Identification of Resistance to Races of *Puccinia graminis* f. sp. *tritici* with Broad Virulence in Triticale (×*Triticosecale*)

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Abstract

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Triticale (×*Triticosecale*), an amphiploid of wheat (mainly *Triticum turgidum*) and cereal rye (*Secale cereale*), is an excellent source of resistance to wheat stem rust, caused by *Puccinia graminis* f. sp. *tritici*. A collection of 567 triticale accessions originating from 21 countries was evaluated at the seedling stage for reaction to races of *P. graminis* f. sp. *tritici* with broad virulence, including TTKSK, TRTTF, and TTTTF. A high frequency (78.4%) of accessions was resistant to race TTKSK, with low infection types ranging from 0; to X. A selection of 353 TTKSK-resistant accessions was evaluated for reaction to three South African isolates of *P. graminis* f. sp. *tritici* with single and/or combined virulences to stem rust resistance genes *SrSatu*, *Sr27*, and *SrKw* present in triticale. Genes *SrSatu*, *Sr27*, and *SrKw* were postulated to be present in 141 accessions and contributed to TTKSK resistance. The remaining 212 resistant accessions may possess uncharacterized genes or combinations of known genes that could not be determined with these isolates. These accessions were further evaluated for resistance to races TTKST, TPMKC, RKQQC, RCRSC, QTHJC, QCCSM, and MCCFC. Resistance remained effective across the entire set of races in the majority of the accessions (n = 200), suggesting that the resistances are effective against a broad spectrum of virulence. In all, 129 (79.6%) resistant accessions with noncharacterized genes were resistant to moderately resistant in field stem rust nurseries at Debre Zeit (Ethiopia) and St. Paul (Minnesota). Results from evaluating F_2 populations derived from resistant–susceptible crosses revealed that resistance to TTKSK in triticale was conferred mostly by single genes with dominant effects.

Stem rust, caused by *Puccinia graminis* f. sp. *tritici*, is one of the most destructive diseases of durum (*Triticum turgidum* L. subsp. *durum*) and common or bread wheat (*T. aestivum* L.) worldwide. In particular, a group of races that emerged recently in eastern Africa possesses virulence to many currently grown wheat cultivars worldwide, and only a few genes in adapted cultivars are effective against these races (6,7,22,27). Since it was first reported in 1999 (24), race TTKSK (Ug99) and its variants have been found throughout eastern and southern Africa (8,14,27,32,33,35) and Iran (15). The lack of resistance in adapted germplasm, coupled with the rapid evolution and spread of this race group, urgently requires the identification and introgression of effective resistance genes into wheat. Wild and cultivated relatives of wheat are known to be good sources of stem rust resistance genes. A number of resistance genes derived from wild relatives of wheat appeared to be more effective against the races in the TTKS race group than *Sr* genes of wheat origin (7,28).

Triticale (×*Triticosecale*) is an intergeneric hybrid between wheat and rye (*Secale cereale*). Triticale was first developed in the late 19th century in Europe (34), and the first commercial cultivars were released in the 1960s (5,10). Triticale is now grown commercially mostly in Europe, China, and Australia, mainly for livestock feed grain or grazing (11). Two types of triticale are grown and used in breeding programs: primary triticale, which are the product of the wheat–rye hybridization followed by chromosome doubling; and secondary triticale, which result from intercrossing primary triticale or crossing primary triticale with wheat or rye (9). Tetraploid (2n = 2x = 28), hexaploid (2n = 6x = 42), and octoploid (2n = 8x = 56) triticale have been developed by crossing rye with diploid, tetraploid, and hexaploid wheat (4) but hexaploids are the main cultivated form. Hexaploid triticale lines are classified as complete or substitution types. Complete types have an entire rye genome, whereas substitution types have at least one set of rye chromosomes replaced by D-genome chromosomes from hexaploid wheat (3). Triticale is also a good resource of genes for wheat improvement, because it can be used as a bridge to transfer desirable characteristics of rye into wheat (25,37). Triticale is a source of resistance to wheat stem rust, and several resistance genes have been described, including *Sr27*, *SrNin*, *SrSatu, SrBj,* and *SrVen* (13). Previous studies demonstrated that chromosomes 2R and 3R are important carriers of stem rust resistance genes in hexaploid triticale (1). The objective of this study was to identify and characterize stem rust resistance in triticale effective against race TTKSK and other races with broad virulence.

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*The *e*-Xtra logo stands for "electronic extra" and indicates that four supplementary figures and one supplementary table are available online.

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Materials and Methods

Plant materials. In total, 567 accessions of triticale from 21 countries deposited at the United States Department of Agriculture–Agricultural Research Service, National Small Grain Collection ([NSGC], Aberdeen, ID) were evaluated in this study (Table 1). Six triticale accessions were selected for inheritance and allelism studies. Four accessions (PI 271074, PI 410803, PI 414970, and PI 428980) were used as the resistant parents and two accessions (PI 386128 and PI 414945) were used as the susceptible parents. In total, eight crosses were developed to investigate the number of genes controlling resistance or to determine the relationship between resistance genes. F_1 plants were grown and selfed to produce F_2 populations. F_2 populations were evaluated for reaction to races TTKSK and TTTTF.

Disease assessment. *Seedling evaluations.* All accessions were evaluated for reaction to three *P. graminis* f. sp. *tritici* races with broad virulence and different geographic origin: TTKSK (Kenya), TRTTF (Yemen), and TTTTF (United States). Accessions exhibiting resistance to race TTKSK were evaluated for their reaction to three South African *P. graminis* f. sp. *tritici* isolates of race BPGSC with virulence, individually or in combinations, to resistance genes *SrSatu*, *Sr27*, and *SrKw* that are known to be present in triticale (isolates UVPgt53 [virulence to *Sr27*], UVPgt56 [virulence to *Sr27* and *SrKw*], and UVPgt57 [virulence to *Sr27*, *SrKw*, and *SrSatu*]). *SrKw* is an uncharacterized gene in the South African triticale 'Kiewiet'. The resistant accessions with uncharacterized genes were further evaluated for resistance to race TTKST (virulence to *Sr24*) (8) from Kenya and six additional U.S. races (TPMKC, RKQQC, RCRSC, QTHJC, QCCSM, and MCCFC). Information about the *P. graminis* f. sp. *tritici* isolates used in the disease phenotyping tests is summarized in Table 2. The fully expanded primary leaves of 5 to 10 seedlings per accession were inoculated 8 to 9 days after planting. Experimental procedures in inoculation and disease assessment were described by Jin et al. (7) and Pretorius et al. (22). Wheat 'McNair 701' (Cltr 15288) was planted in each experiment as the susceptible check. All disease assessments were repeated.

Adult evaluation. A subset of 168 accessions that were selected for resistance to race TTKSK and South African *P. graminis* f. sp. *tritici* races was evaluated in field stem rust nurseries in St. Paul, MN (April to July 2010) and Debre Zeit, Ethiopia (June to October 2010). In St. Paul, the nursery was inoculated with a composite of six U.S. races (TPMKC, RKQQC, RCRSC, QTHJC, QFCSC, and MCCFC). In Debre Zeit, the nursery was inoculated with race TTKSK and a bulk of Ethiopian isolates (with unknown race identities) collected from durum lines at the Debre Zeit Research Center at a ratio of 50/50. Details about the management of nurseries at St. Paul and Debre Zeit, and inoculation and disease assessment procedures, were described by Olivera et al. (18).

Table 1. Number and origin of triticale accessions used to evaluate stem rust resistance in triticale

Location	Number of accessions	Percentage
Russian Federation	123	21.7
Poland	88	15.7
Ukraine	31	5.5
Sweden	32	5.6
Germany	11	1.9
France	11	1.9
Spain	22	3.9
Hungary	26	4.6
Bulgaria	25	4.4
India	26	4.6
China	19	3.4
Australia	25	4.4
U.S.A.	61	10.8
Mexico	59	10.4
Others[a]	7	1.2
Total	567	100

[a] One accession each came from Pakistan, England, Finland, Switzerland, Italy, Portugal, and Romania.

Table 2. Isolate designation, origin, and virulence phenotype of *Puccinia graminis* f. sp. *tritici* races used to evaluate resistance in triticale

Race	Isolate	Origin	Virulence/avirulence formula
TTKSK	04KEN156/04	Kenya	Sr5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 30 31 38 McN/Sr24 36 Tmp
TTKST	06KEN19-V-3	Kenya	Sr5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 24 30 31 38 McN/Sr36 Tmp
TRTTF	06YEM34-1	Yemen	Sr5 6 7b 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McN Tmp/Sr8a 24 31
TTTTF	02MN84A-1-2	United States	Sr5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McN Tmp/Sr24 31
TPMKC	74MN1409	United States	Sr5 7b 8a 9d 9e 9g 10 11 17 21 36 McN Tmp/Sr6 9a 9b 24 30 31 38
RKQQC	99KS76A-1	United States	Sr5 6 7b 8a 9a 9b 9d 9g 21 36 McN/9e 10 11 17 24 30 31 38 Tmp
RCRSC	77ND82A	United States	Sr5 7b 9a 9b 9d 9g 10 17 21 36 McN/6 8a 9e 11 24 30 31 38 Tmp
QTHJC	75ND717C	United States	Sr5 6 8a 9b 9d 9g 10 11 17 21 McN/7b 9a 9e 24 30 31 38 36 Tmp
QCCSM	75WA165-2A	United States	Sr5 9a 9d 9g 10 17 21 24 McN/6 7b 8a 9b 9e 11 30 31 36 38 Tmp
MCCFC	59KS19	United States	Sr5 7b 9g 10 17 McN Tmp/6 8a 9a 9b 9d 9e 11 21 24 30 31 36 38
BPGSC	UVPgt53	South Africa	Sr8a 9a 9b 9d 9g 10 11 McN/5 6 7b 9e 17 21 24 30 31 36 38 Tmp
BPGSC	UVPgt56	South Africa	Sr8a 9a 9b 9d 9g 10 11 McN/5 6 7b 9e 17 21 24 30 31 36 38 Tmp
BPGSC	UVPgt57	South Africa	Sr8a 9a 9b 9d 9g 10 11 McN/5 6 7b 9e 17 21 24 30 31 36 38 Tmp

Table 3. Number and percentage of triticale accessions exhibiting resistant, susceptible, and heterogeneous reaction to *Puccinia graminis* f. sp. *tritici* races TTKSK, TRTTF, and TTTTF

	TTKSK		TRTTF		TTTTF	
IT[a]	*N*	%	*N*	%	*N*	%
0;	57	10.1	38	6.7	60	10.6
;	212	37.5	151	26.6	150	26.5
;1	36	6.4	48	8.5	67	11.9
1	7	1.2	21	3.7	19	3.4
2=	39	6.9	10	1.8	34	6.0
2-	50	8.8	59	10.4	64	11.3
2	26	4.6	76	13.4	40	7.1
2+	2	0.4	3	0.5	4	0.7
3	16	2.8	17	3.0	34	6.0
3+	33	5.8	27	4.8	41	7.3
4	26	4.6	57	10.1	9	1.6
X	14	2.5	0	0.0	1	0.2
Total resistant[b]	443	78.4	406	71.6	439	77.7
Total susceptible[c]	75	13.3	101	17.8	84	14.9
Heterogeneous[d]	47	8.3	60	10.6	42	7.4

[a] Infection types (ITs) observed on seedlings at 14 days post inoculation using a 0-to-4 scale according to Stakman et al. (30); the range of ITs is shown in Supplementary Figure S1.
[b] Resistant corresponds to low ITs of 0, ;, 1, 2, X, or combinations thereof.
[c] Susceptible corresponds to high ITs of 3 or 4.
[d] Accessions that contained both resistant and susceptible plants.

Inheritance studies. To determine the genetic control of resistance to wheat stem rust at the seedling stage, crosses between resistant and susceptible triticale accessions were produced. F_2 populations were evaluated for reaction to races TTKSK and TTTTF to assess gene action and determine the inheritance of resistance based on phenotypic ratios. Tests of allelism were made using F_2 populations derived from crosses between resistant accessions. The χ^2 test was applied to determine the goodness-of-fit to expected genetic ratios in the F_2 generation.

Table 4. Infection types (ITs) to South African races of *Puccinia graminis* f. sp. *tritici* in triticale accessions selected for resistance to race TTKSK, and stem rust resistance (*R*) genes postulated to be present in these accessions

	ITs to *P. graminis* f. sp. *tritici* isolates[a]				
Number[b]	04KEN156/04	UVPgt53	UVPgt56	UVPgt57	Postulated known *R* gene
27	;2=	1	4	4	*SrKw*[c]
2	2-;	11-	1	1	*SrKw* + additional gene
42	;	;	;	4	*SrSatu*[d]
30	;	;	;	1 or 2	*SrSatu* + additional gene[e]
39	;	3+ or 4	3+ or 4	3+ or 4	*Sr27*
1	;	2+	33+	2+, 4	*Sr27* + additional gene
212	…	…	…	…	Uncharacterized genes

[a] ITs observed on seedlings at 14 days post inoculation using a 0-to-4 scale according to Stakman et al. (30), where ITs of ;, 1, 2, or X are considered as a low IT and ITs of 3 or higher are considered as a high IT. Race designation of isolate 04KEN156/04 is TTKSK and race designation of isolates UVPgt53, UVPgt56, and UVPgt57 is BPGSC.
[b] Number of triticale accessions.
[c] ITs were shown in Supplementary Figure S2.
[d] ITs were shown in Supplementary Figure S3.
[e] ITs were shown in Supplementary Figure S4.

Table 5. Infection types (ITs) of triticale (×*Triticosecale*) accessions evaluated to races TTKSK, TTKST, TRTTF, TTTTF, TPMKC, RKQQC, RCRSC, QTHJC, QCCSM, and MCCFC of *Puccinia graminis* f. sp. *tritici* grouped according to the country of origin[a]

Country	PI[b]	Cultivar or line	TTKSK 04KEN156/04	TTKST 06KEN19-V-3	TRTTF 06YEM34-1	TTTTF 01MN84A-1-2	TPMKC 74MN1409	RKQQC 99KS76A-1	RCRSC 77ND82A	QTHJC 75ND717C	QCCSM 75WA165-2A	MCCFC 59KS19
Australia	525197	Muir	0;	;N	;CN	;CN	0;	;N	0;	0;	0;	0;
Australia	587261	81-220	2=	2=; / ;N	2-	2=	12=;	2=	2=	2-	2=	2-;
Bulgaria	564431	11776-163	22+	2+2	4	3+	3	3-3 / 1	3-3	3-	3	3-3
Canada	429049	278-9	2=	2=;	22-	2- / 3	2-;	2=	;2=1	;N	;N	;CN
China	428933	2	;CN	2-	2-1	2-1	2-	2-;	2-;	2-; / ;CN	2-	2-;CN
China	610224	237	3;1	1;3	2 / 3;1	2	1;3	2-	;13	2- / 3	2-	213
France	429013	539	2=	2-	2-	2-1;CN	2-	2-	2-;	2-	2-	;2=
Germany	429097	6A-694	2-;CN1	2=	;CN	;CN1-	2-;	;C	;C	;C2=	;C2=	;2=
Hungary	428980	Szalkas	0;	;N	0;	;CN	;N	0;	0;	0;	0;	0;
India	358312	Triticale 1	23-	213	3-2	1-;CN	31;	2-	;2=	31;	2-2	32; / ;2+
India	429094	75TP-242-JNK6T-227	;CN	;N	;CN	;CN1-	;N	0;	0;	0;	0;	;N
Mexico	611454	Beagle 'S' 505	2-	3-1;	2	2-	2-	;1	;1	2-2;3	;N	2=;
Mexico	611783	710037-10D-2TL-4D-20D-1D-0D	2=	2=	22-	2=	2	;C	;N	;CN	;N	;C
Mexico	611786	710039-0D-4TL-4D-1D-2D-0D	0;	;N	0;	0;	;	;C	0;	0;	;C	0;
Mexico	611798	X-15733-0M-0D-PC291	;13	31;	2	2	1;3	;1	;12= / ;13	;13	;1	1;3
Poland	410803	LT 344/72	2-	2-;	2+	2-	1-2=	0;	;N	;N	;N	;N
Poland	429072	LT 140/72	0;	;N	0;	0;	;N	0;	0;	;N	0;	;N
Poland	429138	LT 332/75	2	2-	4	22-	1;3	22-	2;3	2-; / 23	;13	2+3;
Poland	564439	Lasko	0;	;N	;CN1-	;CN	;N	;N	;N	;CN	;N	;CN
Portugal	611339	Borba	2	31;	3-2	2	123-	;13	;13	;23 / 23	;13	2;3-
Romania	587224	TF 3	0;	;N	2=	;CN	;N	0;	0;	0;	;N	0;
Russian Fed.	386003	31 AD 72	2	2-2	3+	2	2	2- / 3	22- / 3+	2	2	2 / 33-
Russian Fed.	414958	PRAG 31/2	;C	;1-	;C	;C1-	2-;	;C	;CN	;CN	;C	;2=
Russian Fed.	217074	Pisarevs 1	22-	2	2	2-;C	2-	2=	2=	2-	;C	2-
Russian Fed.	428855	HAD 259	2	2-2	22-	2-	2-2	2-;	2-;	22+;	2-;	2;
Russian Fed.	572943	PRAG 46/6	;CN	;N	;CN	;CN1-	;2=	;C1-	;C2=	;C2=	C	;2=
Spain	256033	Triticale 1	22-	2-1;	22-	2-1	2-1	2-;	2-;	2-;	2=;	2-;
Spain	428821	MTE 58	;C1-	;C	;C / 2=	;C1-	;C	;C	;C	;C	;C	;CN
Spain	428897	Sel. 4	;C	;C	;C1-	;C	2-;	2-;	2=;	2=;	;N	;N
Sweden	429063	8A-653	;CN	;N	;C1-2=	;CN1-	;N	0;	0;	0	;N	;N
Ukraine	386127	AD K2	;13	312	22- / 3+	;12- / 3+	31;	3 / 2=	3; / 2=	2- / 32;	31;	31 / 2-
Ukraine	429275	Dneprovskij	2-1	2=; / 33+	2-1;CN	1-;CN	2-; / 3-	2-;	2-;	2-;	;N / 3	;2-
Ukraine	445677	AD 767-16	;13	;23-	4	4	31;	;13	32;	;13 / 3+	;C1	1;3 / 3+
Ukraine	572929	AD 19	;13	2- / 312	2 / 4	;CN / 4	2- / 31;	2-;	2-;	2-;	2-; / ;C	;2-
United States	587536	6TB2Q	0;	;N	0;	;CN	;N	0;	0;	;N	0;	;N
United States	611847	H7089-1-9-5	2=	2=	22+	2	2-	2-;	;2-	2-;	2-;	;2-
United States	634195	Mammoth II	2	3-1	2	;CN2=	2-13	;C	;C	;13	;C	;13-

[a] ITs observed on seedlings at 14 days post inoculation using a 0-to-4 scale according to Stakman et al. (30), where ITs of ;, 1, 2, or X are considered as a low IT and ITs of 3 or higher are considered as a high IT. N denotes excessive necrosis. "/" indicated accessions were heterogeneous with dominant type given first.
[b] Plant introduction (PI) number.

Results

Seedling evaluation. A high frequency of resistance was observed in triticale; 443 (78.4%), 406 (71.6%), and 439 (77.7%) accessions exhibited low infection types (ITs), to *P. graminis* f. sp. *tritici* races TTKSK, TRTTF, and TTTTF, respectively (Table 3). A wide range of ITs (from 0; to X) was observed in the resistant accessions (Table 3; Supplementary Figure S1). However, very low ITs (0; to ;1) were predominant (Table 3; Supplementary Table S1). Resistance genes *SrKw*, *SrSatu*, and *Sr27*, known to be present in triticale, were postulated in 141 of the 353 TTKSK-resistant accessions based on differential reactions to South African *P. graminis* f. sp. *tritici* isolates (Table 4; Supplementary Figures S2 to S4). The remaining 212 resistant accessions may possess combinations of known genes that could not be detected with these isolates, or previously uncharacterized genes. The majority of these accessions (n = 200) exhibited low ITs to all *P. graminis* f. sp. *tritici* races used in this study. A subset of resistant lines showing characteristic ITs to the 10 races evaluated is presented in Table 5.

Adult plant evaluation. In Debre Zeit, triticale entries were evaluated during the main cereal-growing season (May to October). During these months, conditions were conducive for stem rust development, and a high level of disease severity was observed in the nursery. Susceptible checks (wheat 'Red Bobs') ranged from 50 SMS to 70 S across the nursery, and susceptible triticale reached disease severities up to 60 MSS. Race-typing experiments of isolates collected from the Debre Zeit nursery indicated that race TTKSK was the predominant race (19). A high level of stem rust severity was obtained in the St. Paul field nursery. Susceptible checks (wheat 'LMPG-6') exhibited a disease severity across the nursery of 60 S to 80 S, whereas susceptible triticale reached severities from 30 SMS to 50 S. More than 80% of the TTKSK-resistant accessions exhibited resistant (R) to moderately resistant (MR) responses in St. Paul and Debre Zeit nurseries (Table 6). Although the inoculum used in both field nurseries differed in race composition, no major differences were observed in the frequency and level of resistance. In all, 108 (64.3%) and 110 (65.5%) entries displayed disease responses within the range 0 to 20 R in St. Paul and Debre Zeit, respectively (Table 6).

Inheritance and allelism studies. The segregation ratios observed in the F_2 progeny from three crosses between resistant and susceptible accessions fitted 3:1 ratios for resistance/susceptibility to race TTKSK (Table 7), indicating that resistance to race TTKSK at the seedling stage in the selected accessions is controlled by a single gene with complete dominance. The simple inheritance of TTKSK resistance in the selected triticale resistant parents should simplify the transfer of resistance to wheat. In the cross involving accession PI 271074 as resistant parent, the segregation ratio between resistant and susceptible F_2 plants did not fit the single-gene hypothesis (P value = 0.027) due to a higher number of susceptible plants (64:34) (Table 7). The segregation distortion is likely a result of preferential transmission of gametes of the susceptible parent. To identify additional stem rust resistance genes in triticale, we evaluated F_2 populations from crosses between resistant and susceptible parents for their reaction to race TTTTF. One gene with complete dominance effective to race TTTTF was observed in

Table 6. Number and percentage of triticale accessions exhibiting resistant (R), moderately resistant (MR), moderately susceptible (MS), and susceptible (S) response at the adult stage at field stem rust nurseries in St. Paul, MN, and Debre Zeit, Ethiopia

Disease evaluation		St. Paul, MN		Debre Zeit, Ethiopia	
Infection response[a]	Severity[b]	*N*	%	*N*	%
R	0–20	108	64.3	110	65.5
R	21–40	0	0.0	0	0.0
RMR–MRR	0–30	26	15.5	20	11.9
RMR–MRR	31–60	0	0.0	0	0.0
MR	0–30	13	7.7	10	6.0
MR	31–60	0	0.0	1	0.6
MRMS–MSMR	0–30	11	6.5	6	3.6
MRMS–MSMR	31–60	0	0.0	3	1.8
MS	0–30	2	1.2	7	4.2
MS	31–60	1	0.6	0	0.0
MSS–SMS	0–30	3	1.8	4	2.4
MSS–SMS	31–60	2	1.2	2	1.2
S	0–30	0	0.0	4	2.4
S	31–60	2	1.2	1	0.6
Total	…	168	100	168	100

[a] Infection response is determined based on pustule type and size (26).
[b] Stem rust severity following the modified Cobb scale (20).

Table 7. Segregation of F_2 populations of various crosses of triticale to *Puccinia graminis* f. sp. *tritici* races TTKSK and TTTTF

		F_2 plants				
Cross[a]	Race	Resistant	Susceptible	Ratio tested	χ^2	*P* value
PI 386128 (IT = 3+) × PI 271074 (IT = 22-)	TTKSK	64	34	3:1	4.912	0.027
PI 386128 (IT = 3+) × PI 410803 (IT = 2-)	TTKSK	105	28	3:1	1.105	0.293
PI 414945 ((IT = 4) × PI 428980 (IT = 0;)	TTKSK	108	30	3:1	0.783	0.376
PI 414945 (IT = 4) × PI 414970 (IT = 22+)	TTKSK	114	32	3:1	0.740	0.390
PI 386128 (IT = 3+) × PI 271074 (IT = 2)	TTTTF	16	53	1:3	0.121	0.728
PI 386128 (IT = 3+) × PI 410803 (IT = 2-)	TTTTF	72	29	3:1	0.743	0.389
PI 414945 (IT = 4) × PI 428980 (IT = 0;)	TTTTF	65	20	3:1	0.098	0.754
PI 414945 (IT = 4) × PI 414970 (IT = ;)	TTTTF	93	6	15:1	0.006	0.938
PI 271074 (unknown gene) × PI 429151 (*SrSatu*)	TTKSK	107	0	…	…	…
PI 410803 (unknown gene) × PI 429151 (*SrSatu*)	TTKSK	114	0	…	…	…
PI 414953 (*SrSatu*) × PI 428980 (unknown gene)	TTKSK	72	3	15:1	0.648	0.421
PI 414953 (*SrSatu*) × PI 428980 (unknown gene)	TTTTF	464	34	15:1	0.283	0.595
PI 271074 (unknown gene) × PI 410803 (unknown gene)	TTKSK	114	0	…	…	…

[a] Female parent × male parent. PI = plant introduction. Infection types (ITs) observed on seedlings at 14 days post inoculation using a 0-to-4 scale according to Stakman et al. (30).

accessions PI 410803 and PI 428980, whereas one gene with recessive effect was identified in accession PI 271074 (Table 7). Two genes with complete dominance were detected in accession PI 414970, one of which was postulated to be *SrSatu* when evaluated against the three South African isolates. Our results indicated that *SrSatu* is effective to both TTKSK and TTTTF, whereas the other resistance gene in PI 414970 is effective only to race TTTTF. In the allelism test, the F_2 populations derived from the crosses between resistant accessions with uncharacterized genes (PI 271074 and PI 410803) and accessions postulated to carry *SrSatu* produced only resistant progeny to race TTKSK (Table 7). These results indicated that these resistant accessions carry resistance genes that are allelic or tightly linked to *SrSatu*. In addition, the F_2 population derived from the cross between the two resistant accessions carrying uncharacterized genes (PI 271074 and PI 410803) produced only resistant progeny to race TTKSK (Table 7). This indicated that TTKSK resistance in both accessions is allelic. Accession PI 428980 carries a gene effective to race TTKSK that is not allelic to *SrSatu* (Table 7). Due to the limited number of F_2 plants in the TTKSK evaluation, the F_2 progeny of the cross between accessions PI 428980 and PI 414953 (with *SrSatu*) was also evaluated against race TTTTF. In both evaluations, progeny segregation between resistant and susceptible plants fitted the 15:1 ratio, indicating that the genes present in both accessions are not alleles.

Discussion

Race TTKSK of *Puccinia graminis* f. sp. *tritici* and its variants are a serious threat to bread and durum wheat production worldwide because of its wide virulence on many cultivars and rapid spread (27). Collective efforts in the wheat pathology and breeding community are being made to characterize and incorporate resistance genes effective against race TTKSK from durum and bread wheat and its relatives. Resistance to stem rust in triticale has been previously reported (1,13,29,36) but reaction to the recently emerged race TTKSK and its variants has not been characterized. Our results demonstrated that triticale is a rich source of resistance to TTKSK and other races of *P. graminis* f. sp. *tritici*. Previous studies on stem rust resistance in triticale documented a narrow genetic base of stem rust resistance in CIMMYT-derived materials (11,29,36). The accessions we used in this study from NSGC included entries from European countries with large triticale breeding programs (e.g., Russian Federation, Poland, Germany, and France; 17), which may allow the capture of resistance genes different from those present in the CIMMYT triticale.

In all, 141 triticale accessions were postulated to carry *Sr27*, *SrSatu*, or *SrKw* (Table 4). *SrSatu* and *Sr27* are the most common stem rust resistance genes in CIMMYT triticale (12,29,36) and are expected to be widely distributed because CIMMYT materials have played an important role in the improvement of triticale in many countries (36). The 108 triticale accessions resistant to race TTKSK were postulated to have *Sr27*, *SrSatu*, or *SrKw* alone. This result confirmed that *Sr27*, *SrSatu*, and *SrKw* are effective against race TTKSK. However, virulence to *Sr27*, *SrSatu*, and *SrKw* has been reported in Australia and South Africa (12,23,38); therefore, use of these genes should be limited to areas where virulence to these genes is absent in the rust population. 'Abacus', an accession (PI 591912) from Australia, is known to carry resistance genes *SrSatu* and *SrBj* (1). Sixty-three accessions with uncharacterized genes exhibited an IT profile similar to Abacus when evaluated with races TTKSK (IT = ;CN), TRTTF (IT = ;), TTTTF (IT = ;) and the three South African *P. graminis* f. sp. *tritici* isolates (ITs = ; and ;1) of race BPGSC. These accessions may carry *SrBj* but a more definitive postulation of this gene will require evaluation with Australian races with and without virulence to *SrBj* (13).

Triticale accessions with uncharacterized genes exhibited a high level of resistance; that is, to races representing a broad range of virulence at the seedling stage (Table 5). Resistance identified from seedling tests remained highly effective in field evaluations (Table 6). Selection of resistance based on seedling tests is an effective way to identify resistance, because the stem rust resistance genes detected at the seedling stage remain effective at the adult stage. All the stem rust resistance genes described in triticale (13) appeared to be major-effect, all-stage resistance genes. Adult plant resistance genes have not been reported in the species. In this study, we conducted field evaluations of accessions that exhibited resistance to race TTKSK at the seedling stage. To look for genes for adult plant resistance in triticale, accessions susceptible at the seedling stage should be included in field evaluations.

We identified a resistance gene effective to race TTKSK in two resistant parents (PI 271074 and PI 410803) that is allelic or closely linked to *SrSatu* (Table 7). This locus on chromosome 3R carries multiple stem rust resistance alleles, including *SrSatu*, *Sr27*, and *SrLa1* (1,29). One additional resistance gene effective to race TTTTF was present in accession PI 414970. The use of races with different virulence spectra proved to be an efficient tool to identify multiple stem rust resistance genes in individual accessions.

Triticale can contribute novel genes to increase the diversity of stem rust resistance. Efforts should be made to incorporate these effective genes from triticale into adapted common wheat backgrounds. However, the use of triticale genes to improve stem rust resistance in common wheat may also result in a negative impact if not deployed in effective gene combinations. If the same gene is used in both triticale and wheat, the occurrence of virulence to the gene in one crop would endanger the other (1). Resistance genes should be deployed in combination with other effective genes, preferably in backgrounds with complex stem rust resistance in order to prolong their effectiveness. The introgression of stem rust resistance genes from triticale into wheat by chromosomal recombination or translocation is a challenge for wheat breeders and cytogeneticists. The production of wheat–triticale hybrids is associated with a high proportion of aneuploids, sterility of F_1 plants, and low fertility in ensuing generations (16). However, resistance genes from triticale can be introgressed into wheat through hybridization and doubled-haploid breeding (21). The availability of a high-density linkage map in hexaploid triticale (2,31) can serve as a useful tool to facilitate mapping and introgression of stem rust resistance genes.

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