Rosemount in 1978 (Table 2). Terminal rust severities of the sib-lines were regressed against locations. The regression coefficients for Prelude/Thatcher, $b = 0.5217$, and for Baart/Thatcher, $b = 0.2601$, differed significantly from $b = 1.0000$ ($t = 3.6173^{**}$, 93 df, and $t = 8.3709^{**}$, 89 df, for Prelude/Thatcher and Baart/Thatcher, respectively); therefore, differences existed between nurseries. One of these differences was inoculum density (heavier at St. Paul). Climatic data suggested that the environment was favorable for rust development throughout the season at both locations.

The 1978 stem rust progress curves for Thatcher, Prelude, and Baart, at St. Paul and Rosemount, are shown in Fig. 1C and D, respectively. The disease progress curve for Prelude was intermediate between those of Thatcher and Baart. The resistance of Thatcher, as measured by severity, was easier to distinguish at the beginning of the epidemic from Prelude or Baart than when plants were near maturity at both locations. Thatcher had a terminal severity as high as 85% (Table 2).

In 1979, the inoculum density was higher at St. Paul, as shown by the cumulative urediospore count of 27,732 spores per square centimeter at St. Paul, and 4,279 spores per square centimeter at Rosemount. The parents responded to stem rust in 1979 approximately as they did in 1978 (Fig. 1E, F). Prelude was intermediate in response between Baart and Thatcher, except on the last two reading dates at St. Paul, when Prelude had severities similar to Baart (Fig. 1E). Differences in severity among parents and the test lines (Figs. 1E and 2) were greatest when parents and sib-lines were approximately at stage 24 on 28 July.

Even though Baart rusted more severely at St. Paul, there was no significant difference in terminal rust severity between locations in either year ($t = 1.5275$ NS, 14 df, $P > 0.05$, in 1978, and $t = 0.4754$ NS, 10 df, $P > 0.05$, in 1979). Thatcher, however, responded differently to inoculum density. The average terminal rust severity in 1978, for Thatcher at St. Paul, was significantly higher than at Rosemount ($t = 9.2236^{**}$, 46 df, and $t = 6.0910^{**}$, 46 df, for Thatcher on Baart/Thatcher and Prelude/Thatcher blocks, respectively). A $t = 13.3038^{**}$, 10 df, for the same comparison in 1979, indicated that Thatcher rusted significantly more at St. Paul. Prelude also was sensitive to inoculum density, with the terminal severity at St. Paul significantly higher than at Rosemount in both years ($t = 4.58^{**}$, 14 df, in 1978, and $t = 7.6067^{**}$, 10 df, in 1979).

The "single" gene lines used as checks, Prelude, and Baart had a susceptible ("S") field response at both locations throughout the 1978 season, whereas Thatcher was moderately resistant ("MR") to moderately susceptible ("MS"). Near the end of the 1979 season (stage 26), Baart was rated "S", Prelude "S" to "MS", and Thatcher "MS" to "MR".

In the analysis of variance for rust severity at growth stage 24 and

TABLE 2. Wheat stem rust resistance genes, population size, terminal severity at St. Paul (heavy inoculum density) and Rosemount (light inoculum density), and the *t* test of the location mean comparison, for Prelude/Thatcher and Baart/Thatcher progenies, parents, and "single" gene lines in 1978

Postulated Sr gene(s) and checks	No. of lines or replicates ^b	Terminal stem rust severity ^a				<i>t</i> values ^c	No. of lines or replicates ^d	Terminal stem rust severity ^a				<i>t</i> values ^c
		St. Paul		Rosemount				St. Paul		Rosemount		
		Mean	Range	Mean	Range			Mean	Range	Mean	Range	
<i>Sr5</i>	12	76	60-90	75	40-90	0.2489	16	78	65-85	75	60-90	1.0411
<i>Sr12</i>	5	78	75-85	74	60-80	0.8944	3	73	50-85	67	50-75	0.4650
<i>Sr16</i>	9	78	65-95	71	55-95	1.4696	11	85	80-90	76	70-90	2.0580
<i>SrTc</i>	6	78	65-85	71	40-90	0.6956	2	85	...	75
<i>Sr5, Sr12</i>	7	66	50-75	56	30-80	1.0380	5	76	50-85	67	55-75	1.1619
<i>Sr5, Sr16</i>	4	76	50-90	73	55-80	0.3480	3	87	80-90	77	70-85	1.8091
<i>Sr5, SrTc</i>	4	70	60-80	59	40-80	1.1399	1	95	...	80
<i>Sr12, Sr16</i>	3	82	80-85	73	70-80	2.2361	4	64	5-85	78	65-85	0.6809
<i>Sr12, SrTc</i>	12	72	30-90	53	10-80	2.1912*	9	86	80-95	73	45-90	2.3062*
<i>Sr16, SrTc</i>	3	82	70-90	82	70-90	0.0000	3	80	65-95	67	55-75	1.2649
<i>Sr5, Sr12, Sr16</i>	2	68	50-85	73	60-85	0.2350	8	75	55-85	72	50-85	0.5169
<i>Sr5, Sr12, SrTc</i>	5	66	45-90	52	25-70	1.1337	7	80	60-90	63	50-90	2.3455
<i>Sr5, Sr16, SrTc</i>	1	60	...	85	1	80	...	75
<i>Sr12, Sr16, SrTc</i>	1	60	...	50	4	84	75-90	78	65-85	0.9285
<i>Sr5, Sr12, Sr16, SrTc</i>	3	69	60-80	75	60-90	0.6328	0
None	18	76	40-90	80	40-90	0.9647	13	82	60-95	73	50-85	2.0138
Thatcher	24	73	60-85	54	30-85	6.0907**	24	70	60-80	47	35-70	9.2236**
Prelude	8	80	70-90	61	50-75	4.5826**	0
PdSr5Tc	2	80	...	77	70-85	0.3333	0
Baart	0	8	89	85-95	84	75-90	1.5275
BtSr5Tc	0	2	77	70-85	82	80-85	0.6325
743642ASr9g	2	82	75-90	77	75-80	0.6325	2	82	80-85	82	80-85	0.0000
BtSr12Tc	2	85	80-90	85	...	0.0000	2	77	75-80	70	65-85	0.2425
ISr16-Ra	2	42	35-50	72	70-75	3.7947	2	35	25-45	65	60-70	2.6833

^a Based on modified Cobb Scale (14).

^b Prelude/Thatcher progeny.

^c * and ** = $P < 0.05$ and $P < 0.01$, respectively.

^d Baart/Thatcher progeny.

at maturity for St. Paul, 1979 (heavy inoculum density) and terminal for Rosemount, 1979 (light inoculum density), the block \times treatment interactions were not significant ($P > 0.10$) in all cases. This suggested that the oats planted between replicates decreased the movement of inoculum.

There was greater variability among terminal severities at Rosemount than at St. Paul in 1979 (Fig. 2A, C). Differences at stage 24 were not detected in Rosemount because only trace amounts of disease developed in the field. Rust severities at St. Paul varied more between lines at stage 24 than at the end of the season (Fig. 2B, C).

Terminal rust severity on Thatcher was not different from that on Prelude or Baart at St. Paul (Table 3). Under conditions of heavy inoculum density as many as nine of the sib-lines were not distinguishable from either the resistant or susceptible parent, as indicated by Duncan's multiple range test of significance ($P > 0.05$, Table 3). Rust severity of Thatcher, however, was different from that of Prelude and Baart at stage 24 ($P < 0.05$), and seven sib-lines were statistically similar to Thatcher. The severity of Prelude was not different from that of Thatcher and 12 of 15 sib-lines behaved similarly to Thatcher under low inoculum density ($P > 0.05$).

DISCUSSION

The race-specific seedling resistance genes *Sr5*, *Sr12*, *Sr16*, and *SrTc*, of Thatcher were postulated in the progenies. Results of earlier studies indicated that *Sr5*(10,20) and *Sr12*(3) are not related either to the adult plant resistance of Thatcher or the slow rusting character of Era wheat (8). This study indicated that, unlike

Thatcher, the progeny lines that possess only *Sr5*, *Sr12*, *Sr16*, or *SrTc*, regardless of the susceptible parent involved, have a similar disease response under different inoculum concentrations ($P > 0.05$). *SrTc* is a gene characterized by a "23C" to and "X" seedling infection-type on Thatcher, by races virulent on *Sr5*, *Sr9g*, *Sr12*, and *Sr16*. One progeny line with *SrTc* rusted significantly more than Thatcher ($P < 0.05$). Thus, this study (8) produced no evidence that any of the *Sr* genes for stem rust resistance of Thatcher are independently related to the adult plant resistance as determined under different disease intensity in the field.

It has been proposed that pyramiding race-specific genes would result in generalized resistance greater than the summation of the specific resistances due to each gene (12). The data from lines with genes *Sr5*, *Sr12*, *Sr16*, and *SrTc* were grouped into various combinations of 2, 3, or 4. There was no evidence of increased resistance in lines with combinations of the *Sr* genes. In most combinations, unlike that in Thatcher, the amount of disease was similar between locations ($P > 0.05$). Sometimes, the sample size was too small to support statistical inferences (ie, combinations of *Sr5*, *Sr16*, and *SrTc* and *Sr12*, *Sr16*, and *SrTc* lines).

The only lines with combinations of genes that performed like Thatcher were *Sr12* and *SrTc* in both crosses. Some lines with this genetic combinations rusted more at St. Paul than at Rosemount ($P < 0.05$). Earlier reports showed that the adult plant resistance of Thatcher was inherited by two complementary recessive genes (5,6,11,13,18). It is possible that *SrTc* is located on the same chromosome as *Sr12*, and that some of the factors responsible for the adult plant resistance of Thatcher are located between these two genes. There were *Sr12*, *SrTc* lines more resistant than Thatcher in the Prelude/Thatcher cross. Skovmand et al (21) reported that Prelude possessed some genes for slow rusting which in combination with those of Thatcher must have rendered some of *Sr12* *SrTc* lines more resistant than Thatcher. The occurrence of *Sr12* *SrTc* lines that rusted more severely than Thatcher, however, showed that the adult plant resistance of Thatcher was not due to these genes per se (severity at stage 24).

Brennan (1) identified genes on 6A and 2B chromosome substitution lines of Thatcher, that, independently, cause a reduction in number of stem rust pustules. Brennan's results contrasted with those of others in that they indicated that the adult plant resistance of Thatcher, as measured by receptivity (18), or by

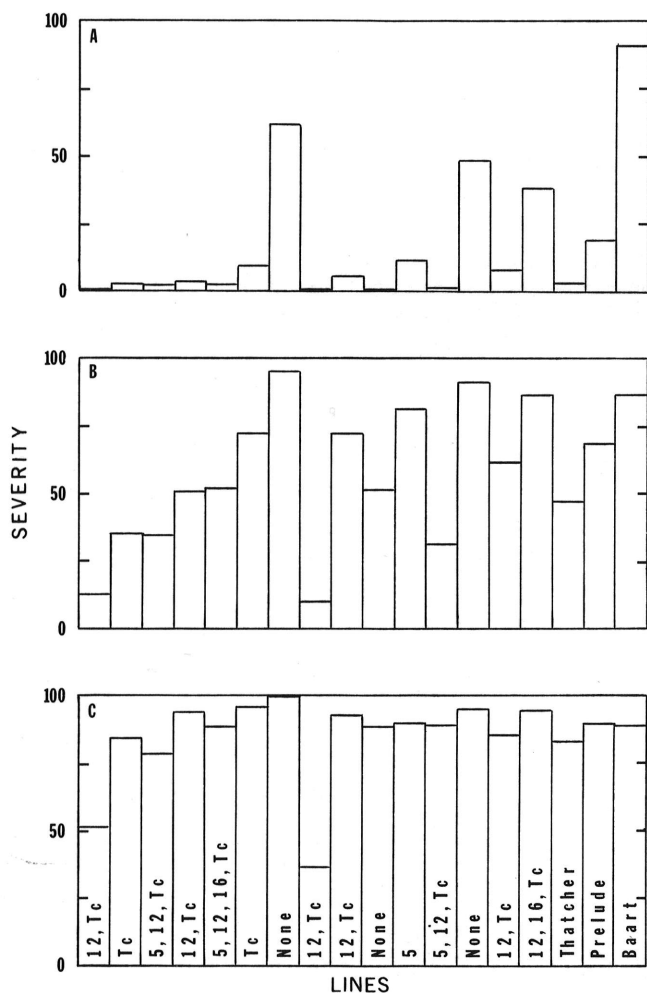


Fig. 2. Wheat stem rust severity in 1979 for the cultivars Thatcher, Prelude, and Baart, and selected sib-lines: A, Terminal severity, at Rosemount; B, At growth state 24 (early milk), at St. Paul; and C, Terminal severity, at St. Paul.

TABLE 3. Wheat stem rust severity at early milk (stage 24) and at maturity at St. Paul, and at maturity at Rosemount, for the parents, Thatcher, Prelude, and Baart, and selected sib-lines, in 1979

Postulated genotype, or cultivar	Stem rust severity ^a		
	St. Paul Stage 24	St. Paul Terminal	Rosemount Terminal
<i>Sr12</i> , <i>SrTc</i>	13 i ^b	53 e	Trace d
<i>SrTc</i>	41 gh	86 cd	3 d
<i>Sr5</i> , <i>Sr12</i> , <i>SrTc</i>	41 fgh	80 d	2 d
<i>Sr12</i> , <i>SrTc</i>	49 efg	96 abc	3 d
<i>Sr5</i> , <i>Sr12</i> , <i>Sr16</i> , <i>SrTc</i>	50 efg	91 abcd	3 d
<i>SrTc</i>	72 bcd	98 ab	8 d
None ^c	96 a	100 a	63 b
<i>Sr12</i> , <i>SrTc</i>	9 i	42 f	Trace d
<i>Sr12</i> , <i>SrTc</i>	72 bcd	95 abc	7 d
None	48 efg	90 abcd	Trace d
<i>Sr5</i>	79 abc	94 abc	13 d
<i>Sr5</i> , <i>Sr12</i> , <i>SrTc</i>	30 h	92 abc	2 d
None	89 ab	98 ab	48 bc
<i>Sr12</i> , <i>SrTc</i>	60 def	87 bcd	9 d
<i>Sr12</i> , <i>Sr16</i> , <i>SrTc</i>	85 abc	96 abc	39 c
Thatcher	46 fgh	86 cd	2 d
Prelude	67 cde	93 abc	19 d
Baart	85 a	92 abc	90 a

^aSeverity = % based on the modified Cobb Scale (14).

^bRust severity values followed by Duncan's multiple range test of significance ($P < 0.05$).

^cNo *Sr* genes for seedling resistance were detected in the greenhouse experiments.

rust rating in the field (5,6,11,13) is due to a complementary recessive gene pair. If only two genes, as proposed by Brennan (1), are involved in the adult plant resistance of Thatcher, then the hypothesis of having one of them located between *Sr12* and *SrTc* is unsatisfactory, because *Sr12* is known to be on chromosome 3B (19).

The lack of correlation between the adult plant resistance and the seedling resistance genes of Thatcher also was demonstrated by a line without the genes *Sr5*, *Sr12*, *Sr16*, or *SrTc* that responded similarly to Thatcher at growth stage 24 and at maturity at St. Paul in 1979. All lines were infected early in the season, so the response of this line was not due to disease escape.

Thatcher responded differently under different inoculum densities in these experiments. The wide variation of stem rust response of Thatcher in the field, which is influenced by the amount of disease pressure, is illustrated by the difference of approximately 20 and 82% in terminal rust severity of Thatcher between St. Paul (heavy inoculum density) and Rosemount (light inoculum density) in 1978 and 1979, respectively. Stem rust races occurring in both years were virulent on all known seedling resistance genes of Thatcher at 23 C. The difference in rust severities at Rosemount between years was due to the reduced amount of exogenous inoculum arriving from the southern USA (A. P. Roelfs, unpublished).

In 1978, each line occurred once in a 1.0-m row plot adjacent to another line. Thus, if a resistant line were between susceptible lines, the inoculum generated by the latter may have affected the inoculum density and the disease response of the former, making selection success low. Nevertheless, resistant and susceptible lines were selected in 1978, based on terminal rust severity and rust severity at stage 27, at the heavy inoculum density location. These lines were retested in 1979, and they proved that the selection was successful.

It is possible that inoculum moved readily from row to row in 1978, and resulted in increased rust severities on some lines. In 1978, terminal rust severity on one line was 72%; however, with some isolation in 1979, it was 42%. In 1979, rows of oats planted between the test plots tended to reduce the plot-to-plot movement of inoculum. This conclusion is supported by the analysis of variance. A nonsignificant block \times treatment interaction term suggested that, among other factors, the inoculum produced on a susceptible line did not move in sufficient amounts to mask the field response of the adjacent lines. Yet, Thatcher had as wide a range of terminal rust severity in 1979 as it did in 1978.

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