Genetics of Stem Rust Resistance in Wheat Cvs. Pasqua and AC Taber

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Accepted for publication 24 November 1997.

ABSTRACT

Liu, J. Q., and Kolmer, J. A. 1998. Genetics of stem rust resistance in wheat cvs. Pasqua and AC Taber. Phytopathology 88:171-176.

Canadian wheat cvs. Pasqua and AC Taber were examined genetically to determine the number and identity of stem rust resistance genes in both. The two cultivars were crossed with stem rust susceptible line RL6071, and sets of random F_6 lines were developed from each cross. The F_6 lines, parents, and tester lines with single stem rust resistance genes were grown in a field rust nursery, inoculated with a mixture of stem and leaf rust races, and evaluated for rust resistance. The same wheat lines were tested by inoculation with specific stem rust races in seedling tests to postulate which *Sr* genes were segregating in the F_6 lines. Segregation of F_6 lines indicated that Pasqua had three genes that conditioned field resistance to stem rust and had seedling genes *Sr5*, *Sr6*, *Sr7a*, *Sr9b*, and *Sr12*. Leaf rust resistance gene *Lr34*, which is in Pasqua, was associated with adult-plant stem rust resistance in the segregating F_6 lines. Adult-plant gene *Sr2* was postulated to condition field resistance in AC Taber, and seedling genes *Sr9b*, *Sr11*, and *Sr12* also were postulated to be in AC Taber.

Additional keywords: CIMMYT germ plasm, *Puccinia graminis* f. sp. *tritici*, specific resistance, Thatcher wheat.

Resistance to stem rust (*Puccinia graminis* Pers. f. sp. *tritici* Eriks. & E. Henn.) is a high priority in spring wheat (*Triticum aestivum* L.) breeding programs throughout western Canada. Prior to the release of resistant cultivars, stem rust epidemics caused regular yield losses in western Canada. The last major epidemics of stem rust on spring wheat were caused by race 15B during the 1950s (7,8). All cultivars released after the race 15B epidemics have been highly resistant to stem rust.

Two major sources of stem rust resistance historically have been used in spring wheat breeding programs in North America. Adult-plant resistance from cv. Yaroslav Emmer was transferred via the common wheat line H-44-24a (17) to cv. Renown (18), which was the first stem rust and leaf rust resistant cultivar released by the Cereal Research Centre in Winnipeg, MB, Canada, in 1937. Cvs. Regent, Redman, and Selkirk are derivatives of Renown, with adult-plant stem rust resistance from Yaroslav Emmer (15). This gene was designated *Sr2* (12,18). The other source of stem rust resistance has been cv. Thatcher, in which resistance was derived from cv. Iumillo durum (10). Resistance in Thatcher also is most effective in the adult-plant stage. Cultivars with either source of resistance have been highly resistant to stem rust for the past 40 years.

Since the late 1960s, cultivars based on the Thatcher derivative Neepawa (Napayo, Katepwa, Columbus, Kenyon, Minto, Roblin, and AC Cora) have been the predominant high-quality bread wheats grown in western Canada. These cultivars were developed by incorporating additional genes for stem rust, leaf rust, or sprouting resistance into Neepawa. Cv. Pasqua was developed by crossing BW63, a Neepawa derivative with five leaf rust resistance genes, with cv. Columbus, which is a Neepawa derivative that has improved sprouting resistance.

The Canada Prairie Spring (CPS) wheat class was initiated during the mid-1980s in western Canada. These wheats have higher yield potential and lower protein content compared to Neepawa-type wheats. CPS wheats have a quality type suited for flat breads and Asian noodles and have a high proportion of wheats from the International Wheat and Maize Improvement Center (CIMMYT), Mexico D.F., in their background. Cv. AC Taber was developed by backcrossing common bunt resistance into CPS cv. Biggar (13).

Stem rust resistance in current bread and CPS wheats eventually may be threatened by the introduction of a new virulent race. In 1991, race QCC, which is virulent to stem rust resistance gene *Rpg1* in cultivated barley, became common in North America (9). Barley cultivars with *Rpg1* had been resistant to prevalent stem rust races prior to the introduction of QCC. Introduction of other stem rust races with virulence to commonly grown spring wheats may occur. Identification of stem rust resistance genes in current cultivars will facilitate incorporation of additional effective genes into breeding programs. The objectives of this study were to identify the stem rust resistance genes in cvs. Pasqua and AC Taber, which are representative of western Canada bread and CPS wheats, respectively.

MATERIALS AND METHODS

Spring wheat cvs. Pasqua (Pasqua = BW63*2/Columbus; BW63 = Neepawa + leaf rust resistance genes *Lr11*, *Lr14b*, *Lr22a*, *Lr30*, and *Lr34*; and Columbus = Neepawa*6/RL4137) and AC Taber (13) (AC Taber = Tobari/Romany*3//BW553; and BW533 = Red Bobs*2/PI 78383//8*Neepawa) were crossed with RL6071, a stem rust susceptible line from cv. Marquis (5). Random F_6 lines (108 total) were developed from RL6071/Pasqua, and 76 lines from RL6071/AC Taber were developed by single-seed descent from the F_2 to F_5 generations. Plants with winter habit were discarded in each generation in the AC Taber cross. Approximately 50 seeds from each F_5 plant were planted as F_6 lines in 2-m rows in a field rust nursery. Spreader rows of stem rust susceptible wheat and barley cultivars were grown perpendicular to rows of the F_6 lines, parents, and single-gene *Sr* lines: *Sr5*: Prelude*6/Reliance; *Sr6*: Mida/McMurachy/Exchange//6*Prelude; *Sr7a*: Na101/6*Marquis;

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Publication no. P-1997-1224-01R
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Sr9b: Prelude*4/2/Marquis*6//K.117A; *Sr11*: Chinese Spring*9/Timstein; and *Sr12*: Chinese Spring*5/Thatcher 3B. The spreader rows were inoculated with a mixture of stem rust races TMR, RHT, QTH, RKQ, and TPM (*P. graminis* f. sp. *tritici* nomenclature [21]) and a bulk collection of leaf rust races from western Canada (14). Stem rust ratings were recorded when the susceptible parent, RL6071, had a severity (20) and response (25) rating of 60% moderately susceptible to susceptible (60 MS-S). The F_6 lines from RL6071/Pasqua also were scored for leaf rust severity and leaf-tip necrosis (the *Ltn* gene), a condition associated with the presence of the adult plant leaf rust resistance gene *Lr34* (23), which is in Pasqua (4).

The F_6 lines from both crosses, parents, cv. Thatcher, line RL6058 (a Thatcher backcross line with *Lr34*), and single-gene *Sr* lines also were tested as seedlings in a greenhouse with different *P. graminis* f. sp. *tritici* races to postulate the identity of specific resistance genes segregating in the F_6 lines. Seeds (12 to 20) of each F_6 line were planted in clumps in fiber flats filled with a sand-peat-soil mixture or in a greenhouse bed. Plants were grown at 20 ± 2°C, with 8 h of supplemental fluorescent light (276 µmol m^{-2} s^{-1}) per day. Eight to ten days after seeding, seedlings were inoculated by atomizing urediniospores suspended in Soltrol light mineral oil (Novartis Canada Ltd., Mississauga, ON). Inoculated plants were air-dried for 1 to 2 h to allow full evaporation of oil from leaf surfaces and incubated in a dew chamber (Percival model ID-60, Boone, IA) at 100% relative humidity for 16 h in darkness at 20°C. After incubation, the sets were covered with transparent plastic sheets for about 4 h to prevent excessively rapid drying of the plants. Infection types (ITs) on primary leaves were rated 14 to 15 days after inoculation, using a scale of 0 to 4 (25): ITs 0 (immune), ; (fleck), 1 (small uredinia with necrosis), 2 (small uredinia with chlorosis), and 3 (small uredinia without chlorosis or necrosis) were considered resistant, and ITs 3^+ to 4 (large uredinia without chlorosis or necrosis) were considered susceptible. The identity of *Sr* genes in the F_6 lines was postulated by comparison of ITs with the single-gene *Sr* lines. Goodness-of-fit to segregation ratios in the population of F_6 lines from each cross was determined by chi-square tests (26). In both seedling- and adult-plant tests, a small number of random lines segregated for stem rust reaction. The heterogeneous lines were excluded from data analysis.

RESULTS

Cv. Pasqua. In the field nursery, Pasqua and RL6058 exhibited high levels of resistance to *P. graminis* f. sp. *tritici*, with only trace (TR) levels of stem rust uredinia (Table 1). Thatcher had an intermediate level of field resistance. The stem rust severity and response of RL6071/Pasqua F_6 lines varied from TR to 70% susceptible (70 S) (Table 1). Of the 108 F_6 lines tested, 14 were as resistant as Pasqua, and 13 were as susceptible as RL6071 (Table 2). The segregation of 95 resistant lines (TR-50 MS) to 13 susceptible lines (40-70 S) fit a 7:1 ratio, which indicated Pasqua had three genes that conditioned field resistance to *P. graminis* f. sp. *tritici*. The F_6 lines segregated for *Ltn* in a 1:1 ratio ($\chi^2 = 0.083$, $P = 0.90$ to 0.75) (Table 3). Because all of the lines with *Ltn* were leaf rust resistant, *Ltn* could be used to identify lines with *Lr34*. A contin-

TABLE 1. Seedling-plant infection types[a] and adult-plant field reactions[b] to *Puccinia graminis* f. sp. *tritici* in wheat cultivars or lines Pasqua, AC Taber, Thatcher, RL6058, and RL6071; selected F_6 lines RL6071/Pasqua and RL6071/AC Taber (with postulated *Sr* genes in parentheses); and lines with single *Sr* genes

Cultivar/line	Resistant parent	MCC[c]	HFH	RKQ	TPM	MPN	RHT	Field rust severity (%) and response
Pasqua		0;	0;	0;	0;	…[d]	…	TR
AC Taber		;	;12^-	12^-	12^-	;12^-	1^+2	10 R
Thatcher		;1	0;	2^+3	3^+	;1	;23	30 MS
RL6058 (*Lr34*)		0;	0;	0;	0;	…	…	TR–MR
RL6071		3^+	4	4	4	4	4	60 MS–S
Sr5		4	0;	4	4	…	…	70 S
116 (*Sr5*, *Ltn*)	Pasqua	3^+	0;	4	4	…	…	5 MR
10 (*Sr5*, *Sr7a*)	Pasqua	4	0;	2	4	…	…	30 MS–60 S
Sr6		;	;	3^+4	;	…	…	50 MS
64 (*Sr5*, *Sr6*)	Pasqua	0;	0;	4	;	…	…	5–30 MR–MS
67 (*Sr5*, *Sr6*, *Ltn*)	Pasqua	0;	0;	4	0;	…	…	TR
Sr7a		3^+4	4	2^-	4	…	…	20–30 MR–MS
69 (*Sr7a*, *Ltn*)	Pasqua	3^+4	4	12^+	4	…	…	10 MR–MS
23 (*Sr5*, *Sr7a*, *Sr12*)	Pasqua	;12	0;	22^+	4	…	…	40 MR–60 S
Sr9b		12^-	3^+4	4	2	12	4	50 MS–70 S
109 (*Sr9b*)	Pasqua	22^+	4	33^+	23^-	…	…	50 MS–70 S
36 (*Sr5*, *Sr9b*, *Ltn*)	Pasqua	22^+	0;	3^+4	12	…	…	TR–5R
2 (*Sr9b* + *Sr2*)	AC Taber	2	4	4	122^+	2	4	10–20 MR
64 (*Sr9b*)	AC Taber	;1	4	4	122^+	12	4	50 MS
Sr11		;	;1	;1	4	4	;1^-	50 MS–70 S
44 (*Sr11*)	AC Taber	2	2^+3c	2^+3c	4	3^+4	12^-	80 MS
10 (*Sr11*, *Sr12*)	AC Taber	;1	;1	$22^\pm$	4	2	12^-	40 MS–S
Sr12		;22^+	$2^\pm3$	4	4	;12	3^+4	40–50 S
113 (*Sr12*, *Ltn*)	Pasqua	;1	2^+3	3^+4	4	…	…	TR
47 (*Sr5*, *Sr12*)	Pasqua	;1	0;	4	4	…	…	40 MS–S
11 (*Sr12*)	AC Taber	;12^+	;$2^\pm$	3^+4	4	$22^\pm$	4	40 MS–S
68 (*Sr11*, *Sr12* + *Sr2*)	AC Taber	12	2	$22^\pm$	4	2	12^-	20 MR–40 MS

[a] Infection types on primary leaves were rated 14 days after inoculation on a scale of 0 to 4 (25).
[b] Field reactions to a mixture of *P. graminis* f. sp. *tritici* races in a field rust nursery. Percent rust severity ranged from a trace (TR) to 100% on individual plants. R = resistance (flecks and small uredinia with necrosis); M = mixed infections (small and moderate uredinia); MR = moderately resistant (large necrotic flecks and uredinia); MS = moderately susceptible (moderate to large uredinia with chlorosis); and S = susceptible (large uredinia).
[c] Stem rust race *P. graminis* f. sp. *tritici* nomenclature (21).
[d] Not tested.

gency chi-square test (Table 3) showed a strong association between field stem rust resistance and *Ltn* ($\chi^2 = 25.56$, $P < 0.001$) in the population of random lines. Of the 26 F_6 lines classified as TR, 22 had *Ltn*, whereas none of the 13 lines classified as susceptible had *Ltn*.

The RL6071/Pasqua F_6 lines, parents, cv. Thatcher, and line RL6058 were tested at the seedling stage with different *P. graminis* f. sp. *tritici* races. Pasqua and RL6058 had IT 0; to all races used (Table 1). Thatcher had IT 0; to HFH, IT ;1 to 2^+3 to races MCC, RKQ, MPN, and RHT, and IT 3^+ to TPM. Of 104 F_6 lines tested with race MCC, 73 were highly resistant (IT 0;), 18 were moderately resistant (IT 2 to 2^+), and 13 were susceptible (IT 3^+4) (Table 2). The segregation of 91 resistant lines (IT 0 to 2^+) to 13 susceptible lines (IT 3^+4) fit a three-gene ratio (7:1). When inoculated with race TPM, the F_6 lines segregated 75 resistant to 28 susceptible lines to fit a two-gene ratio (3:1).

The genes conditioning resistance to TPM were two of the three genes conferring resistance to MCC, because all 75 lines resistant to TPM also were resistant to MCC. Of the resistant lines, 25 had IT 1^+ to 3^- and 50 had IT 0;. The gene conditioning IT 1^+ to 3^- should be *Sr9b*, because some F_6 lines (e.g., lines 36 and 109 in Table 1) resistant to TPM had the characteristic IT 1^+2 of the single-gene line *Sr9b* (Table 1). The 50 F_6 lines that had low IT 0; to TPM should have either only *Sr6* or both *Sr6* and *Sr9b*. When tested with HFH, a race avirulent to *Sr6* but virulent to *Sr9b*, 81 F_6 lines had IT 0;, 11 had IT 2 to 3, and 13 had IT 3^+4 (Table 2). The segregation of 92 resistant lines (IT 0; to 2^+3) to 13 susceptible lines (IT 3^+4) gave a good fit to a 7:1 ratio, which indicated that Pasqua had two genes conditioning IT 0; and one gene conditioning intermediate IT 2^+3 to HFH. One of the genes giving IT 0; should be *Sr6*, which also conferred resistance to MCC and TPM, and the other must be *Sr5*, because lines 10 and 116 had low ITs identical to the single-gene line *Sr5* (Table 1). This gene conditions IT 0; to HFH but is ineffective against MCC and TPM.

The third gene that conditioned an intermediate level of resistance to HFH was one of the three genes conferring resistance to MCC, because all F_6 lines giving IT 2^+3 to HFH also were resistant to MCC. This gene is most likely *Sr12*, because F_6 lines with only *Sr12* (e.g., line 113) or together with *Sr5* and *Sr6* (e.g., line 47) were identified in the population of random lines (Table 1). The F_6 lines segregated to fit a single-gene ratio when inoculated with RKQ, which is virulent to *Sr5*, *Sr6*, *Sr9b*, and *Sr12*. This gene appeared to be *Sr7a*, because F_6 lines resistant to RKQ had the characteristic IT 2 to 2^+ of the single-gene line *Sr7a*. Results from the seedling tests indicated that Pasqua has at least five seedling genes, which are postulated to be *Sr5*, *Sr6*, *Sr7a*, *Sr9b*, and *Sr12*, for stem rust resistance (Tables 1 and 2).

The presence of *Sr6* in Pasqua was demonstrated further in an additional seedling test, in which RL6071/Pasqua F_6 lines postulated to have gene *Sr6* but lacking *Sr7a* were tested with races RCR and QTH. Race RCR is avirulent to *Sr6* and virulent to *Sr5*, *Sr9b*, and *Sr12*. *Sr6* is temperature sensitive, conditioning IT 0; to 1 at low incubation temperatures ($\lesssim$20°C) but high IT 3^+4 at temperatures $\gtrsim$24°C (18). Race QTH is virulent to all five stem rust resistance genes identified in Pasqua with the selected *P. graminis* f. sp. *tritici* races (Table 4). The inoculated plants were incubated at 25 ± 2°C and 18 ± 2°C, respectively. Of 26 lines tested with RCR, three lines (i.e., lines 3, 67, and 91) had high IT 3^+4 after incubation at high temperatures and low IT ; at low temperatures, which indicated the presence of *Sr6* (Table 4). Twenty-three lines exhibited an intermediate level of resistance (IT ;12) to RCR at high temperatures and a low IT 0; at low temperatures, which also indicated that these lines had resistance gene(s) in addition to *Sr6*. As expected, all lines tested with QTH gave IT 3^+4 at high temperatures. However, 5 of 26 F_6 lines tested (e.g., lines 3 and 90 in Table 4) had intermediate IT 2^+3 to QTH at low temperatures, which indicated that Pasqua may have additional genes for stem rust resistance.

The F_6 lines with *Ltn* and postulated *Sr* genes were compared for IT with lines that lacked *Ltn* (Table 1). No differences in seedling IT could be attributed to the presence of *Ltn* in the F_6 lines. Lines with combinations of *Sr5*, *Sr7a*, *Sr9b*, *Sr12*, and *Ltn* had ITs very similar to lines with the same *Sr* genes but lacking *Ltn*.

Cv. AC Taber. In the field test, AC Taber had a stem rust severity and response of 10 R (Table 1). The field reaction of the RL6071/AC Taber F_6 lines ranged from 5 R to 70 S. The segregation of 33 resistant lines (5 R to 50 MR) to 34 susceptible lines (40 MS to 70 S) fit a 1:1 ratio, which indicated that AC Taber had one gene conditioning field resistance to *P. graminis* f. sp. *tritici* (Table 5).

In the greenhouse seedling test, AC Taber had low IT ; to race MCC and intermediate IT ;12^- to races HFH, RKQ and TPM (Table 1). The F_6 lines from RL6071/AC Taber segregated 65 resistant (IT ;1 to 2^+) to 11 susceptible (IT 3^+4) to fit a three-gene ratio (7:1) when inoculated with MCC (Table 5). When tested with TPM, the F_6 lines segregated 43 resistant lines (IT ;12 to 2^+) to 34 susceptible lines (IT 3^+4) to fit a 1:1 ratio, which indicated there was one gene for resistance. This gene, presumably *Sr9b*, was one of the three genes conferring resistance to MCC, because all 43 lines that were resistant to TPM also were resistant to MCC. When

TABLE 2. Segregation for seedling-plant infection[a] type and adult-plant resistance to *Puccinia graminis* f. sp. *tritici* in F_6 lines of RL6071/Pasqua

Race[b]	Postulated *Sr* genes	No. of lines and infection type (R^c:S^d)	Expected ratio (R:S)	*P*[e]
MCC	*6, 9b, 12*	91:13	7:1	>0.95
		73:18:13 (0;) (22^+) (3^+4)	6:1:1	0.50–0.25
HFH	*5, 6, 12*	92:13	7:1	>0.95
		81:11:13 (0;) (2–3) (3^+4)	6:1:1	0.90–0.75
RKQ	*7a*	54:50 (1–2^+) (3^+4)	1:1	0.90–0.75
TPM	*6, 9b*	75:28 (0;–2^+) (3^+4)	3:1	0.75–0.50
Field test[f]	*Thatcher + Lr34*	95:13	7:1	>0.95

[a] Infection types on primary leaves were rated 14 days after inoculation on a scale of 0 to 4 (25).
[b] Stem rust race *P. graminis* f. sp. *tritici* nomenclature (21).
[c] Resistant line.
[d] Susceptible line.
[e] Probability of χ^2 value.
[f] A mixture of stem rust races was used to initiate a rust epidemic.

TABLE 3. Adult-plant field reactions[a] to *Puccinia graminis* f. sp. *tritici* and relationship with the presence (+) or absence (–) of leaf-tip necrosis in F_6 lines of RL6071/Pasqua

Reaction to stem rust	Leaf-tip necrosis +	Leaf-tip necrosis –	Total	χ^2	*P*
TR	22	4	26		
MR–MS	33	36	69		
S	0	13	13		
Total	55	53	108	25.564	<0.001

[a] Field reactions to a mixture of *P. graminis* f. sp. *tritici* races in a field rust nursery. Percent rust severity ranged from a trace (TR) to 100% on individual plants. R = resistance (flecks and small uredinia with necrosis); M = mixed infections (small and moderate uredinia); MR = moderately resistant (large necrotic flecks and uredinia); MS = moderately susceptible (moderate and large uredinia with chlorosis); and S = susceptible (large uredinia).

tested with race HFH, the F_6 lines segregated 60 resistant (IT;1 to 2^+) to 17 susceptible (IT 3^+4) to fit a two-gene 3:1 ratio (Table 5). The genes conferring resistance to HFH were two of the three genes that conferred resistance to MCC, because all 60 F_6 lines with low to intermediate IT to HFH also were resistant to MCC. Based on IT, one of the two genes is likely *Sr12*, because F_6 lines with *Sr12* alone or with another gene (e.g., lines 11 and 68 in Table 1) were identified in the population of random lines. The second gene appeared to be *Sr11*, because F_6 lines (e.g., line 44 in Table 1) had low IT to the same races as the *Sr11* single-gene line. The presence of *Sr11* in AC Taber was confirmed further by testing the F_6 lines with RKQ, which is virulent to *Sr9b* and *Sr12* but avirulent to *Sr11*. The F_6 lines segregated 34 lines resistant to 43 lines susceptible to RKQ, which fit a single-gene ratio that confirmed the presence of *Sr11*. A greenhouse evaluation of RL6071/AC Taber F_6 lines with the selected *P. graminis* f. sp. *tritici* races indicated that AC Taber has at least three seedling genes, which are postulated to be *Sr9b*, *Sr11*, and *Sr12*, for stem rust resistance (Tables 1 and 5). The adult-plant resistance of the F_6 lines was not correlated with the presence of any postulated seedling-resistance genes. The resistant F_6 lines had a resistance response similar to *Sr2*. Adult-plant resistance in AC Taber may be conditioned by *Sr2*.

DISCUSSION

Field stem rust resistance in Pasqua was conditioned by three adult-plant resistance genes. Field resistance in the F_6 lines was not correlated with the presence of any of the identified seedling *Sr* genes. The adult-plant genes were most likely derived from Thatcher. Brennan (1) determined that the adult-plant resistance of Thatcher was due to two genes. Hayes et al. (10) found that the adult-plant stem rust resistance in a Marquis/Iumillo line, the source of Thatcher resistance, was due to two genes. The presence of *Ltn*, a marker for *Lr34*, correlated strongly with field stem rust resistance in the F_6 lines. The stem rust resistance associated with *Lr34* must be an important part of the effective stem rust resistance in Pasqua. RL6058 (Thatcher + *Lr34*) had better seedling resistance to individual stem rust races compared to Thatcher and a higher level of field resistance. Dyck (2) used the associated stem rust resistance to map *Lr34* to chromosome 7D. The complete association between *Lr34* and the increased stem rust resistance seen in RL6058 was not observed in the seedling ITs of the RL 6071/Pasqua F_6 lines, however. Some of the lines with *Ltn* had only intermediate levels of field stem rust resistance. Dyck (3) obtained similar results with random lines derived from RL 6071/Roblin and speculated that RL6071 may have a gene that inhibits the stem rust resistance associated with *Lr34*.

Lr34 by itself may not necessarily express stem rust resistance; in a Thatcher background, it may act as an enhancer of stem rust resistance genes normally suppressed in Thatcher. Chromosome 7DL of Thatcher-type wheats carries a gene that acts as a suppressor of resistance to specific races of stem rust (11). The substitution of chromosome 7D of Canthatch (Canthatch = Thatcher + *Sr7a*) by 7D of Chinese Spring, which has *Lr34*, resulted in better stem rust resistance compared to Canthatch. The 7D substitution lines had resistance equal to Canthatch nullisomic for this chromosome, which because of the absence of the 7DL suppressor showed greater resistance than Canthatch (E. R. Kerber, *unpublished data*). The third gene in Pasqua, which conditioned field resistance, may be a gene derived from Thatcher that was expressed due to the enhancement or nonsuppressing effect of *Lr34*. It is unlikely that *Lr34* by itself conditions stem rust resistance, because Chinese Spring is susceptible to stem rust. All of the suppressed stem rust resistance genes in Thatcher may not be present in Pasqua. This may explain why F_6 lines of RL6071/Pasqua with *Ltn* did not have lower seedling ITs compared to lines without *Ltn*.

In this study, the identity of homozygous F_6 lines was postulated based on comparison of IT responses to different stem rust races by the single-gene lines. Identification of the resistance genes based on this method was complicated by the numbers of genes that segregated in both crosses relative to the number of F_6 lines that were available, the possible interactions between the seedling resistance genes that could affect the IT, and the unknown effects of segregating genetic backgrounds and adult-plant resistance genes on ITs in the F_6 lines. Ideally the two cultivars, Pasqua and AC Taber, or selected derived F_6 lines, would be intercrossed with the single-gene lines, and F_2 populations from the intercrosses would be evaluated for segregation of rust resistance. This is the most conclusive method of resistance gene identification; however, it is not always practical given the number of stem rust resistance genes that may be present in wheat cultivars.

Seedling genes *Sr5*, *Sr6*, *Sr7a*, *Sr9b*, and *Sr12* were postulated to be in the RL 6071/Pasqua F_6 lines. *Sr5* originally was derived from Kanred, a parent of Thatcher. *Sr6* is present in McMurachy, which is in the pedigree of RL 4137, the sprouting resistant line that was a parent of Columbus. *Sr6* was transferred to Pasqua from RL 4137 via Columbus. *Sr7a* was backcrossed into Thatcher to develop Canthatch, and Canthatch was used in the development of BW63, a parent of Pasqua. *Sr9b* is linked to *Lr13*, which is also

TABLE 4. Seedling-plant infection type[a] responses (at two temperatures) to races QTH[b] and RCR of *Puccinia graminis* f. sp. *tritici* in selected F_6 lines of RL6071/Pasqua and single-gene lines

	QTH		RCR	
Line	25°C	20°C	25°C	20°C
Sr6	4	4	4	0;1
Sr7a	4	4	2	2
Sr9b	4	4	4	4
Sr12	4	4	4	4
3	3^+	2^+3	3^+	;
55	34	4	12	0;
67	4	4	34	;
90	34	2^+3	;12	0;
91	4	4	4	;

[a] Infection types on primary leaves were rated 14 days after inoculation on a scale of 0 to 4 (25).
[b] Stem rust race *P. graminis* f. sp. *tritici* nomenclature (21).

TABLE 5. Segregation for seedling-plant infection type[a] and adult-plant resistance to *Puccinia graminis* f. sp. *tritici* in F_6 lines of RL6071/AC Taber

Race[b]	Postulated *Sr* genes	No. of lines and infection type (R^c:S^d)	Expected ratio (R:S)	*P*[e]
MCC	*9b*, *11*, *12*	65:11 (;1–2^+) (3^+4)	7:1	0.75–0.50
HFH	*11*, *12*	60:17 (;1–2^+) (3^+4)	3:1	0.75–0.50
RKQ	*11*	34:43 (12–2^+)(3^+4)	1:1	0.50–0.25
TPM	*9b*	43:34 (;12–2^+)(3^+4)	1:1	0.50–0.25
Field test[f]	*2*	33:34	1:1	>0.95

[a] Infection types on primary leaves were rated 14 days after inoculation on a scale of 0 to 4 (25).
[b] Stem rust race *P. graminis* f. sp. *tritici* nomenclature (21).
[c] Resistant line.
[d] Susceptible line.
[e] Probability of χ^2 value.
[f] A mixture of stem rust races was used to initiate a rust epidemic.

in Pasqua (4). *Sr9b* originally may have been derived from Frontana, the source of *Lr13* (6). *Sr12* was derived from Iumillo durum and is present in Thatcher and Neepawa (15,19). Pasqua may have additional stem rust resistance genes as evidenced by the resistant ITs seen in some F_6 lines to race QTH at 18°C; however, we were unable to identify additional *Sr* genes with our collection of *P. graminis* f. sp. *tritici* races.

The single-gene line with *Sr7a* had an intermediate level of field stem rust resistance, but its presence did not correlate with field resistance in the F_6 lines. The single-gene lines with *Sr5*, *Sr6*, *Sr9b*, or *Sr12* had moderately susceptible to susceptible field reactions. Field resistance could not be attributed to any of the seedling *Sr* genes in the F_6 lines. Singh and McIntosh (24) found that *Sr7a* and *Sr12* alone did not confer resistance; however, the adult-plant resistance of Thatcher-derived cv. Chris was associated with the presence of both genes. Nazareno and Roelfs (19) indicated that the combination of *Sr12* and an unidentified gene, *SrTc*, may be related to adult-plant resistance in Thatcher. We found no association between *Sr12* and field stem rust resistance. Use of different stem rust races in various studies of adult-plant stem rust resistance make direct comparisons of the results difficult.

The field resistance of the F_6 lines of RL 6071/AC Taber was characteristic of the *Sr2* adult-plant gene (18). Both AC Taber and the resistant F_6 lines developed a mixture of small to large pustules, with varying amounts of necrosis and chlorosis above the nodes. Because field resistance could not be correlated with any of the seedling resistances, it is likely that AC Taber has *Sr2*. This gene occurs in many wheats and is present in many CIMMYT selections. McIntosh et al. (18) stated that *Sr2* is arguably the most important gene for stem rust resistance on a worldwide basis. Wheats with *Sr2* were moderately susceptible to race 15B during the epidemics of the 1950s; however, with this exception, the gene has provided durable resistance since being introduced into common wheat.

F_6 lines of RL 6071/AC Taber postulated to have *Sr9b* and *Sr12* singly were identified. These lines had IT responses similar to single-gene lines with *Sr9b* and *Sr12*. F_6 lines postulated to have *Sr11*, however, had intermediate IT ;12 to 2^+3c compared to the single-gene line with *Sr11*, which had a low IT ; to ;l. The expression of *Sr11* may be influenced by host genetic background effects. Roelfs and McVey (22) noted that *Sr11* usually had IT ;2^- in I*Sr11*-Ra or IT 12^- in line Ag. These ITs were similar to the ITs of the F_6 lines postulated to have *Sr11*. *Sr11* might have a lower IT in the Chinese Spring*9/Timstein single-gene line used in this study. *Sr11* was identified in Romany (5), which is in the background of AC Taber.

AC Taber previously was found to have *Lr13* and *Lr14a* (16). As noted above, *Lr13* is linked with *Sr9b*. Gene *Lr14a* was derived from Yaroslav Emmer along with *Sr2*, and wheats with *Lr14a* often also have the linked gene *Sr17* (18). Although race RKQ is avirulent to *Sr17*, lines with this gene singly could not be postulated in the F_6 random line population. Therefore, it is unlikely that *Sr17* is present in AC Taber. A recombination event between the *Sr17* and *Lr14a* loci may have occurred in the development of AC Taber.

In recent years, TPM and QCC have been the predominant stem rust races in Manitoba and Saskatchewan (9). Genes *Sr6*, *Sr9b*, *Sr11*, and *Sr12* condition effective resistance to these races. The corresponding single-gene lines did not show high levels of field resistance in the rust nursery tests, because the spreader rows were inoculated with a mixture of stem rust races that were virulent to these genes. Thatcher adult-plant resistance plus *Sr6*, *Sr9b*, and *Sr12* would provide effective field resistance in Pasqua to races TPM and QCC, whereas *Sr2*, *Sr9b*, *Sr11*, and *Sr12* would provide effective field resistance to these races in AC Taber.

Both Pasqua and AC Taber were postulated to have genes *Sr9b* and *Sr12* but differed for genes *Sr5*, *Sr6*, *Sr7a*, and *Sr11*. In addition, the two cultivars differed for adult-plant stem rust resistance. Because many western Canada bread wheats have Thatcher in their pedigrees and also have *Lr34*, it is likely that the Thatcher adult-plant resistance plus the effects associated with *Lr34* are important in the stem rust resistance of these wheats. Because CIMMYT germ plasm is very common in the CPS breeding programs in western Canada, it is likely that *Sr2* is in many of the cultivars of this wheat class. If stem rust races with virulence to the Thatcher adult-plant resistance and *Sr2* become common in western Canada, it will be necessary to incorporate additional stem rust resistance genes into the breeding germ plasm for both classes of wheat.

ACKNOWLEDGMENTS

Contribution 1713, Agriculture and Agri-Food Canada. We thank K. Dunsmore for supplying stem rust cultures, P. Seto-Goh for technical assistance, and E. R. Kerber for useful discussion.

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