Evaluation and Characterization of Seedling Resistances to Stem Rust Ug99 Races in Wheat–Alien Species Derivatives

S. S. Xu,* Y. Jin, D. L. Klindworth, R. R.-C. Wang, and X. Cai

ABSTRACT

Stem rust (caused by *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn.), a devastating disease of wheat (*Triticum aestivum* L.), was effectively controlled worldwide for the past 50 yr by deployment of stem rust resistance (*Sr*) genes in wheat cultivars. However, a new stem rust race, TTKSK (known as Ug99 or TTKS) that emerged in eastern Africa, is a cause of concern because it has broad virulence to currently deployed *Sr* genes. To identify potentially new sources of effective *Sr* genes against Ug99, we evaluated and characterized the seedling responses to TTKSK of 62 wheat lines derived from crosses of common or durum wheat (*T. turgidum* L. ssp. *durum*) with the species *Thinopyrum junceum*, *Th. intermedium*, *Th. bessarabicum*, *Th. elongatum*, *Th. ponticum*, *Elymus rectisetus*, *Aegilops caudata*, and *Ae. speltoides*. For stem rust evaluation, we first tested all lines for reactions to races TTTT and TTKSK. Lines initially showing resistance to TTKSK were then retested with eight races, including three races in the TTKS lineage (TTKSK, TTKST, and TTTSK) and five North American races (QFCS, QTHJ, RCRS, RKQQ, and TPMK). Thirty wheat–alien species derivatives had resistance to TTKSK, TTKST, and TTTSK. The comparisons of wheat–alien species derivatives and their parental lines for reactions to different races suggested that 12 partial amphiploids or amphiploids and four disomic addition lines may carry novel genes for stem rust resistance. These resistant lines represent materials for introducing stem rust resistance genes into wheat breeding.

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Abbreviations: CIMMYT, International Maize and Wheat Improvement Center; CS, Chinese Spring; IT, infection type; LDN, Langdon.

Stem rust, caused by *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn., is a major, devastating disease of common or bread wheat (*Triticum aestivum* L., $2n = 6x = 42$, AABBDD genome) and durum wheat (*T. turgidum* L. ssp. *durum*, $2n = 4x = 28$, AABB). Leonard and Szabo (2005) listed major losses to stem rust that occurred in the twentieth century, primarily before 1960, in Europe, China, Australia, and North America. By the 1990s, the incidence of stem rust had dramatically fallen, due in large part to the deployment of stem rust resistance (*Sr*) genes in cultivars (Singh et al., 2006). One of the most important *Sr* genes was *Sr31*, which was deployed worldwide in many cultivars (Singh et al., 2006). In 1999, virulence to *Sr31* was detected in nurseries in Uganda (Pretorius et al., 2000) and the race was designated as Ug99. Based on the North American stem rust nomenclature system (Roelfs and Martens, 1988), Wanyera et al. (2006) designated this virulence type as TTKS. With the recent identification of new variants of TTKS, the original race Ug99 was redesignated as TTKSK (Jin et al., 2008b).

Published in Crop Sci. 49:2167–2175 (2009).
doi: 10.2135/cropsci2009.02.0074
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Race TTKSK is causing alarm for three reasons. First, this race has broad virulence to currently deployed *Sr* genes (Jin et al., 2007; Singh et al., 2006). Jin and Singh (2006) found that among North American cultivars, only 16% of hard red spring wheats, 48% of hard red winter wheats, and 28% of soft winter wheats had resistance to race TTKSK. Second, race TTKSK has continued to evolve. In 2006–2007, variants of TTKSK, designated TTKST and TTTSK (i.e., with added virulence to *Sr24* and *Sr36,* respectively) were detected in Kenya (Jin et al., 2008b; 2009). The third concern was the rapid movement of TTKSK from Africa. A predicted path for dispersal of TTKSK from eastern Africa to the Arabian Peninsula and ultimately to the Indian subcontinent, was proposed by Singh et al. (2006). Race TTKSK has closely followed this path, appearing in Yemen in 2006 (Jin et al., 2008a) and Iran in 2007 (Nazari et al., 2009).

Host resistance genes provide excellent control of stem rust. Thus, the most effective measure to prevent epidemics is to deploy *Sr* genes that are effective against TTKSK and its variants in wheat cultivars and breeding lines. Such an effort is currently being undertaken at the International Maize and Wheat Improvement Center (CIMMYT) and other wheat breeding programs (Singh et al., 2008). However, the number of *Sr* genes in wheat that are effective against TTKSK and its variants is limited. There is a need to expand the *Sr* gene resources by searching for further resistance genes in species related to, and crossable with, wheat. In the wheat gene pool, a number of progenitor and relative species are known to be potential sources of *Sr* genes. Among 50 *Sr* genes listed in the current *Catalogue of Gene Symbols for Wheat* (McIntosh et al., 2008), 18 were derived from the progenitor and related species of wheat and 15 are effective against race TTKSK (Singh et al., 2006; Xu et al., 2008).

In our research program "Improvement of Hard Red Spring and Durum Wheat for Disease Resistance and Quality Using Genetics and Genomics," we have developed and collected a number of wheat–alien species derivative lines developed from crosses of common wheat or durum wheat with *Aegilops speltoides* Tausch ($2n = 2x = 14$, SS), *Thinopyrum intermedium* (Host) Barkworth & D. R. Dewey ($2n = 6x = 42$, EEEEStSt or JJEEStSt) (Cauderon et al., 1973; Sun, 1981), *Th. ponticum* (Podp.) Z-W. Liu & R.-C. Wang [syn. *Agropyron elongatum* (Host) Beauv., *Elytrigia pontica* (Podp.) Holub., *Lophopyrum ponticum* (Podp.) Á. Löve, $2n = 10x = 70$, EEEEEEEEEE] (Sun, 1981; Kibirige-Sebunya and Knott, 1983), *Th. elongatum* (Host) D.R. Dewey ($2n = 2x = 14$, EE) (Dvořák and Knott, 1974), *Th. junceum* (L.) Love ($2n = 6x = 42$, EEEEEE or JJJJEE) (Charpentier, 1992), *Th. bessarabicum* (Savul. & Rayss) Á. Löve ($2n = 2x = 14$, JJ) (Zhang et al., 2002), *Ae. caudata* L. [syn. *Ae. markgrafii* (Greuter) K. Hammer ($2n = 2x = 14$, CC)] (Bluethner et al.,1988), *Elymus rectisetus* (Nees) Á. Löve & Connor ($2n = 6x = 42$, StStYYWW) (Xue and Wang, 1999), and *Haynaldia villosa* (L.) Schur (syn. *Dasypyrum villosum*, $2n = 2x = 14$, VV) (Chen et al., 1995). Most of these lines have been evaluated for resistance to several important wheat diseases such as tan spot [caused by the fungus *Pyrenophora tritici-repentis* (Died.) Drechsler, anamorph *Drechslera triticirepentis* (Died.) Shoemaker] (Oliver et al., 2006, 2008), Stagonospora nodorum blotch [caused by *Stagonospora nodorum* (Berk.) E. Castell. & Germano, teleomorph *Phaeosphaeria nodorum* (E. Müll.) Hedjar] (Oliver et al., 2006, 2008), Fusarium head blight [*Fusarium graminearum* Schwabe, teleomorph *Gibberella zeae* (Schw.) Petch.] (Oliver et al., 2005), and barley yellow dwarf viruses (Banks et al., 1993; Zhang et al., 1996b). Although some of the lines were evaluated for resistance to several races of stem rust (Banks et al., 1993), the lines were not evaluated for resistance to TTKSK and its variants. In this study, we evaluated these wheat–alien species derivatives and their wheat parental lines for reaction to TTKSK and other races; we then discuss the possible source and novelty of the *Sr* genes in some of the resistant lines.

MATERIALS AND METHODS

Plant Materials

Plant materials used in this study included 5 bread wheat cultivars and lines, 5 durum wheat cultivars and lines, 62 wheat–alien species derivatives (18 partial amphiploids, 7 amphiploids, 33 disomic addition lines, and 4 alien translocation lines), and 1 *E. rectisetus* accession (Table 1). The wheat or wheat–alien species derivative lines were originally developed and/or cytogenetically characterized in different research programs (see references in Table 1). 'Langdon' (LDN) durum–derived amphiploids and the LDN 5D(5B) disomic chromosome substitution line were developed by L.R. Joppa in the USDA–ARS, Northern Crop Science Laboratory, Fargo ND. The common wheat–*Th. ponticum* partial amphiploid SS5 (PI 604926) was a selection in a collection of interspecific hybrids assembled by W.J. Sando, currently held by the USDA germplasm collection. The wheat–*Haynaldia villosa* 6VS/6AL translocation line was originally developed by Chen et al. (1995). Three translocation lines (KS10-2, KS24-1, and LMq-28) with *Sr43* were obtained from D.R. Knott, Department of Plant Sciences, University of Saskatchewan, Saskatoon, SK, Canada. All other partial amphiploids, amphiploids, disomic addition lines, and their parental lines were held by one of the authors (R. R.-C. Wang).

All the disomic addition lines (Table 1) were cytologically verified by mitotic chromosome counts on root tips (Xu and Joppa, 2000). The chromosome numbers of translocation line XC02B-93 and the *T. aestivum/Th. intermedium* partial amphiploid Zhong 8 were also determined.

Stem Rust Races and Inoculation Procedure

The following races (isolates), maintained at the USDA–ARS Cereal Disease Laboratory, St Paul, MN, were used for this study: TTTT (01MN89A-1-2), QFCS (06ND76C), QTHJ (75ND717C), RCRS (77ND82A), RKQQ (99KS76A-1), TPMK (74MN1407), TTKSK (04KEN156/04), TTKST (06KEN19v3), and TTTSK (07KEN24-4). All of the lines were tested for resistance to races TTTT and TTKSK. Lines initially

Table 1. The wheat–alien species derivatives and their wheat parental lines used in this study.

Type (no. of lines)	Line name or accession no.[†]	Pedigree or description	$2n$[‡]	No. of lines	References
Common wheat (5)	LMPG-6	Susceptible check	42	1	
	'Alcedo', 'Chinese Spring' (CS), 'Fukuhokomugi', 'Genaro'	Parents of wheat-alien species derivatives	42	4	
Durum wheat (5)	'Langdon' (LDN)	Parent of LDN-derived amphiploid	28	1	
	LDN 5D(5B)	LDN 5D(5B) disomic substitution line and parent of LDN 5D(5B)–derived amphiploid	29	1	Joppa and Williams (1988); Li et al. (2006)
	ST464-C1	ST464 derived monogenic line postulated to carry *Sr13*	28	1	Klindworth et al. (2007)
	KL-B	'Khapli' emmer derived monogenic line postulated to carry *Sr13*	28	1	Klindworth et al. (2007)
	Rusty	Susceptible check	28	1	Klindworth et al. (2006)
Partial amphiploid (18)	AJAP2, AJAP4, AJAP7, AJAP8	CS/*Thinopyrum junceum*	56, 58	4	Charpentier (1992); Wang et al. (2003)
	Zhong 1, Zhong 4–7	*Triticum aestivum*/*Th. intermedium*	56	5	Banks et al. (1993)
	Zhong 8	*T. aestivum*/*Th. intermedium*		1	
	TAF 46	*T. aestivum*/*Th. intermedium*	56	1	Cauderon et al. (1973)
	78829	*T. aestivum*/*Th. intermedium*	56	1	Zhang et al. (1996a,b)
	7631, 693, 784	*T. aestivum*/*Th. ponticum*	56	3	Zhang et al. (1996a,b)
	SS5 (PI 604926)	CS/*Th. ponticum*//Arlando/ Leapland/Comet125	56	1	Sando (Oliver et al., 2006)
	40767-1	*T. aestivum*/*Th. ponticum*	56	1	Zhang et al. (1996a,b)
	OK 7211542	*T. aestivum*/*Th. ponticum*	56	1	Sando (Zhang et al., 1996b)
Amphiploid (7)	W95001	CS/*Th. bessarabicum*	56	1	Zhang et al. (2002)
	J83Ae164, J83Ae598, J83Ae663	Langdon (LDN) / *Ae. speltoides*	41, 42	3	L.R. Joppa (unpublished)
	J83Ae613, J83Ae778, J83Ae793	LDN 5D(5B) /*Ae. speltoides*	42	3	L.R. Joppa (unpublished)
Disomic addition (33)	AJDAj1– AJDAj9, AJDAj11, HD3505, HD3508, HD3515	CS/*Th. junceum*	44	13	Charpentier (1992); Wang et al. (2003)
	AI (B)–A VIII (G)	Alcedo/*Ae. caudata*	44	6	Bluethner et al. (1988); Friebe et al. (1992)
	A1026, A1034, A1057	Fukuhokomugi/*Elymus rectisetus* JC1050	44	3	Xue and Wang (1999)
	W5354, W7232, W7246, W5366, W5326, W7250, W5336	CS/*Th. bessarabicum*//Genaro (1J- 7J)	44	7	Zhang et al. (2002); Li et al. (2007)
	W0622, W0889–W0891	CS*2/*Th. elongatum* (1E, 2E, 6E, 7E)	44	4	Dvořák and Knott (1974); Li et al. (2007)
Translocation line (4)	KS10-2, KS24-1, LMq-28	*T. aestivum*/*Th. ponticum* translocation with *Sr43*	42	3	Kibirige-Sebunya and Knott (1983)
	XC02B-93	6VS/6AL translocation/Yangmai5// Sheng32109		1	Chen et al. (1995)

[†] Line name or accession numbers were based on the literatures as indicated in the references or were provided by seed providers.

[‡] The $2n$ chromosome numbers were based on the literatures as indicated in the references or were provided by seed providers.

showing resistance to TTKSK were retested with the three races of the TTKS lineage (TTKSK, TTKST, and TTTSK), and the lines with adequate seed stocks were also tested with the five North American races (QFCS, QTHJ, RCRS, RKQQ, and TPMK). In each trial, 6 to 8 plants per line were inoculated following the procedure of Jin et al. (2007). Briefly, urediniospores were suspended in a light mineral oil and applied to 7- to 9-d-old seedlings. Following inoculation, seedlings were incubated in the dark in a dew chamber for 14 h at 18°C, followed by 3 to 4 h of fluorescent light. Plants were removed to a greenhouse at 18 to 20°C with a 16-h photoperiod. Plants were scored for infection types (ITs) 14 d post inoculation using the system of Stakman et al. (1962). ITs 0, ;, 1, 2, or any combination of these indicated resistance, and ITs 3 or 4 indicated susceptibility.

RESULTS AND DISCUSSION

Infection type data for the first test of all 73 lines with races TTTT and TTKSK and the chromosome numbers of all lines are shown in Table 2. The IT data for the TTKS lineage (TTKSK, TTKST, and TTTSK) and five North American races (QFCS, QTHJ, RCRS, RKQQ, and TPMK) in the second trial are listed in Table 3. There were four *Th. junceum* partial amphiploids in the first trial. Two (AJAP2 and AJAP4) were susceptible to TTKSK, but the other two (AJAP7 and AJAP8) gave ITs 2 and were also resistant to TTTT (Table 2). The partial amphiploids were produced using 'Chinese Spring' (CS) as the wheat parent (Charpentier, 1992); and since CS was susceptible to TTKSK, resistance to TTKSK in the partial amphiploids

Table 2. Infection types produced by various amphiploids, partial amphiploids, disomic addition and translocation lines, and miscellaneous parental lines to races TTTT and TTKSK of *Puccinia graminis* f. sp. *tritici*.

Line	Pedigree	2*n*[†]	Infection types to race[‡]	
			TTTT	TTKSK
‘Chinese Spring’ (CS)	*Triticum aestivum*	42	4	4
AJAP2	CS/ *Thinopyrum junceum* partial amphiploid	56	4	4
AJAP4	CS/*Th. junceum* partial amphiploid	56	3	4
AJAP7	CS/*Th. junceum* partial amphiploid	56	2++/3	2
AJAP8	CS/*Th. junceum* partial amphiploid	58	2++	2
AJDAj1	CS/*Th. junceum* disomic addition	44	4	4
AJDAj2	CS/*Th. junceum* disomic addition	44	4	4
AJDAj3	CS/*Th. junceum* disomic addition	44	4	4
AJDAj4	CS/*Th. junceum* disomic addition	44	4	4
AJDAj5	CS/*Th. junceum* disomic addition	44	4	4
AJDAj6	CS/*Th. junceum* disomic addition	44	4	4
AJDAj7	CS/*Th. junceum* disomic addition	44	4	4
AJDAj8	CS/*Th. junceum* disomic addition	44	4	4
AJDAj9	CS/*Th. junceum* disomic addition	44	4	4
AJDAj11	CS/*Th. junceum* disomic addition	44	4	4
HD3505	CS/*Th. junceum* disomic addition	44	2+	2
HD3508	CS/*Th. junceum* disomic addition	44	3	4
HD3515	CS/*Th. junceum* disomic addition	44	4	4
Zhong 1	*T. aestivum/Th. intermedium* partial amphiploid	56	2+	2+
Zhong 4	*T. aestivum/Th. intermedium* partial amphiploid	56	;	;
Zhong 5	*T. aestivum/Th. intermedium* partial amphiploid	56	0;	;
Zhong 6	*T. aestivum/Th. intermedium* partial amphiploid	56	0;	;
Zhong 7	*T. aestivum/Th. intermedium* partial amphiploid	56	0;	;
Zhong 8	*T. aestivum/Th. intermedium* partial amphiploid	56	;	;
78829	*T. aestivum/Th. intermedium* partial amphiploid	56		;
TAF 46	*T. aestivum/Th. intermedium* partial amphiploid	56		2-;
7631	*T. aestivum/Th. ponticum* partial amphiploid	56		2
40767-1	*T. aestivum/Th. ponticum* partial amphiploid	56		2+
693	*T. aestivum/Th. ponticum* partial amphiploid	56		2
784	*T. aestivum/Th. ponticum* partial amphiploid	56		;2-
OK 7211542	*T. aestivum/Th. ponticum* partial amphiploid	56		2-
SS5 (PI 604926)	CS/*Th. ponticum*//Arlando/Leapland/Comet125	56	;1/3;	;1-
W0622	CS*2/*Th. elongatum* AABBDD + 1” (1E)	44	3	3
W0889	CS*2/*Th. elongatum* AABBDD + 1” (7E)	44		2
W0890	CS*2/*Th. elongatum* AABBDD + 1” (6E)	44		4
W0891	CS*2/*Th. elongatum* AABBDD + 1” (2E)	44		4
W5348	CS/*Th. bessarabicum* AABBDDJJ amphiploid	56	2+3-	2+
W5418	‘Genaro’	42	;1	2++
W5354	CS/*Th. bessarabicum*//Genaro (AABBDD + 1J)	44	4	2+
W7232	CS/*Th. bessarabicum*//Genaro (AABBDD + 2J)	44	3+	2++
W7246	CS/*Th. bessarabicum*//Genaro (AABBDD + 3J)	44	2	23
W5366	CS/*Th. bessarabicum*//Genaro (AABBDD + 4J)	44	;	23
W5326	CS/*Th. bessarabicum*//Genaro (AABBDD + 5J)	44	3/2	3-
W7250	CS/*Th. bessarabicum*//Genaro (AABBDD + 6J)	44	3	2++
W5336	CS/*Th. bessarabicum*//Genaro (AABBDD + 7J)	44	2;	2
W2895	*Elymus rectisetus* JC1050	42	–	;
‘Fukuhokomugi’	*T. aestivum*	42	4	4
A1026	Fukuhokomugi/*E. rectisetus* JC1050 disomic addition	44	4	4
A1034	Fukuhokomugi/*E. rectisetus* JC1050 disomic addition	44	4	4
A1057	Fukuhokomugi/*E. rectisetus* JC1050 disomic addition	44	4	4

Table 2. Continued.

Line	Pedigree	$2n$†	Infection types to race‡	
			TTTT	TTKSK
‘Alcedo’	*T. aestivum*	42	4	4
AI (B)	Alcedo/*Aegilops caudata* disomic addition	44	4	4
AII (C)	Alcedo/*Ae. caudata* disomic addition	44	2	2-
AIII (D)	Alcedo/*Ae. caudata* disomic addition	44	1+	2-;
AV (E)	Alcedo/*Ae. caudata* disomic addition	44	3-	4
AIV (F)	Alcedo/*Ae. caudata* disomic addition	44	4	4
AVIII (G)	Alcedo/*Ae. caudata* disomic addition	44	4	3+
XC02B-93	6VS/6AL translocation line/Yangmai5//Sheng32109	42	4	4
KS10–2	KS10-2/*4 ‘Thatcher’ (*Th. ponticum* translocation; Sr43)	42		;
KS24-1	KS24-1 (*Th. ponticum* translocation; Sr43)	42		;1
LMq-28	L ‘Marquis’ Marquis *6/28 *Th. ponticum* (Sr43)	42		;2-
‘Langdon’ (LDN)	*T. turgidum* ssp. *durum*	28	;	2C
LDN 5D(5B)	LDN 5D(5B) disomic substitution	29	1+	2+
J83Ae613	LDN 5D(5B)/*Ae. speltoides* PI 369572 amphiploid	42	1	2
J83Ae598	LDN/*Ae. speltoides* PI 369581 amphiploid	41	;	;
J83Ae164	LDN/*Ae. speltoides* PI 369600 amphiploid	42	–	;1
J83Ae663	LDN/*Ae. speltoides* PI 369609 amphiploid	42	1	;
J83Ae778	LDN 5D(5B)/*Ae. speltoides* PI 393494 amphiploid	42	0;	0;
J83Ae793	LDN 5D(5B)/*Ae. speltoides* PI 442448 amphiploid	42	;	;
LMPG-6	Susceptible hexaploid check	42	3+	4
Rusty	Susceptible durum wheat check	28	4	4
KL-B	‘Khapli’ emmer–derived monogenic line postulated to carry *Sr13*	28	2-	2++
ST464-C1	ST464-derived monogenic line postulated to carry *Sr13*	28	2-	2+

†The $2n$ chromosome numbers of all disomic addition lines, translocation line XC02B-93, and partial amphiploid Zhong 8 were verified in this study; the chromosome numbers of all other lines were based on the literatures as indicated in the references or were provided by seed providers in Table 1 donors.

‡Infection types follow Stakman et al. (1962) where 0,;, 1, 2, or combinations were considered low infection types, and 3 to 4 were considered high infection types; C = chlorosis; – = missing data.

was attributable to *Th. junceum*. When the 13 *Th. junceum* disomic addition lines were tested to TTKSK in the first test, only one line, HD3505, was resistant. In the second test, HD3505 was resistant to races in the TTKS lineage but was susceptible to most of the North American races. Partial amphiploids AJAP7 and AJAP8 were resistant to all races in the second trials (Table 3), indicating potentially useful sources of resistance different from the resistance gene in HD3505.

Five of the six Zhong-series wheat–*Th. intermedium* partial amphiploids in the first trial displayed IT ; to TTKSK (Table 2), whereas the sixth line, Zhong 1, gave IT 2+ (large 2). When these six lines were tested with the additional races, Zhong 1 was found to be susceptible to RKQQ and moderately susceptible to TTKST, TTTSK, and QTHJ (Table 3). However, the other five lines (Zhong 4–Zhong 8) were clearly resistant to all races, the highest IT being 2− (small 2). Whereas these lines should be valuable sources of stem rust resistance, their similar responses indicated they may have the same gene(s). The wheat–*Th. intermedium* partial amphiploids 78829 had fleck ITs to TTKSK in the first trail (Table 2), and it had fleck and ;2 ITs to TTKST and TTTSK, respectively, in the second trial (Table 3). The wheat–*Th. intermedium* partial amphiploid TAF46 was moderately resistant to TTKSK (2−;) in the first trial (Table 2). In the second trial (Table 3), it also was moderately resistant to TTKST (2+) and TTTST (2+), respectively. The and Baker (1970) showed that the resistance gene *Sr44* was present in the 7Ag chromosome addition line derived from TAF46. This gene is the only designated wheat *Sr* gene derived from a TAF46-derived addition line (Cauderon et al., 1973; McIntosh et al., 1995; Friebe et al., 1996). Because Zhong 4, 5, 7, and 8 exhibited very different reactions to TTKSK, TTKST, and TTTSK from TAF46, they likely carry a *Sr* gene(s) different from *Sr44* in TAF46.

These wheat–*Th. intermedium* partial amphiploids generally contain the complete wheat genome and seven pairs of chromosomes from *Th. intermedium* (Banks et al., 1993). Based on meiotic paring in the hybrids among eight partial amphiploids (Zhong 1–7 and TAF46), Banks et al. (1993) suggested that these partial amphiploids can be divided into three different groups: A (Zhong 1 and Zhong 2), B (Zhong 3–7), and TAF46. The partial amphiploids in group B differed by only one chromosome pair but differed from group A and TAF46 by two to five pairs of *Th. intermedium* chromosomes. Zhang et al. (1996b) reported that Zhong 3, 4, 5, and 7 carried five pairs of St-genome

Table 3. Infection types produced by resistant amphiploids, partial amphiploids, and disomic addition lines, and translocation lines to eight races of stem rust.

Line	Infection type to race[†]							
	TTKSK	TTKST	TTTSK	QFCS	QTHJ	RCRS	RKQQ	TPMK
AJAP7	2	2	2	2+	2	2	2	2++
AJAP8	2+	2+	2+	2	2	2	22+	2++
HD3505	;2–	3–	2–	2	4	2–/4	3	4
Zhong 1	2+	3–	3–	2	3	2	3+	2+
Zhong 4	0	;	;	;	;1	;	;1	;1
Zhong 5	;	;	;	;	0;	;	2-	;
Zhong 6	;	;	;	0;	;	;1	2–	2–
Zhong 7	;	;	;	0;	0;	;	2–;	0;
Zhong 8	;	;	;	;	;2–	;	2–	;
78829	;2–	;	;2					
TAF46	2+	2+	2+					
7631	2+	2+	3–					
40767-1	;/;2+	;/3–;	;/3–					
693	2+	2+	2+					
784	;	0	;					
OK721142	2	2	2					
W0889	2	2+	2+					
SS5	;2–	2	2	0	0;	2–	;	;
W5336	2–	2–	2–	;	;1	;	;	2
W5418[‡]	3	3	3	0;	2	2–	2–	2–
AII (C)	2	2	2+	;1	2–	2	2–	2–
AIII (D)	;12–	;2–	;2	;	3–	X	0;	1N
KS10-2	;	;2+	;1					
KS24-1	;1	;2+	;2					
LMq-28	;2	;2+	;2–					
J83Ae613	–	2–	2–	;	;1	;1	;1	1
J83Ae598	;	;	;	;	–	;1	–	;
J83Ae164	;2–	;2–	–	0;	;	;	;	1
J83Ae663	;2–	–	0;	0	;	;	;	;
J83Ae778	0;	;	0;	0;	;	;	–	;
J83Ae793	;2–	;2-	;	–	0	0;	;	;

[†] Infection types follow Stakman et al. (1962) where 0, ;, 1, 2, or combinations were considered low infection types, and 3 to 4 were considered high infection types; X = mesothetic; N = necrotic; – = missing data.

[‡] Wheat cultivar Genaro (W5418) was listed for comparison of its response to stem rust with *Th. bessarabicum* 7J disomic addition line (W5336).

chromosomes, one St/E Robertsonian translocation, and one St/E intercalary translocation, whereas Zhong 6 carried six pairs of St-genome chromosomes and one St/E Robertsonian translocation. However, TAF46 carried four pairs of E-genome and three pairs of St-genome chromosomes. Thus, Zhong 4, 5, 6, and 7 might carry the same *Sr* gene(s) due to their similar chromosome complements. Because Zhong 8 gave very similar ITs to Zhong 4, 5, 6, and 7 with all nine races (Table 2 and 3), it probably carries a similar set of *Th. intermedium* chromosomes to the five B group accessions. Thus, each of these partial amphiploids likely carries a novel gene(s) for a high level of stem rust resistance. Because neither parent was available for our tests, there is a slight possibility that the resistance was derived from a hexaploid wheat parent.

Six partial amphiploids (7631, 40767-1, 693, 784, OK 7211542, and SS5) derived from *Th. ponticum* were included in the study (Tables 2 and 3). They were all resistant to TTKSK in the first test. In the second test, 784 gave similar high levels of resistance reactions to TTKSK, TTKST, and TTTSK as Zhong 4, Zhong 5, Zhong 6, Zhong 7, and Zhong 8, whereas the responses of other five lines were similar to Zhong 1 and TAF46 (Table 3). Zhang et al. (1996a,b) reported that 784 and 40767-1 contained 21 pairs of A, B, D chromosomes, 6 pairs of St chromosomes, and 1 pair of E chromosomes; OK 7211542 contained 20 pairs of A, B, D chromosomes, 7 pairs of St chromosomes, and 1 pair of E chromosomes; and 7631 and 693 contained 20 pairs of wheat chromosomes and 8 pairs of E-genome chromosomes. The partial amphiploid SS5 (PI 604926) carries 14 *Th. ponticum* chromosomes and 42 wheat chromosomes, but the genome identities of the seven pairs of *Th. ponticum* chromosomes have not been determined (Oliver et al., 2006). Similar to the wheat–*Th. intermedium* partial amphiploids, these wheat–*Th. ponticum* partial amphiploids may be a source of novel genes for stem rust resistance.

Four disomic addition lines derived from *Th. elongatum* were included in the tests (Tables 2 and 3). They carried chromosomes 1E, 2E, 6E, and 7E from *Th. elongatum*. Only W0889, the 7E disomic addition line, was resistant to TTKSK, TTKST, and TTTSK (Tables 2 and 3). Three of the stem rust resistance genes, that is, *Sr25* and *Sr43* from *Th. ponticum* and *Sr44* from *Th. intermedium*, involved group 7 chromosome translocations (Knott, 1988; Friebe et al., 1996). It is possible that the 7E disomic addition line may carry a *Sr* gene that is the same as one of the three *Sr* genes (*Sr25*, *Sr43*, and *Sr44*) derived from group 7 chromosomes of *Th. ponticum* and *Th. intermedium*.

A CS–*Th. bessarabicum* amphiploid (W5348) and disomic addition lines for all seven J-genome chromosomes, were tested (Tables 2). The CS–*Th. bessarabicum* amphiploid gave IT 2+ to TTKSK in the first trial. The ITs of all seven disomic addition lines were similar to 'Genaro' (W5418), a wheat parent of the disomic addition lines. Furthermore, when tested with TTKSK, TTKST, and TTTSK in the second trial, with the exception of the 7J addition line W5336, all disomic additions were susceptible. The 7J addition line

W5336 had similar ITs to races QFCS and TPMK to Genaro, but the addition line had much lower ITs to the other six races than Genaro (Table 3), suggesting that chromosome 7J may carry a resistance gene(s) different from that in Genaro. Because stem rust resistance genes from *Th. bessarabicum* have not been reported in the literature, the *Th. bessarabicum* 7J addition line may be a novel source of stem rust resistance.

Elymus rectisetus accession JC1050 gave IT ; to TTKSK (Table 2). There were three wheat–*E. rectisetus* disomic addition lines in the first trial, and all were susceptible to both TTKSK and TTTT, indicating that the resistance gene(s) in *E. rectisetus* must be located on chromosome(s) other than those present in the disomic addition lines.

The *Ae. caudata* disomic addition lines were derived from crosses to *T. aestivum* cultivar Alcedo. Alcedo was susceptible to TTKSK, so any *Ae. caudata* disomic addition line with resistance to TTKSK must have a resistance gene(s) located on an *Ae. caudata* chromosome. Disomic addition lines AII and AIII containing the *Ae. caudata* chromosomes C and D, respectively, were resistant to TTKSK (Table 2). AII (C) was resistant to all races in the second trial, whereas AIII (D) was resistant to all races except QTHJ (IT 3−) and had a mesothetic (X) reaction to RCRS (Table 3), suggesting that the two addition lines may carry different resistance genes. Friebe et al. (1992) suggested that the *Ae. caudata* chromosomes C and D may correspond to the chromosomes within the homoeologous group 5 and 6, respectively. Because stem rust resistance genes from *Ae. caudata* have not been reported previously, AII (C) and AIII (D) are potential sources of novel resistance genes.

The three translocation lines (KS10-2, KS24-1, and LMq-28) carrying *Sr43* derived from *Th. ponticum* were resistant to TTKSK, TTKST, and TTTSK (Table 2 and 3). The lines KS10-2 and KS24-1 had slightly higher levels of resistance than LMq-28, which may be attributed their 'Thatcher' background (Jin and Singh, 2006). LMq-28 carries *Sr43* in a 'Marquis' background (Knott et al., 1977; Kibirige-Sebunya and Knott, 1983), and Marquis is known to carry *Sr7b, Sr18, Sr19*, and *Sr20* (Anderson et al., 1971). Since all four genes are ineffective against TTKSK (Jin et al., 2007), the reaction of LMq-28 to TTKSK and its variants probably correctly indicates the IT of these races to *Sr43*.

Among the wheat relatives, *Ae. speltoides* has been an excellent source of genes for stem rust resistance. Three *Sr* genes, *Sr32* (Friebe et al., 1996), *Sr39* (Friebe et al., 1996), and *Sr47* (Faris et al., 2008), have been transferred into common wheat and durum wheat. All three confer resistance to TTKSK (Jin et al., 2007; Faris et al., 2008). In this study, six amphiploids (J83Ae598, 164, 613, 663, 778, and 793) involving *Ae. speltoides* as the alien parents and either Langdon or Langdon 5D(5B) disomic substitution line as the tetraploid wheat parent were tested (Tables 2 and 3). All six amphiploids exhibited high levels of resistance with IT ; predominating in the test (Tables 2 and 3). Langdon derives stem rust resistance from 'Khapli' emmer (Heermann and Stoa, 1956), the source of *Sr13* (Knott, 1962). Hexaploid monogenic-*Sr* lines carrying *Sr13* gave seedling IT 2+ to TTKSK (Jin et al., 2007). In this study, two durum monogenic lines, ST464-C1 and KL-B, postulated to carry *Sr13*, gave seedling ITs of 2+ and 2++ to TTKSK, respectively (Table 2). Both Langdon and its disomic substitution of chromosome 5D for 5B gave similar ITs 2C and 2+ to TTKSK similarly to ST464-C1 and KL-B (Table 2). Thus, all six Langdon-*Ae. speltoides* had lower ITs than could be explained by the presence of *Sr13* alone, suggesting that they carry an additional gene(s) controlling resistance to TTKSK and other races.

The wild relative species of cultivated wheats are valuable sources of novel genes for many desirable wheat traits. Due to their wild grassy characteristics, related species are usually not suitable for direct evaluation and characterization of those traits. However, the wheat–alien species derivatives such as amphiploids or partial amphiploids, and chromosome addition, substitution, and translocation lines are usually in semidomesticated or domesticated backgrounds and can be easily used for evaluation and characterization. Such materials have played an important role in wheat improvement (Jones et al., 1995; Jiang et al., 1994). The sources of resistance to Ug99 and other races identified in this study will be useful in resistance breeding in both common and durum wheat. Even though it is difficult to utilize the resistant lines identified in this study, including wheat–alien species amphiploids and diosomic addition lines, directly in wheat breeding, they can be hybridized with wheat for chromosome manipulation and elimination enabling the retention of chromosome regions with desirable attributes while eliminating the unwanted chromatin.

Acknowledgments

We thank Drs. Chao-Chien Jan and Lili Qi for critically reviewing the manuscript. This material is based on work supported by the USDA-ARS CRIS Project No. 5442-22000-033-00D and Cornell University Project "Durable Rust Resistance in Wheat".

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