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Genetic resources for stem rust resistance in cultivated and wild tetraploid wheats

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Abstract. New emerging races of *Puccinia graminis* f. sp. *tritici* are a serious threat to durum and bread wheat production worldwide because of their virulence on many cultivars and rapid spread. Our research objective was to indentify new sources of stem rust resistance in cultivated and wild tetraploid wheats that could be utilized in durum breeding. We characterized 3500 durum (*T. turgidum* ssp. *durum*) and 360 emmer wheat (*T. turgidum* ssp. *dicoccum*) accessions for stem rust resistance in multiple field and seedling evaluations. Search for resistance through seedling evaluation was also conducted in 1770 accessions of wild and cultivated *T. turgidum* ssp. and *Aegilops* ssp. Accessions exhibiting a high level of stem rust resistance to TTKSK (or Ug99 race) and other races were observed in all the species evaluated. Studies on the inheritance of TTKSK resistance revealed that resistance was conferred mostly by one and two genes. Our studies concluded that wild and cultivated tetraploids are a rich source of resistance to race TTKSK, and may contribute with novel stem rust resistance genes.

Keywords. Genetic resources – Resistance genes – *Puccinia graminis* f. sp. *tritici* – Ug99.

Ressources génétiques de la résistance à la rouille noire dans les blés tétraploïdes cultivés et sauvages

Résumé. *De nouvelles races émergentes de Puccinia graminis f. sp. tritici posent une grave menace pour la production de blé dur et de blé tendre dans le monde entier en raison de leur virulence sur de nombreux cultivars et de leur propagation rapide. L'objectif de cette recherche est d'identifier de nouvelles sources de résistance à la rouille de la tige des blés tétraploïdes cultivés et sauvages qui pourraient être utilisées pour l'amélioration du blé dur. Nous avons caractérisé 3500 accessions de blé dur (T. turgidum ssp. durum) et 360 d'amidonnier (T. turgidum ssp. dicoccum) pour la résistance à la rouille noire par de nombreuses évaluations sur le terrain et au niveau des semis. La recherche de la résistance à travers l'évaluation des semis a également été menée sur 1770 accessions de T. turgidum ssp. et Aegilops ssp sauvages et cultivées. Des accessions présentant un niveau élevé de résistance à la rouille noire TTKSK (ou race Ug99) et à d'autres races ont été observées dans toutes les espèces étudiées. Les études sur l'héritage de la résistance TTKSK ont révélé que la résistance est principalement conférée par un ou deux gènes. Nos études ont permis de conclure que les tétraploïdes sauvages et cultivés sont une riche source de résistance à la race TTKSK, et que leurs gènes pourraient être utilisés pour améliorer la résistance à la rouille de la tige.*

Mots-clés. *Ressources génétiques – Gènes de résistance – Puccinia graminis f. sp. tritici – Ug99.*

I – Introduction

Stem or black rust, caused by *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn. (Pgt), is one of the most destructive diseases of durum wheat [*Triticum turgidum* L. ssp. *durum* (Desf.) Huns.] and bread wheat (*T. aestivum* L.) worldwide. The recent emergence of TTKS (or Ug99 race) group in Eastern Africa with broad virulence to wheat cultivars worldwide (Jin *et al.*, 2007) represents a new threat to wheat production at a global scale. Since first reported in 1999 (Pretorius *et al.*, 2000), TTKSK and its variants have been found throughout eastern and southern Africa (Jin *et al.*, 2008; Singh *et al.* 2011; Viser *et al.* 2011; Wanyera *et al.* 2006; Wolday *et al.*, 2011), and Iran (Nazari *et al.*, 2009). In addition to TTKSK, Pgt races found in Ethiopia that are more adapted to durum and have combined virulence to important durum resistance genes, such as *Sr13* and *Sr9e*, increase the vulnerability of durum to stem rust. The limited availability of resistance to TTKSK in adapted germplasm (Jin *et al.* 2007) coupled with its rapid evolution and spread urgently requires the identification and introgression of effective resistance genes from all genepools of wheat.

Tetraploid wheats with AABB genome (*Triticum turgidum* L.) comprise eight cultivated and wild subspecies. The only wild form is wild emmer [*T. turgidum* ssp. *dicoccoides* (Körn. ex Aschers. & Graebn.) Thell.], the progenitor of cultivated tetraploid and hexaploid wheat (Zohary, 1970). In addition to durum wheat, there are four other free-threshing cultivated subspecies of *T. turgidum* including Persian wheat [*T. turgidum* L. subsp. *carthlicum* (Nevski) Á. Löve and D. Löve], Polish wheat [*T. turgidum* L. subsp. *polonicum* (L.) Thell.], Oriental wheat [*T. turgidum* L. subsp. *turanicum* (Jakubz.) Á. Löve and D. Löve], and Poulard wheat (*T. turgidum* L. subsp. *turgidum*) (van Slageren, 1994). These tetraploid wheats are ancient cereal crop species derived from cultivated emmer wheat [*T. turgidum* L. subsp. *dicoccum* (Schrank) Thell.] (Feldman *et al.*, 1995). Tetraploid wheats have contributed with important genes for stem rust resistance, such as *Sr2, Sr9d, Sr9e, Sr12, Sr13, Sr14*, and *Sr17* (Heermann and Stoa, 1956; McFadden, 1930; McIntosh *et al.*, 1995), but have not been extensively characterized for resistance to the new races on the TTKSK group.

Aegilops is the most closely related genus to *Triticum* (Gill and Friebe, 2002) and comprises 23 species that include diploid, tetraploid, and hexaploid genomes (van Slageren, 1994). *Aegilops* species are known to be rich sources of resistance to various pathogens and pests, including stem rust (Alam and Gustafson 1988; Anikster *et al.* 2005; Gill *et al.* 1985; Pasquini 1980), and many resistance genes have been transferred into wheat. However, limited information for resistance to race TTKSK is available except for *Ae. tauschii* (Rouse *et al.* 2011).

The objective of this study is to identify and characterize new sources of stem rust resistance against race TTKSK and other races with broad virulence in *T. turgidum* L. ssp. and *Aegilops* ssp., and to investigate the genetic bases of stem rust resistance.

II – Material and methods

1. Germplasm

A total of 5359 accessions of seven subspecies of *T. turgidum* deposited at the USDA-ARS National Small Grain Collection (NSGC) (Aberdeen, ID) were evaluated in this study. The collection includes: 3500 accessions of durum wheat, 359 of cultivated emmer, 880 of wild emmer, 77 of Persian wheat, 63 of Polish wheat, 66 of Oriental wheat, and 414 of Poulard wheat. We also evaluated 1220 *Aegilops* accessions including 260 of *Ae. biuncialis,* 151 of *Ae. cylindrica*, 182 of *Ae. geniculata*, 202 of *Ae. neglecta*, 73 of *Ae. peregrina*, and 233 of *Ae. triuncialis*. Thirteen accessions (4 durum, 4 emmer, 2 wild emmer, 1 Persian wheat, 1 Polish wheat, and 1 Poulard wheat) were selected for inheritance and allelism studies based on their reaction to races TTKSK, TRTTF, and TTTTF. Crosses were developed to investigate the number of genes conferring resistance to race TTKSK. F_1 plants were grown and selfed to produce F_2 populations. Individual F_2 plants were then selfed to produce $F_{2:3}$ families.

2. Disease assessment

Adult evaluation. All the durum and emmer entries were evaluated for resistance in field tests in the stem rust nursery at Debre Zeit, Ethiopia. Accessions rated as resistant with 30% or less stem rust severity and moderately or lower susceptible infection response in the Debre Zeit field nursery were further evaluated in the Debre Zeit and St. Paul nurseries in two growing seasons. In St. Paul, the nursery was inoculated with a composite of six US races (TPMKC, RKQQC, RCRSC, QTHJC, QFCSC, and MCCFC). The Debre Zeit nursery was artificially inoculated with race TTKSK and a bulk of Ethiopian isolates collected from durum lines 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.* (2012a). Plants were evaluated for their infection responses (pustule type and size) (Roelfs *et al.*, 1992), and disease severity following the modified Cobb scale (Peterson *et al.*, 1948). Infection responses R and RMR were considered as indicative of resistance, and infection responses MR, MRMS, and MS with 30% or less stem rust severity were considered intermediate.

Seedling evaluation. The entire *T. turgidum* ssp. collection of the NSGC was evaluated for reaction to three Pgt races with broad virulence and different geographic origin: TTKSK (Kenya), TRTTF (Yemen), and TTTTF (United States). Accessions exhibiting resistance to race TTKSK were further characterized against race JRCQC (Ethiopia), a race with virulence combination to *Sr9e* and *Sr13* that are important for stem rust resistance in durum, and to six representative US races (TMPKC, RKQQC, RCRSC, QTHJC, QCCLC, and MCCFC). All the *Aegilops* accessions were evaluated only against races TTKSK, TRTTF and TTTTF. The race designation is based on the letter code nomenclature system (Roelfs and Martens, 1988; Roelfs *et al.*, 1993), modified to further delineate races in the TTKS group (Jin *et al.*, 2008). Information about the stem rust isolates used in the disease phenotyping tests is summarized in Table 1. Five seedlings per accession were inoculated on the fully expanded primary leaves 8 to 9 days after planting. Experimental procedures in inoculation and disease assessment were done as described by Jin *et al.* (2007). Wheat cultivar McNair 701 (Cltr 15288) was used as the susceptible control. All the assessments were done with one replicate and were repeated once.

3. Inheritance studies

To determine the genetic control of resistance to wheat stem rust at the seedling stage, crosses between resistant and susceptible accessions were evaluated. F_1 plants were evaluated for the response to races TTKSK to assess gene action. F_2 and $F_{2:3}$ progenies were evaluated against race TTKSK to determine the inheritance of resistance based on phenotypic ratios. Twenty plants from each $F_{2:3}$ family were tested. According to Hanson (1958), this $F_{2:3}$ family size has a 99% probability of distinguishing between segregating and non-segregating families for monogenic inheritance.

Table 1. Isolate designation, origin, and virulence phenotype of *P. graminis* f. sp. *tritici* races used to evaluate resistance in *T. turgidum* ssp and *Aegilops* spp.

Race[1]	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*
TRTTF	06YEM34-1	Yemen	*Sr5 6 7b 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McN Tmp / Sr8a 24 31*
JRCQC	09ETH08-3	Ethiopia	*Sr6 9e 9g 10 11 17 21 McN Tmp / Sr5 7b 8a 9a 9b 9d 24 30 31 36 38*
TTTTF	02MN84A-1-2	USA	*Sr5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McN Tmp / Sr24 31*
TPMKC	74MN1409	USA	*Sr5 7b 8a 9d 9e 9g 10 11 17 21 36 McN Tmp / Sr6 9a 9b 24 30 31 38*
RKQQC	99KS76A-1	USA	*Sr5 6 7b 8a 9a 9b 9d 9g 21 36 McN / 9e 10 11 17 24 30 31 38 Tmp*
RCRSC	77ND82A	USA	*Sr5 7b 9a 9b 9d 9g 10 17 21 36 McN / 6 8a 9e 11 24 30 31 38 Tmp*
QTHJC	75ND717C	USA	*Sr5 6 8a 9b 9d 9g 10 11 17 21 McN / 7b 9a 9e 24 30 31 36 38 Tmp*
QFCSC	06ND76C	USA	*Sr 5 8a 9a 9d 9g 10 17 21 McN / 6 7b 9b 9e 11 24 20 31 36 38 Tmp*
MCCFC	59KS19	USA	*Sr5 7b 9g 10 17 McN Tmp / 6 8a 9a 9b 9d 9e 11 21 24 30 31 36 38*

[1] Race designation based on the letter code nomenclature system (Roelfs and Martens, 1988; Roelfs et al., 1993), modified to further delineate races in the TTKS group (Yin et al., 2008).

III – Results

1. Resistance in durum and emmer wheat

Resistance to wheat stem rust at the adult stage was observed in durum in the Debre Zeit nursery, as 914 (26.1%) entries exhibited a resistant to moderately resistant response (Table 2). These entries were further evaluated in Debre Zeit and St. Paul nurseries in two additional growing seasons. Two hundred eighty (8.0%) entries exhibited a resistant to moderately resistant response in all the field evaluations (Table 2). The highest frequencies of resistance were observed in entries from Africa (Ethiopia and Egypt) and North America (Mexico and USA). From these 280 field-resistant entries, 123 exhibited resistant reactions to all the Pgt races used in the seedling evaluation (Table 2). These accessions likely possess useful resistance genes and could be used in durum improvement for stem rust resistance. Ten entries were susceptible in all seedling evaluations (Table 2). This result may indicate the presence of genes for adult plant resistance (APR) in these accessions.

A high frequency of resistance at the adult stage was observed in emmer wheat, as 164 (50.3%) accessions exhibited a resistant to moderately resistant response in the first evaluation at the Debre Zeit nursery (Table 2). However, only 39 (10.9%) accessions remain resistant to moderately resistant in all the field evaluations at Debre Zeit and St. Paul nurseries (Table 2). The highest frequencies of resistance in emmer were from Ethiopia and the Middle East. Twenty-eight of these resistant accessions in field evaluations exhibited a resistant reaction to all Pgt races at the seedling stage. Selection of resistance based on seedling tests can be effective, as resistance detected at the seedling stage remains effective at the adult stage. Only four accessions that were susceptible to races TTKSK, TRTTF, and TTTTF in seedling evaluations remained resistant to moderately resistant across the two evaluations performed at the adult stage (Table 2).

Table 2. Number and percentage of durum (*Triticum turgidum* ssp. *durum*) and emmer (*T. turgidum* ssp. *dicoccum)* entries resistant (R) to moderately resistant (MR) to wheat stem rust in field evaluations, and resistant (R) and susceptible (S) in seedling evaluations.

	Durum		Emmer	
	No.	**%**	**No.**	**%**
Total number of entries	3500	100.0	359	100.0
R to MR[1] in Debre Zeit nursery	330	9.4	51	14.2
R to MR in St. Paul nursery	425	12.1	85	23.7
R to MR in all field evaluations	280	8.0	39	10.8
R against all Pgt races at seedling stage[2]	123	3.5	28	7.8
S against all Pgt races at seedling stage	10	0.3	4	1.1

[1] *Accessions characterized as resistant to moderately resistant with a maximum 30% stem rust severity and maximum moderately susceptible infection response.*

[2] *Entries evaluated against races TTKSK, TRTTF, TTTTF, JRCQC, TPMKC, RKQQC, RCRSC, QTHJC, QFCSC, and MCCFC.*

2. Resistance in wild emmer, Persian, Polish, Oriental, and Pollard wheat

Seedling resistance was observed in these five *turgidum* ssp., as 250 (17.9%), 319 (25.2%), and 304 (21.5%) accessions exhibited a resistant reaction to race TTKSK, TRTTF, and TTTTF, respectively (Table 3). The highest frequency of TTKSK resistance was observed in Persian wheat (44.6%), whereas low frequencies were observed in Pollard (12.3%) and Oriental wheat (9.4%). The percentage of resistance to the three Pgt races was similarly high in wild emmer and Polish wheat. However, in Persian, Oriental, and Pollard wheat, the percentage of resistance varied markedly depending on the pathogen race (Table 3). One hundred and one (6.7%) accessions were resistant to all the races evaluated (Table 3). The characteristic infection types (IT) of wild emmer, Polish, Oriental, and Pollard wheat resistant accessions to the three races evaluated ranged from $2^=$ to 2^+ (Table 3). However, most of the Persian wheat resistant accessions exhibited intermediate types (IT ;32 and 3-2;). Thirteen wild emmer and 62 cultivated tetraploid accessions were resistant against all Pgt races evaluated (data not shown).

3. Resistance in *Aegilops* ssp.

A high frequency of resistance was observed in this group of *Aegilops* spp. as 896 (73.2%), 767 (62.7%) and 849 (69.3%) accessions exhibited low infection types to races TTKSK, TRTTF, and TTTTF, respectively (Table 4). Five hundred nine (41.6%) accessions were resistant to the three races. With the exception of *Ae. biuncialis,* all species exhibited a frequency of resistant accessions to race TTKSK over 80% (Table 2). We observed a high degree of association for resistance to the three Pgt races in *Ae. geniculata* and *Ae. neglecta*; over 75% of the accessions were resistant against races TTKSK, TRTTF, and TTTTF. However, race specificity was apparent in accessions of the remaining species. In particular, *Ae. cylindrica* had only one accession that was resistant to race TRTTF.

Table 3. Number and percentage of *T. turgidum* ssp. *carthlicum,* ssp. *polonicum,* ssp. *turanicum,* and ssp. *turgidum* accessions exhibiting resistant, susceptible, and heterogeneous[1] reaction to *P. graminis* f. sp. *tritici* races TTKSK, TRTTF, and TTTTF.

	TTKSK		TRTTF		TTTTF	
	No.	%	No.	%	No.	%
T. turgidum ssp. *dicoccoides*	152	17.2	178	25.1	123	14.4
T. turgidum ssp. *carthlicum*	33	44.6	12	16.4	19	27.1
T. turgidum ssp. *polonicum*	15	24.6	14	22.6	13	21.7
T. turgidum ssp. *turanicum*	6	9.4	1	1.6	0	0.0
T. turgidum ssp. *turgidum*	44	12.3	114	31.8	146	40.7
TOTAL	250	17.9	319	25.2	304	21.5

[1] *Accessions that contained both resistant and susceptible plants.*

4. Inheritance of stem rust resistance

The infection type displayed by the F_1 plants from the crosses between resistant and susceptible accessions, and the segregation ratios observed in the resulting F_2 and $F_{2:3}$ progenies indicate that resistance to race TTKSK at the seedling stage in *T. turgidum* ssp. is controlled mostly by single gene (Table 5). Two resistant genes effective against TTKSK was observe only in two wild emmer and one durum accessions. Genes with complete dominance, partial dominance, and recessive effects were observed in the selected resistant parents (Table 5).

Table 4. Number and percentage of *Aegilops* accessions exhibiting resistant reaction to *P. graminis* f. sp. *tritici* races TTKSK, TRTTF, and TTTTF at the seedling stage.

Species	Genome	Access.	TTKSK		TRTTF		TTTTF		3 races	
		No.	No.	%	No.	%	No.	$	No.	%
Ae. cylindrical	DDCC	151	133	88.1	1	0.7	102	67.5	1	0.7
Ae. geniculata	MMUU	183	145	79.2	159	86.9	156	85.2	136	74.7
Ae. triuncialis	UUCC	353	290	82.2	198	56.1	315	89.2	166	47.0
Ae. biuncialis	UUMM	262	75	28.6	179	68.3	82	31.3	34	13.0
Ae. neglecta	UUMM	202	189	93.6	183	90.6	170	84.2	158	78.2
Ae. peregrina	SSUU	73	64	87.7	47	64.4	24	32.9	14	19.2
Total		1224	896	73.2	767	62.7	849	69.3	509	41.6

IV – Discussion

The TTKS race group of *Puccinia graminis* f. sp. *tritici*, and races found in Ethiopia that are more adapted to durum (Olivera *et al.*, 2012b), pose serious challenges to durum production at a global scale. The limited number of stem rust resistance genes effective against these new emerging Pgt races requires the search of additional stem rust genes that are effective against them. Results from this study demonstrate that cultivated and wild tetraploid wheats (*T. turgidum* ssp.) are a good reservoir of genes and could be used in durum improvement for stem rust resistance. Two hundred eighty (8.0%) durum accessions exhibited a resistant to moderately resistant in all field evaluations (Debre Zeit, Ethiopia and St. Paul, MN). These frequencies of resistance are much lower to the ones reported for North American (Pozniak *et al.*, 2008), and CIMMYT and Egypt (Singh *et al.*, 2011) durum lines at the field stem rust nursery in Njoro, Kenya (TTKSK and TTKSKT inoculum). These results confirmed that Pgt races present at the Debre Zeit (Ethiopia) nursery are more adapted to durum wheat and overcome the TTKSK resistance present in many of the durum lines. The highest frequency of durum resistant accessions is from cultivars and breeding lines from USA and Mexico, and landraces and old cultivars from Ethiopia and Egypt. Ethiopian durum cultivars and landraces have been previously reported as a good source of stem rust resistance (Admassu *et al.*, 2012; Beteselassie *et al.*, 2007; Bonman *et al.*, 2007; Denbel and Badebo, 2012). Ethiopia is a center of diversity of tetraploid wheat (Harlan, 1969) and the majority of the durum varieties are landraces (Tessema *et al.*, 1993) that have been co-evolving for centuries with local pathogen populations. Efforts should be made in incorporating these effective resistance genes into modern durum cultivars. Stem rust resistance in North American durum cultivars largely relies on *Sr13* and *Sr9e* (Klindworth *et al.*, 2007). However, the occurrence of a high frequency of resistant accessions originated from North American breeding programs indicates that additional effective genes are present in these germplasms.

Table 5. Segregation of $F_{2:3}$ families of various crosses of *T. turgidum* ssp. to race TTKSK of *Puccinia graminis* f. sp. *tritici*.

	Resistant	$F_{2:3}$ families[1]			Ratio tested		Genes	
Species	line	HR	Seg.	HS	(HR:Seg:HS)	*p*	Number	Effect
Durum	PI 428549	33	63	39	1:2:1	0.567	1	D
Durum	PI 298547	53	69	16	7:8:1	0.027	2	D
Durum	PI 479959	45	102	43	1:2:1	0.585	1	D
Durum	PI 519559	25	56	17	1:2:1	0.191	1	D
Emmer	PI 101971	31	48	28	1:2:1	0.522	1	PD
Emmer	PI 217640	37	80	33	1:2:1	0.644	1	PD
Emmer	PI 298582	22	45	19	1:2:1	0.821	1	R
Emmer	PI 319869	22	38	19	1:2:1	0.843	1	R
Wild emmer	PI 466946	46	74	9	7:8:1	0.179	2	PD
Wild emmer	PI 466960	42	69	16	7:8:1	0.003	2	PD
Persian	PI 387696	20	33	17	1:2:1	0.784	1	D
Polish	PI 384339	22	40	12	1:2:1	0.203	1	PD
Poulard	PI 384339	32	83	30	1:2:1	0.213	1	R

[1] HR=homozygous resistant; Seg=segregating; HS=homozygous susceptible;
D=Dominant; PD=Partially Dominant; R=Recessive.

Cultivated emmer accessions highly resistant in field and seedling evaluations have been observed in this study, and can contribute genes for stem rust resistance in durum. Most of the field resistant emmer accessions remain resistant against all Pgt races evaluated at the seedling stage. Selection of resistance based on seedling tests can be effective, as resistance detected at the seedling stage remains effective at the adult stage. Emmer wheat has contributed race specific stem rust resistance genes; *Sr13* and *Sr14* from Khapli (Heermann and Stoa, 1956), *Sr9e* from Vernal, and *Sr9d* and *Sr17* from Yaroslav (McIntosh *et al.*, 1995). The infection types observed in the 28 emmer accessions resistant to all the Pgt races evaluated indicate that resistance genes present in these accessions were likely different from the abovementioned genes. Emmer is also the donor of *Sr2* (McFadden, 1930), the most important APR gene for stem rust resistance in wheat. A selected group of emmer and durum accessions are being investigated for the presence of *Sr2* or additional APR genes based on stem rust evaluations in seedling and adult plant stages as well as available markers (Mago *et al.*, 2011).

Wild emmer, Persian, Polish, Oriental, and Poulard wheats may provide additional diversity of resistance to race TTKSK and other Pgt races from different origins and broad virulence spectra. Resistance to stem rust in these wild and cultivated tetraploids has been previously reported (Anikster *et al.*, 2005; McVey, 1991; Nevo *et al.*, 1991). The results from our study revealed that these subspecies exhibited different frequencies of resistance to race TTKSK. The highest frequency of resistance was observed in Persian wheat (45%), followed by Polish wheat (25%). These frequencies are comparable to the one reported by Olivera *et al.* (2012a) in cultivated emmer wheat (32.2%). These frequencies of resistance in cultivated and wild tetraploid wheats are lower than that reported by McVey (1991) using North American races, suggesting that race TTKSK overcame many of the genes present in these subspecies. According to infection type patterns, wild emmer exhibited the highest level of diversity for stem rust resistance (data not shown), and a high level of race specificity as a limited number of accessions were resistant to all races evaluated.

In the six tetraploid *Aegilops* species we evaluated, a high frequency of resistance against races with broad virulence spectrum was observed in all species. High frequencies of resistance against Ug99 have been also reported in diploid *Aegilops* species (Olivera *et al.*, 2007; Rouse *et al.*, 2011), confirming that this genus, closely related to *Triticum*, can contribute with potential new genes for stem rust resistance. We have selected resistant and susceptible parents from all evaluated species to produce biparental crosses in order to study the genetics of TTKSK resistance in these species. Gene introgression from these tetraploid *Aegilops* ssp. will likely not be a straightforward process, and cytogenetic manipulation will be required.

One of our major research objectives is to develop several mapping populations for all the *T. turgidum* subspecies level to determine the inheritance of TTKSK resistance and then mapping the resistance genes identified. Our results indicate that resistance to race TTKSK at the seedling stage is mostly conferred by single genes with both dominant and recessive action (Tables 5). The simple inheritance of TTKSK resistance in these species should simplify the transfer of resistance to durum and bread wheat.

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