DEVELOPMENT AND CHARACTERIZATION OF WHEAT GERMPLASM FOR RESISTANCE TO STEM RUST UG99 IN WHEAT

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

World wheat production is currently threated by stem rust (caused by *Puccinia graminis* f. sp. *tritici*) Ug99 race (TTKSK). The ongoing global effort to combat Ug99 is focusing on the identification and deployment of Ug99-resistant genes (*Sr*) into commercial cultivars. The objectives of this study were to identify TTKSK-effective *Sr* genes in untapped durum and common wheat germplasm and introgression of TTKSK-effective *Sr* genes from tetraploid wheat (*Triticum turgidium*) and *Aegilops tauschii* into hexaploids through production of synthetic hexaploid wheat (SHW). For identification of TTKSK-effective *Sr* genes, 177 durum and common wheat cultivars and lines were first evaluated using three highly virulent races TTKSK, TRTTF, and TTTTF and 71 cultivars and lines with TTKSK resistance were identified. The TTKSK-resistant cultivars and lines were then evaluated using six local races and the molecular markers that are diagnostic or tightly linked to the known TTKSK-effective *Sr* genes. The race specification and marker analysis showed that several previously deployed TTKSK-effective *Sr* genes such as *Sr2*, *Sr24* and *Sr42* were present in some of the cultivars and lines. A number of resistant cultivars and lines derived from wheat relatives such as *Thinopyrum ponticum*, Th. *elongatum*, *Th. intermedium*, and *Ae. speltoides* may carry novel *Sr* genes. For SHW development, 200 new SHW lines were developed by crossing 181 tetraploid wheat accessions to 14 *Ae. tauschii* accessions. Sixty-six of the new SHW lines, 14 previously-developed SHW lines, and their parents were evaluated for resistance to TTKSK, TRTTF, TTTTF and six other races and genotyped using molecular markers linked to the known genes in *T. dicoccum* and *Ae. tauschii*. The evaluation data showed that 44 SHW lines were resistant to TTKSK. The race specification and marker analysis showed that *Sr2* from *T. dicoccum* and *Sr33* from *Ae. tauschii* were present in some of the SHW lines and a number of SHW lines have novel genes conferring

TTKSK resistance. The durum and wheat cultivars and lines and SHW lines with known and novel *Sr* genes conferring resistance to TTKSK will be useful resources for improving wheat resistance to TTKSK and other emerging races of stem rust.

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CHAPTER 1. GENERAL INTRODUCTION

Stem rust, caused by *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn., is one of the most devastating diseases in wheat. Serious epidemics of this disease occurred in many wheat-growing countries from the 1920s and 1960s (Leonard and Szabo, 2005). With the eradication of the alternate host (*Berberis vulgaris* L.) and the release of the resistant wheat cultivars, stem rust has been under control for more than 30 years (Singh et al., 2006). However, emergence of the new race Ug99, which was detected in 1999 in Uganda (Pretorius et al., 2000), caused alarm worldwide because Ug99 has broad virulence to current *Sr* genes deployed in leading cultivars, rapid mutation, and rapid movement from East Africa to other wheat-growing regions (Singh et al., 2006, 2011; Xu et al., 2009).

Use of host resistance is considered the most effective and economic strategy to control stem rust. Development of the resistant cultivars using Ug99-effective *Sr* genes is now essential in many wheat breeding programs worldwide. However, the lack of Ug99-resistance genes hinders the progress in developing resistant cultivars. Thus, extensive efforts are needed to identify and characterize new sources of Ug99 resistance from untapped wheat germplasm lines, and transfer them into adapted wheat germplasm. USDA-ARS wheat germplasm improvement programs recently have collected and developed a number of durum and common wheat cultivars and lines. Some of the lines were wheat-alien species derivatives (i.e. chromosome addition, substitution, and translocation lines) from interspecific hybridization between wheat and its relatives. Evaluation and characterization of these germplasm for their resistance to Ug99 and other will provide useful information for effective utilization of these germplasm for improving wheat for resistance to Ug99.

In the primary gene pool of wheat, tetraploid wheat (*T. turgidum* L.) and *Aegilops tauschii* Coss. are useful resources for germplasm improvement of hexaploid common wheat (*T. aestivum* L.). Several recent studies demonstrated that Ug99-resistant genotypes were richly present in *Ae. tauschii* and seven tetraploid subspecies (*T. turgidum* subsp. *carthlicum*, *dicoccum*, *dicoccoides*, *durum*, *polonicum*, *turgidum*, and *turanicum*). Transfers of genes from *Ae. tauschii* and tetraploid wheat to common wheat can be accomplished either through interploidy hybridization followed by backcrossing or by production of synthetic hexaploid wheat (SHW) (×*Aegilotriticum* spp., $2n = 6x = 42$, AABBDD) (Mujeeb-Kazi et al., 1996). Compared with direct hybridization and backcrossing, SHW has the advantages of allowing for utilizing the genes from both the tetraploid and *Ae. tauschii* parents, evaluating value of the genes in combination, and performing large scale testing.

The objectives of this study were to: 1) evaluate durum and common wheat cultivars and lines, and wheat-alien species derivatives for reaction to Ug99 and other major virulent races and to investigate Sr genes present in resistant germplasm using molecular markers; 2) develop new SHW lines by crossing a large number of unique genotypes from the seven tetraploid subspecies to Ae. tauschii; and 3) evaluate expression of the stem rust resistance in the new SHW lines.

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CHAPTER 2. LITERATURE REVIEW

Wheat and Wheat Gene Pools

Taxonomy, genetics, and importance of wheat

The genus *Triticum*, including six wheat species that originated from the Levant area of the Middle East, botanically belongs to tribe Triticeae in the family Poaceae (Gramineae). The six wheat species are classified into three sections including *Monococcon* Dumort., *Dicoccoidea*, and *Triticum* Flaksb. The three sections contain diploid species *T. monococcum* L. and *T. urartu* Tumanian ex Gandilyan, tetraploid species *T. turgidum* L. and *T. timopheevii* (Zhuk.) Zhuk., and hexaploid species *T. aestivum* L. and *T. zhukovskyi* Menabde & Ericzjan, respectively (van Slageren,1994). Modern wheat crops mainly consist of tetraploid durum wheat [*T. turgidum* subsp. *durum* (Desf.) Husnot, $2n = 4x = 28$, AABB)] and hexaploid common wheat (*T. aestivum* L. subsp. *aestivum*, $2n = 6x = 42$, AABBDD), accounting for 4 and 96% of the total wheat acreage, respectively (Gill et al., 2004). Durum wheat is an allotetraploid ($2n = 4x = 28$) with A and B genomes, whereas common wheat is an allohexaploid ($2n = 6x = 42$) with the A, B, and D genomes. The 14 and 21 pairs of chromosomes in durum and common wheat, respectively, are placed into seven homoeologous groups (Sears and Okamoto, 1956; Sears, 1966; Kimber and Sears, 1987). Both durum and common wheat behave as a diploid species at meiosis due to the *Ph1* (pairing homoeologous) gene on chromosome arm 5BL, which prohibits pairing between homoeologous chromosomes (Riley and Chapman, 1958; Gill et al., 2004).

Cultivated wheat is a major staple food for 35% of the world's population (Ogbonnaya et al., 2013). Among the three major grain crops (i.e. wheat, corn, and rice), wheat has the largest acreage (220 million ha in 2011) and it ranks third in world crop production (704 million tons in 2011). Due to population growth, world wheat production needs to be continuously increased.

The strategies for increasing wheat production are to increase planting acreage and yield potential. An overview of wheat production in the past 20 years (1992-2011, http://faostat.fao.org/) showed that increase of wheat production has relied on per acre yield increase, since acreage varied little. However, increase of wheat yield is becoming a challenging task due to gradual depletion of available germplasm resources (Zamir, 2001; Reif et al., 2005; Warburton et al., 2006), climate change (Lobell et al., 2011), disease and insect epidemics (Duveiller et al., 2007), and abiotic stresses (Collins et al., 2008) such as drought (Nicolas et al., 1984) and waterlogging (Setter and Waters, 2003). Therefore, it is essential to use various genetic resources to broaden the genetic variability of wheat through the identification and introgression of genes for higher yield, improved quality, and resistance to various abiotic and biotic stresses.

Wheat gene pool

In addition to *Triticum* species, the tribe Triticeae contains over 300 species classified under more than 20 genera such as *Aegilops*, *Agropyron*, *Dasypyrum*, *Elymus*, *Hordeum*, *Leymus*, *Secale*, *Thinopyrum*, etc. (Dewey, 1984). Except for *Triticum* species and *Ae. tauschii* Cosson, all other Triticeae species carry genomes homoeologous with the wheat genomes A, B, and D, and they have variable crossibility with cultivated wheat (Cai et al., 2005). According to Harlan and de Wet (1971) cultivated wheat and its relatives in the tribe Triticeae can be classified into three gene pools (Jiang et al., 1994).

The primary gene pool of common wheat includes cultivars, breeding lines, and landraces, diploid wheat species with AA genomes (i.e. *T. monococcum*), tetraploid subspecies with AABB genomes (i.e. *T. turgidum* subsp. *carthlicum*, *dicoccum*, *dicoccoides*, *durum*,

paleocolchicum, *polonicum*, *turgidum*, and *turanicum*), hexaploid subspecies with AABBDD genomes (i.e. *T. aestivum* subsp. *compactum*, *macha*, *spelta*, and *sphaerococcum*), the D-genome donor species *Ae. tauschii*, and synthetic hexaploid wheat (×*Aegilotriticum* spp.) derived from crossing tetraploid wheat with AABB genomes with *Ae. tauschii*. The secondary gene pool includes the species carrying at least one of A, B, or D genomes of common wheat, such as *T. timopheevii* (AAGG), *T. zhukowskyi* (AAAAGG), and triticale (×*Triticosecale* Wittmack) (AARR, AABBRR, and AABBDDRR). The diploid *Aegilops* species with the S genome, such as *Ae. speltoides*, which has been considered a progenitor of the B genome of common wheat (Kilian et al., 2007), is also classified to the secondary gene pool (Jiang et al., 1994). The tertiary gene pool contains all other species in Triticeae that have no homologous genomes with common wheat, such as the species in *Agropyron*, *Dasypyrum*, *Elymus*, *Hordeum*, *Leymus*, *Secale*, *Thinopyrum*, etc. (Jiang et al., 1994; Friebe et al., 1996).

Exploitation of Wheat Gene Pools for Germplasm Improvement

Utilization of the primary gene pool for wheat improvement

Since the emergence of genetics and modern breeding technology in the early 20th century, wheat improvement has mainly focused on the utilization of landraces, cultivars, and their derivatives in the primary gene pool. Wheat improvement has been effectively achieved by simple and multiple crosses among selected parental cultivars and lines, followed by subsequent selection using various conventional breeding methodologies such as pedigree selection, mass selection, and backcross. A number of well-known and unique wheat landraces and cultivars and their derivatives have been extensively used as parents both regionally and globally. A semi-dwarf wheat cultivar ‘Norin 10’ originally developed in Japan in 1935, was extensively utilized

to develop new cultivars by Dr. N. E. Borlaug and his colleagues at the International Maize and Wheat Improvement Center (CIMMYT) in the 1950s. The widespread utilization of semi-dwarf wheat cultivars developed from Norin 10 triggered the first 'Green Revolution' in the 1960s (Reitz and Salman, 1968). In the early 1990s, a severe Fusarium head blight (FHB) (caused by *Fusarium graminearum* Schwabe) outbreak occurred in North America and the disease epidemic now occurs in most wheat-growing regions (Bai and Shaner, 2004). The Chinese wheat cultivar 'Sumai 3' developed in 1970 is highly resistant to FHB (He et al., 2001). At the present time, Sumai 3 and its derivatives have become major parents for developing FHB-resistant cultivars in most breeding programs. Since 'Alsen', the first hard red spring wheat cultivar (Frohberg et al., 2006) carrying the Sumai3-derived FHB-resistant QTL derived from Sumai 3 was released in 2000, at least 15 cultivars such as Howard, Glenn, Barlow, Prosper, and Tom and numerous breeding lines have been developed in the U.S.

The widespread use of varieties derived from landraces, cultivars, and adapted elite germplasm has resulted in a reduction of genetic diversity in cultivated wheat (Reif et al., 2005). The narrow genetic base makes wheat crops vulnerable to climate change and various and to disease and insect epidemics (Zamir, 2001; Niu et al., 2013). It also limits substantial improvement of wheat yield and quality through breeding. Thus, enormous efforts to increase genetic diversity in cultivated wheat have been made through the development of new germplasm using related species from the three gene pools. A number of useful traits from related species have transferred into common wheat and durum wheat (See reviews by Ogbonnaya et al., 2013; Mujeeb-Kazi et al., 2013).

Introgressions of useful genes from related species in the primary gene pool to durum and common wheat have been performed mainly by direct interspecific and intergeneric

hybridization and followed by backcrosses (Cox, 1997). The genes *GPC-B1* for high protein content (Joppa and Cantrell, 1990), *Yr15* for resistance to stripe rust (McIntosh et al., 1996), and two major FHB resistance QTLs (Otto et al., 2002; Stack and Faris, 2006; Chen et al., 2007) were initially transferred into durum from wild emmer (*T. turgidum* subsp. *dicoccoides*) using direct backcrossing. Many other disease and insect resistance genes, including *Pm16*, *Pm30*, *pm42*, *Lr23*, *Yr15*, and *YrH52* from wild emmer; *Sr2*, *Sr13*, *Sr14*, and *Hdic* from cultivated emmer; *H13*, *H22*, *H24*, *H26*, Lr39, *Lr40*, *Lr41*, and *Lr42* from *Ae. tauschii*; and *Lr35*, *Sr22* and *Sr35* from *T. monococcum* were transferred into common wheat using direct hybridization and/or backcrossing (See review by Ogbonnaya et al., 2013; Saintenac et al., 2013). Many of these genes have been extensively used in wheat breeding. Several genes, such as *GPC-B1* and *Sr2*, are now present in many bread wheat cultivars and *Sr13* is present in most North America durum cultivars (Simons et al., 2011).

In addition to direct hybridization and backcrossing, amphiploidization offers another important approach for gene introgression from the related species in the primary gene pool to common wheat (Cox, 1997). Synthetic hexaploid wheat (SHW), which is the spontaneous or colchicine-induced amphidiploids from the hybrids between tetraploid wheat subspecies (*T. turgidum* subsp.) with AABB genome and *Ae. tauschii* ($2n = 2x = 14$, DD), are particularly useful in gene introgression of desirable genes from tetraploid wheat and *Ae. tauschii* to common wheat because they have the same genome constitution as common wheat (Xu et al., 2004). A recent review by Ogbonnaya et al. (2013) indicated that over 1,500 SHW lines have been developed worldwide since McFadden and Sears (1944) created the first SHW in the 1940s. These SHW lines represent an important genetic resource for the improvement of common wheat. Many of the SHW lines were unique sources of genes for disease and insect resistance

from *Ae. tauschii*, such as *Pm2*, *Gb3*, *Gb7*, *Cre3*, *Sr33*, *Sr45*, *Sr46*, *H26*, *H32*, *Stb5*, *Rkn*, and *Dn3* (See review by Ogbonnaya et al., 2013; Saintenac et al., 2013). Several genes have been deployed into commercial cultivars through SHW lines, such as *Gb3* for resistance to greenbug in winter wheat cultivars 'TAM110' (Lazar et al., 1997) and 'TAM112' (PI 643143), which provide effective protection from greenbug in the southern Great Plains (Lu et al., 2010). For practical utilization of SHW germplasm in wheat breeding, four high-yielding wheat cultivars, the 'Chuanmai' series, which now are grown more than 100,000 ha, were developed by backcrossing CIMMYT SHW lines with adapted Chinese cultivars (Yang et al., 2009).

Utilization of secondary and tertiary gene pools for wheat improvement

Gene introgression from alien species in the secondary and tertiary gene pools into cultivated wheat is much more difficult and complex than that from the primary gene pool. Alien gene introgression in wheat has been performed using chromosome engineering, which involves production of intergeneric hybrids, amphidiploids, and chromosome addition, substitution, and translocation lines (Qi et al., 1997). Since the 1950s, numerous species in the genera *Aegilops*, *Agropyron*, *Dasypyrum*, *Elymus*, *Hordeum*, *Leymus*, *Secale*, *Thinopyrum*, etc. have been successfully hybridized with durum or common wheat (See reviewed by Mujeeb-Kazi et al., 2013). A large number of amphiploids and alien chromosome disomic addition (DA) lines have been produced from the intergeneric hybrids using chromosome doubling and subsequent chromosome elimination through backcrosses, respectively (Banks et al., 1993; Jiang et al., 1994; Larkin et al., 1995; Zhang et al., 1996; Qi et al., 1997; Xu et al., 2009; Niu et al., 2011; Mujeeb-Kazi et al., 2013). Many amphiploids and DA lines have been evaluated for the presence of useful genes located on the specific alien chromosomes and have been used to

transfer the alien genes into the wheat genome through induced translocations (i.e homoeologous recombination).

Wheat-alien species DA lines carrying the entire wheat genome and a pair of chromosomes from alien species have been directly used to develop translocations (i.e. homoeologous recombination) between the alien chromosome and its wheat homoeologs chromosome in the wheat. However, homoeologous chromosome pairing rarely occurs due to the presence of *Ph1* in the wheat genome and special techniques are needed to induce chromosome translocation (Qi et al., 2007). The most common approaches to induce homoeologous recombination is to use the *Ph1* gene inhibitor (Ph^I), *Ph1*mutants (*ph1b* and *ph1c*), or *Ph1*-deficient aneuploids. Numerous translocation lines carrying desirable genes have been developed by using *ph1b*-induced homoeologous recombination (See reviewed by Jiang et al., 1994; Friebe at al., 1996; Mujeeb-Kazi et al., 2013). Particularly, the use of *ph1b* mutants in combination with molecular markers and fluorescent genomic *in situ* hybridization (GISH) has proven efficient in selecting translocation lines carrying smaller alien segments (Niu et al., 2011; Klindworth et al., 2012). The new translocation lines carrying *Sr25*, *Sr26*, *Sr32*, *Sr39*, *Sr43*, and *Sr50* for stem rust resistance on short alien segments were developed using *ph1b*-induced homoeologous recombination and these lines are currently being used in wheat breeding. Compared to the *ph1b* mutant, Ph^I from *Ae. speltoides* (Chen et al., 1994) induces translocations in the presence of *Ph1* and a single dose of Ph^I, but it is less efficient and rarely used (Jiang et al., 1994). However, Wang et al. (2003) successfully developed two wheat-*Th. junceum* translocation lines carrying a gene(s) for salt tolerance on a short *Th. junceum* chromosome segment by crossing a wheat-*Th. junceum* DA line to the $Ph1^I$.

In durum wheat, because both *Ph*^{I} and *ph1b* are not available, *Ph1*-deficient aneuploids, such as the durum 5D(5B) disomic substitution (DS) line have been used for alien gene introgression. Dr. L. R. Joppa developed a durum-*Ae. speltoides* 2B/2S translocation line (DAS15) carrying the stem rust-resistant gene *Sr47* located on a large 2S chromosome segment using the durum DS line Langdon 5D(5B) (Faris et al., 2008). Klindworth et al. (2012) further reduced the *Ae. speltoides* chromatin surrounding *Sr47* using the Rusty durum 5D(5B) DS line to induce new homoeologous recombination and recovered several durum lines with very short alien segments carrying *Sr47* from the original translocation DAS15.

Homoeologous recombination may occur in the derivatives of wheat-alien hybrids at a low frequency and can result in spontaneous wheat-alien chromosome translocations (Jiang et al. 1994). The wheat cultivar 'Agent' is a spontaneous wheat-*Th. ponticum* 3D/3Ae#1 translocation carrying a leaf rust resistance gene (*Lr24*) (Smith et al., 1968). Spontaneous wheat-alien translocations could arise from the misdivision of a wheat and an alien univalent chromosome and the subsequent exchange of the telocentric chromosome arms at the centromeres (Sears, 1972; Jiang et al., 1994). The wheat-rye 1BL·1RS translocation that is widely used around the world originated by the centromeric-breakage and reunion mechanism (Mettin et al., 1973; Zeller, 1973; Jiang et al., 1994). However, the homoeologous recombination that occurs through this mechanism is a random and sporadic event. To effectively utilize this mechanism for targeted introgression of alien genes, Friebe et al. (2005) crossed wheat monosomics for group-1 (1A, 1B, and 1D) chromosomes to wheat-*Elymus trachycaulus* chromosome 1H^{t} DA line. They observed that the 1H^{t} and 1A univalents misdivided at anaphase I/telophase I in 6–7% of the pollen mother cells in the hybrids. The frequency of Robertsonian translocations was 1–4% in progenies derived from plants monosomic for group-1chromosomes of wheat (1A, 1B, and 1D)

and $1H^t$ of *E. trachycaulus*. Monosomics has also been used as a tool for developing several compensating Robertsonian translocations carrying several stem rust resistance genes, including *Sr44* from *Th. intermedium* (Liu et al., 2013), *Sr51* from *Ae. searsii* (Liu et al., 2011a), *Sr52* from *Dasypyrum villosum* (Qi et al., 2011), and *Sr53* from *Ae. geniculata* Roth (Liu et al., 2011b).

In addition to the techniques described above, several other approaches such as ionizing radiation (Sears, 1956), somatic cell fusion (Xia et al., 2003), tissue culture (Lapitan et al., 1984), and gametocidal genes (Endo, 1988; Tsujimoto and Tsunewaki, 1988) have been used for alien gene introgression. However, most of the resulting translocations induced by these approaches were between non-homoeologous chromosomes, and therefore are non-compensating; these types of changes are usually not agronomically acceptable (Sharma and Knott, 1966; Sears, 1972). Thus, these approaches are infrequently utilized for alien gene introgressions.

The wheat-alien chromosome translocation lines developed through these various methods substantially increase genetic diversity of wheat and some of them have been successfully incorporated into wheat cultivars. The wheat-rye T1BL·1RS translocation, which carries genes for resistance to powdery mildew (*Pm8* and *Pm17*), stripe rust (*Yr9*), stem rust (*Sr31*), and leaf rust (*Lr26*) and for wide adaptation and high yield, has been widely deployed in wheat cultivars (Jiang et al., 1994). Several disease-resistance genes such as *Pm21* from *H. villosa* (Chen et al., 1995), and *Sr24* and *Sr26* (McIntosh et al., 1976) from *Th. ponticum* have been widely deployed in wheat cultivars. Two Chinese winter wheat cultivars ‘Shanrong 1’ and ‘Shanrong 3’, which were developed from somatic cell fusion between wheat and *Th. ponticum*, carry a gene for salt tolerance from *Th. ponticum* and are now the major cultivars grown in the saline region of China (Xia et al., 2003). Although most of the other wheat-alien chromosome

translocation lines have not been deployed, they provide a valuable base of germplasm for future improvement of wheat for resistance to various biotic and abiotic stresses.

Wheat Stem Rust

Economic importance of stem rust in wheat

Stem rust, caused by the fungal species *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn., is a destructive disease for wheat. Heavy losses of wheat production were caused by the stem rust epidemics that occurred from the 1920s to the 1960s worldwide, including in the U.S., China, Europe, Australia, and India (Leonard and Szabo, 2005). In the U.S., statewide losses of 56% and 53% of the wheat crop in North Dakota and Minnesota, respectively, were documented in the stem rust epidemic of 1935 (Leonard, 2001). In North Dakota, the last serious stem rust epidemics caused losses of 38% and 43% of the total crop in 1953 and 1954, respectively.

Since the last major epidemic in North America, extensive efforts have been made to control stem rust through the deployment of cultivars carrying effective stem rust resistance (*Sr*) genes and the eradication of the alternate host of stem rust, the common barberry (*Berberis vulgaris* L.). Through these measures, stem rust had been effectively controlled for more than 30 years, until a new stem rust pathotype, which is commonly known as Ug99, was detected in Uganda in 1999 (Pretorius et al., 2000). Most *Sr* genes deployed in cultivars worldwide are ineffective against Ug99, which is now a major threat to world wheat production (Singh et al., 2011a). Thus, the emergence of Ug99 has made stem rust once again one of the most important diseases that currently jeopardize global wheat production.

Pathogen

Classification and nomenclature system

The stem rust pathogen was first designated as *Puccinia graminis* Pers. by Christiaan H. Persoon in 1794 (Schafer et al., 1984). Based on the host plant species, the pathogen was sub-classified to six formae speciales (f. sp.) including *P. graminis* f. sp. *tritici*, *secalis*, *avenae*, *agrostidis*, *poae*, and *airae* for wheat (*Triticum*), rye (*Secale*), barley (*Hordeum*), oat (*Avena*), bentgrass (*Agrostis*), bluegrass (*Poa*), and hairgrass (*Aira caespitosa*), respectively (Leonard and Szabo, 2005). The wheat stem rust pathogen *P. graminis* f. sp. *tritici* (Pgt) is composed of different physiologic races or pathotypes. A race is a uniform isolate with a certain pattern of infection types to a number of differential lines containing a single *Sr* gene. Roelfs and Martens (1988) established an international nomenclature system designating *P. graminis* f. sp. *tritici* races by combining 12 differential lines based on the nomenclature system developed by Roelfs and McVey (1979). The 12 differential lines were originally divided into three differential sets with four differentials in each set (Roelfs and Martens, 1988). A certain pattern of infection types to the four differentials in each set is given a letter code, which indicates different virulence to the differentials within each set. For example, a race with a higher letter code T can infect more differentials than that with a low letter code B in the same set (Roelfs and Martens, 1988). As new races have been steadily discovered, Jin et al. (2008a) expanded the system into five differential sets containing 20 differentials, thus a race is currently designated using five letters (Table 2.1).

Table 2.1. An international nomenclature system designating *P. graminis* f. sp. *tritici* (Pgt) races†

	Differential subset	Infection type produced on host lines with *Sr* gene				Ug99‡
	1	*Sr5*	*Sr21*	*Sr9e*	*Sr7b*	T
	2	*Sr11*	*Sr6*	*Sr8a*	*Sr9g*	T
Pgt code	3	*Sr36*	*Sr9b*	*Sr30*	*Sr17+13*	K
	4	*Sr9a*	*Sr9d*	*Sr10*	*SrTmp*	S
	5	*Sr24*	*Sr31*	*Sr38*	*SrMcn*	K
B		L§	L	L	L	
C		L	L	L	H§	
D		L	L	H	L	
F		L	L	H	H	
G		L	H	L	L	
H		L	H	L	H	
J		L	H	H	L	
K		L	H	H	H	
L		H	L	L	L	
M		H	L	L	H	
N		H	L	H	L	
P		H	L	H	H	
Q		H	H	L	L	
R		H	H	L	H	
S		H	H	H	L	
T		H	H	H	H	

† Sources: Roelf and Martens (1998) and Jin et al. (2008b).
‡ An example of Pgt code for Ug99.
§ L and H indicate low and high infection type, respectively.

Life cycle and infection process

Puccinia graminis f. sp. *triticii* is an obligate biotrophic fungus that acquires nutrients and reproduces on a living host. It is also a heteroecious fungus that requires two different hosts in the life cycle (Roelf, 1985; Roelf et al., 1992; Leonard and Szabo, 2005). The life cycle and infection process of the pathogen have been fully studied and extensively reviewed in the literature (Leonard and Szabo, 2005). The full life cycle of the pathogen includes a non-sexual reproductive cycle on wheat or related species and a sexual reproductive cycle on barberry.

According to the stage of spore production, the pathogen can be divided into five spore stages, including urediniospores, teliospores, basidiospores, pycniospores, and aeciospores (Roelf, 1985; Leonard and Szabo, 2005).

The urediniospores infect the host plant and form pustules (uredinium) on the stems or leaves in the summer; the uredinium spread the urediniospores to infect the host plant again or other host or spread to far-distant host plants by prevailing wind (Roelf, 1985). In the early fall or late summer, the uredinium change mechanisms to produce teliospores, which have a darker color, thicker cell wall, and two cells, instead of the urediniospores. Teliospores undergo the karyogamy process, in which two nuclei in each cell are fused, and start dormancy in the winter (Roelf, 1985; Roelf et al., 1992). When the spring comes, each cell of the teliospore with fused nuclei will grow the hypha shape basidium (promycelium), which contains four haploid nuclei through meiosis. Each haploid nuclei will form a basidiospore containing two nuclei through mitosis. The basidiospore will infect the upper surface leaves of the barberry plant and form pycnium in spring, which will produce pycniospores as male gametes (+) and flexuous hyphae as female gametes (-). After the fusion of pycniospores and flexuous hyphae, a dikaryotic aecium forms. The Aecia then produce the aeciospores, which have the ability to infect the host plant and form the uredinium that produces urediniospores (Roelf, 1985; Roelf et al., 1992; Leonard and Szabo, 2005).

In the early infection stage, urediniospores attached on the host stems or leaves will germinate under favorable conditions, including mild temperature, sufficient water on the stem or leaf surface, and darkness (Roelf, 1985; Roelf et al., 1992). After the spores geminate, the urediniospore produces the germ tube that grows along a right angle to the stoma under favorable conditions such as light. After arriving at the stoma, the end of the germ tube will form an

appressorium to cover the stoma. Appressorium leg formed from appressorium will pass through stoma into cavity under the epidermis. A substomatal vesicle formed from end of appressorium leg with nuclei derived from appressorium will produce infection hypha, which form haustorial mother cell at its end. The haustorial mother cell penetrates the mesophyll cell wall of the host, and releases its nuclei into the cytoplasm of the mesophyll cell to form the haustorium. The haustorium absorbs nutrients from the host cell and forms the hypha that will break out of the host cell and release the urediniospore again (Roelf, 1985; Roelf et al., 1992; Leonard and Szabo, 2005).

Genetics of the pathogen

Puccinia graminis f. sp. *tritici* contains 18 chromosomes (Boehm et al., 1992) with a genome size of 88.6 Mb (Duplessis et al., 2011). Its avirulence and virulence to wheat are genetically controlled by avirulence genes (*Avr*) in the rust genome and their inheritance fits to the Mendelian laws (Johnson and Newton, 1940; Johnson, 1954; Loegering and Powers, 1962; Zambino et al., 2000). Zambino et al. (2000) investigated virulence phenotypes of F_1 and 81 F_2 progeny from two *P. graminis* f. sp. *tritici* strains on 10 wheat differentials carrying individual *Sr* genes. They observed that segregation of avirulence to virulence was 3:1 on eight differentials, indicating that the avirulence phenotype was dominant and controlled by a single avirulence gene. However, they found that the segregations of avirulence to virulence on the other two differentials were 15:1 and 3:13, respectively, and they suggested that there were possibly two segregating genes: one dominant for avirulence and one dominant for avirulence inhibition. Therefore, although a single avirulence gene generally controls avirulence and virulence,

interactions of two or more avirulence genes may also affect expression of avirulent/virulent phenotypes.

The interactions between the avirulence genes of *P. graminis* f. sp. *tritici* and the *Sr* genes in wheat fit to the classical gene-for-gene model developed by Flor (1971). To distinguish the *Avr* genes of *P. graminis* f. sp. *tritici* from other formae speciales of *P. graminis*, Zambino et al. (2000) proposed to name avirulence genes using a four letter prefix to indicate avirulence on a particular host, such as '*Avr*T', '*Avr*S', '*Avr*H', and '*Avr*A' for wheat (*Triticum*), rye (*Secalis*), barley (*Hordeum*), and oats (*Avena*), respectively, and a suffix to indicate the name of the compatible *Sr* gene. As a large number of molecular markers were developed from the rust genome (Zhong et al., 2009), many *AvrT* genes have been mapped. Zambino et al. (2000) used 970 AFLP and RAPD markers to establish a genetic linkage map consisting of seven linkage groups and mapped eight *AvrT* genes (*AvrT6, AvrT8a, AvrT9a, AvrT10, AvrT21, AvrT28, AvrT30*, and *AvrTU*) to linkage groups.

Host resistance

Host resistance and resistance expression

Major hosts of *P. graminis* f. sp. *tritici* include wheat (*Triticum*) species and many wild relatives of wheat. Anikster (1984) reported 28 species in eight genera that can host *P. graminis* f. sp. *tritici* under natural conditions. The hosts range of *P. graminis* f. sp. *tritici* is much wider under artificial inoculation conditions than it is under natural conditions. A survey showed that 78 species in 34 genera may be host under artificial inoculation (Anikster, 1984).

Host resistance is classified as either race-specific or non-race specific. Race-specific resistance governed by a single host gene was the consequence of interaction between a host

resistance gene and a corresponding avirulence gene in the pathogen (Dyck and Kerber, 1985; Singh et al., 2011b). The mechanism of race-specific resistance to stem rust strictly follows gene-for-gene model, i.e. a gene governing resistance in the host will have a corresponding gene governing avirulence in the pathogen (Flor, 1971). As with the avirulence genes in the pathogen, most of the host's resistance genes to stem rust are dominant (Roelfs, 1988). The race-specific resistance genes usually control resistance in both the seedling and adult stages. Non-race specific resistance, also called durable resistance or horizontal resistance, is conferred by multiple genes. The term 'adult plant resistance (APR)', which is also called slow rusting, can be considered non-race specific resistance (Roelf et al., 1992; Singh et al., 2011b). The symptoms of APR show moderately susceptible to susceptible reactions in both the seedling and adult stages, but the number of pustules (disease severity) are reduced (Singh et al., 2011a).

To date, a total of 63 *Sr* genes have been identified in the A, B and D genomes of wheat and its closely related species in the primary gene pool, or transferred to the wheat genomes from alien genomes of the species in the secondary and tertiary gene pools (Table 2.2). Fifty-seven of the genes are designated *Sr1* through *Sr57* in the *Catalogue of Gene Symbols for Wheat* (McIntosh et al., 2013). Most of the *Sr* genes are race-specific, except for four APR genes including *Sr2*, *Sr55*, *Sr56*, and *Sr57*.

Table 2.2. Chromosome location and original source of *Sr* genes.

Sr gene	Chr loc ‡	Original source	References
Sr2†	3BS	*T. turgidum* subsp. *dicoccum*	Knott (1968)
Sr5	6DS	*T. aestivum* subsp. *aestivum*	McIntosh et al. (1995)
Sr6	2DS	*T. aestivum* subsp. *aestivum*	McIntosh et al. (1995)
Sr7a	4AL	*T. aestivum* subsp. *aestivum*	McIntosh et al. (1995)
Sr7b	4AL	*T. aestivum* subsp. *aestivum*	McIntosh et al. (1995)
Sr8a	6AS	*T. aestivum* subsp. *aestivum*	McIntosh et al. (1995)
Sr8b	6AS	*T. aestivum* subsp. *aestivum*	McIntosh et al. (1995)
Sr9a	2BL	*T. aestivum* subsp. *aestivum*	McIntosh et al. (1995)

Table 2.2. Chromosome location and original source of *Sr* genes (continued).

Sr gene	Chr loc ‡	Original source	References
Sr9b	2BL	*T. aestivum* subsp. *aestivum*	McIntosh et al. (1995)
Sr9d	2BL	*T. turgidum* subsp. *dicoccum*	McIntosh et al. (1995)
Sr9e	2BL	*T. turgidum* subsp. *dicoccum*	McIntosh et al. (1995)
Sr9f	2BL	*T. aestivum* subsp. *aestivum*	McIntosh et al. (1995)
Sr9g	2BL	*T. turgidum* subsp. *durum*	McIntosh et al. (1995)
Sr10	2B	*T. aestivum* subsp. *aestivum*	McIntosh et al. (1995)
Sr11	6BL	*T. aestivum* subsp. *aestivum*	McIntosh et al. (1995)
Sr12	3BS	*T. turgidum* subsp. *durum*	McIntosh et al. (1995)
Sr13†	6AL	*T. turgidum* subsp. *dicoccum*	Knott (1962)
Sr14†	1BL	*T. turgidum* subsp. *dicoccum*	Knott (1962)
Sr15	7AL	*T. aestivum* subsp. *aestivum*	Watson and Luig (1966)
Sr16	2BL	*T. aestivum* subsp. *aestivum*	Loegering and Sears (1966)
Sr17	7BL	*T. turgidum* subsp. *dicoccum*	McIntosh et al. (1967)
Sr18	1D	*T. aestivum* subsp. *aestivum*	Baker et al. (1970)
Sr19	2BS	*T. aestivum* subsp. *aestivum*	Anderson et al. (1971)
Sr20	2BL	*T. aestivum* subsp. *aestivum*	Anderson et al. (1971)
Sr21	2AL	*T. monococcum* subsp. *monococcum*	The (1973)
Sr22†	7AL	*T. monococcum* subsp. *monococcum*	The (1973)
Sr23	2BS	*T. aestivum* subsp. *aestivum*	McIntosh and Luig (1973)
Sr24†	3DL	*Th. ponticum*	McIntosh et al. (1976)
Sr25†	7DL	*Th. ponticum*	McIntosh et al. (1976)
Sr26†	6AL	*Th. ponticum*	McIntosh et al. (1976)
Sr27†	3A	*S. cereale*	Marais et al. (1994)
Sr28†	2BL	*T. aestivum* subsp. *aestivum*	Rouse et al. (2012)
Sr29†	6DL	*T. aestivum* subsp. *aestivum*	Dyck and Kerber (1977)
Sr30	5DL	*T. aestivum* subsp. *aestivum*	Knott and McIntosh (1978)
Sr31	1BL	*S. cereale*	Friebe et al. (1996)
Sr32†	2A, 2B, 2D	*Ae. speltoides*	McIntosh et al. (1995)
Sr33†	1DS	*Ae. tauschii*	Jones et al. (1991)
Sr34	2A,2D	*Ae. comosa*	Friebe et al. (1996)
Sr35†	3AL	*T. monococcum* subsp. *monococcum*	Saintenac et al. (2013)
Sr36†	2BS	*T. timopheevii* subsp. *timopheevii*	McIntosh et al. (1995)
Sr37†	4BL	*T. timopheevii* subsp. *timopheevii*	McIntosh et al. (1995)
Sr38	2AS	*Ae. ventricosa*	McIntosh et al. (1995)
Sr39†	2BS	*Ae. speltoides*	Niu et al. (2011)
Sr40†	2BS	*T. timopheevii* subsp. *armeniacum*	Dyck (1992)
Sr41	4D	*T. aestivum* subsp. *aestivum*	Riede et al. (1995b)

Table 2.2. Chromosome location and original source of *Sr* genes (continued).

Sr gene	Chr loc ‡	Original source	References
Sr42	6DS	*T. aestivum* subsp. *aestivum*	Ghazvini et al. (2012)
Sr43†	7DS	*Th. ponticum*	Kim et al. (1993); Niu et al. (2013)
Sr44†	7DS	*Th. intermedium*	Friebe et al. (1996); Liu et al. (2013)
Sr45†	1DS	*Ae. tauschii*	Marais et al. (1998)
Sr46†	2DS	*Ae. tauschii*	E.S. Lagudah personal communication
Sr47†	2BL	*Ae. speltoides*	Klindworth et al. (2012)
Sr48†	2AL	*T. aestivum* subsp. *aestivum*	Bansal et al. (2009)
Sr49	5BL	*T. aestivum* subsp. *aestivum*	U. Bansal 2010 personal communication
Sr50 †	1DS	*S. cereale*	Anugrahwati et al. (2008)
Sr51	3A, 3B, 3D	*Ae. searsii*	Liu et al. (2011a)
Sr52	6AS	*D. villosum*	Qi et al. (2011)
Sr53	5D	*Ae. geniculata*	Liu et al. (2011b)
Sr54	2DL	*T. aestivum* subsp. *aestivum*	Ghazvini et al. (2013)
Sr55	4DL	*T. aestivum* subsp. *aestivum*	Herrera-Foessel et al. (in preparation)
Sr56	5BL	*T. aestivum* subsp. *aestivum*	Bansal et al. (2008)
Sr57	7DS	*T. aestivum* subsp. *aestivum*	Singh et al. (in preparation)
SrCad†	6DS	*T. aestivum* subsp. *aestivum*	Hiebert et al. (2011)
SrTmp†	unknown	*T. aestivum* subsp. *aestivum*	Roelfs and McVey (1979)

† Those genes confer resistance to race TTKSK.
‡ Chromosomal location.

Expression of stem rust-resistant genes

Numerous studies show that certain environment and genetic factors can affect the expression of some *Sr* genes. Among the environmental factors, temperature is most noticeable because several *Sr* genes such as *Sr5, Sr6, Sr13,* and *Sr43* are temperature-sensitive. *Sr6* and *Sr43* provided resistance to many races at around 20 ºC but they became infective at 26 ºC (Dyck and Kerber 1985; Niu et al., 2013). Similarly, *Sr5* was considered an immunity gene to stem rust (McIntosh et al., 1995) but it broke down at 30 ºC (Luig and Rajaram, 1972). On the contrary, *Sr13* breaks down at low temperatures such as 18 ºC (Roelfs and McVey, 1979).

The interaction of two or more *Sr* genes may enhance resistance as compared to the monogenic resistance level (Dyck and Kerber, 1985). Knott (1957) suggested that *Sr9b*, *Sr10*,

Sr11 and *Sr12* act as modifiers to enhance the resistance level of *Sr7a* to race 15B (Roelfs, 1988). Klindworth et al. (2011) found that at 25°C, monogenic lines carrying *Sr6* and *Sr9b* were susceptible (IT 3) and resistant (IT 2) to TPPKC, respectively, but the hybrid of the monogenic lines (*Sr6sr6Sr9bsr9b*) had a higher level of resistance (IT ;), indicating that the interaction between *Sr6* and *Sr9b* enhanced the level of resistance.

Unlike gene interactions enhancing resistance, certain suppressors on the D genome can suppress the expression of the *Sr* genes on the A and/or B genomes in hexaploid wheat, and vice versa (Bai and Knott, 1992; Assefa and Fehrmann, 2004; Innes and Kerber, 1994; Kerber and Green, 1980; Williams et al., 1992). Kerber and Green (1980) first identified a suppressor gene on the long arm of chromosome 7D in the wheat cultivar Canthatch, Williams et al. (1992) inferred that the suppressor may inhibit three recessive genes on the A and/or B genomes. Many hexaploid synthetic wheat lines derived from the crosses between resistant tetraploid wheat and susceptible *Ae. tauschii* or from susceptible tetraploid wheat and resistant *Ae. tauschii* were susceptible or had a lower level of resistance than their resistant parents, indicating the suppressor may be present on the A and/or B and D genome (Innes and Kerber, 1994; Assefa and Fehrmann, 2004).

Genetic background frequently affects expression of certain *Sr* genes. Particularly, during the process of transferring a resistance gene to a susceptible parent, the resistance level of the backcrossed progeny is often lower than that of the original stock. Knott (1957) noted that after transferring *Sr7* to Marquis through five backcrosses, it was difficult to select the progeny carrying the gene because the plant with the highest level of resistance was close to susceptible. Luig and Rajaram (1972) backcrossed *Sr5* to line W2691/W3498 and compared the resistant

level at five, seven, and nine backcrosses. They found that the resistance level of the progeny with *Sr5* was lower with increasing numbers of backcrosses.

Disease control

The methods of stem rust control include cultural management, chemical control, eradication of alternate host, and utilization of the resistant cultivars (Roelf et al., 1992). Cultural control is part of field and crop management such as the quantity of fertilizer, times of irrigation, and density of crop per unit-area. It is infeasible to control wheat stem rust using cultural management since stem rust is only one of many wheat diseases. Growers have no reason to change their conventional field and crop management unless a severe epidemic of stem rust occurs (Roelf et al., 1992). Chemical control using fungicides is effective to prevent stem rust infection and development. However, high cost and environmental concerns can limit growers use of fungicide to control stem rust. Because of these limitations in cultural management and chemical control, eradication of the alternate host barberry, and deployment of cultivars with stem rust-resistant genes are the two major approaches to control stem rust (Roelf et al., 1992; Leonard and Szabo, 2005). The eradication of barberry blocks sexual reproduction of the stem rust pathogen, thus reducing genetic variation of the pathogen, and eliminating the source of stem rust spores produced on barberry (Leonard and Szabo, 2005).

Compared to other approaches, the utilization of resistant cultivars is the most economic and effective control method for stem rust. Since the 1950s, a systematic deployment of effective *Sr* genes into commercial cultivars has been carried out by wheat breeder in all of the wheat-growing regions that are vulnerable to stem rust (Roelfs, 1985; Roelf et al., 1992; Leonard and Szabo, 2005). In the northern Great Plains of North America, a hard red spring wheat cultivar

‘Selkirk’ (released in 1953 in Canada) carrying *Sr2, Sr6, Sr7b, Sr9d, Sr17,* and *Sr23* for resistance to race 15B was widely grown until it was replaced by new high-yield cultivars (Roelf, 1985). Wheat cultivar ‘Era’ (Roelf et al., 1992) with *Sr5, Sr 6, Sr12,* and *Sr17* and ‘Waldron’ with *Sr5, Sr11,* and *SrWld-1* were developed in 1972 (Heiner and McVey, 1971) and 1969 (Riede, et al., 1995a), respectively, and widely grown for a decade until they were replaced by new high yield cultivars (Roelfs, 1985). Since 1971, *Sr26* has been deployed in Australian wheat cultivars and was successfully used to control a stem rust epidemic (Roelfs et al., 1992). Several other important *Sr* genes such as *Sr24, Sr31,* and *Sr42* have been widely deployed into bread wheat cultivars worldwide and *Sr13* has been deployed in various durum cultivars. The extensive and widespread deployment of *Sr* genes in durum and common wheat cultivars has controlled stem rust worldwide for more than 30 years until the emergence of Ug99 in East Africa in the late 1990s (Singh et al., 2006).

Ug99 Lineage Races and Their Control

Ug99 lineage races

In Uganda in 1998, a large number of cultivars containing *Sr31* were observed to be susceptible to stem rust. Pretorius et al. (2000) identified a new race with virulence to *Sr31* and designated the race as Ug99 in 1999. Wanyera et al. (2006) designated Ug99 as TTKS using the North American stem rust nomenclature system (Roelfs and Martens, 1988). Jin et al. (2008a) re-designated Ug99 as TTKSK by adding the fifth set of differentials. The emergence of TTKSK poses a serious threat to world wheat production because this race has broad virulence to most of the *Sr* genes deployed in modern wheat cultivars (Pretorius et al., 2000). A survey by CIMMYT in 2007 showed that only 5 - 10% of cultivars from 22 counties were resistant to TTKSK (Singh

et al., 2011a). Jin and Singh (2006) showed that among 450 cultivars and breeding lines in the U.S. only 16% of hard red spring wheat, 48% of hard red winter wheat, and 27% of soft winter wheat were resistant to TTKSK.

Race TTKSK has the ability to evolve new virulence to deployed *Sr* genes. In 2006 and 2007, two new variants of TTKSK, designated TTKST and TTTSK, respectively, were detected in Kenya. These two races are virulent to *Sr24* and *Sr36*, respectively (Jin et al., 2008a, 2009). Studies showed that the genes conferring TTKSK resistance in most American wheat cultivars and breeding lines were *Sr24*, *Sr36*, and $Sr1RS^{Amigo}$ (Jin and Singh, 2006; Olson et al., 2010). Because the genes conferring TTKSK resistance in most of the common wheat cultivars in the U.S. were *Sr24* and *Sr36* (Jin and Singh, 2006; Olson et al., 2010), the new variant races have made wheat more vulnerable to stem rust. In addition, five other races detected in Africa, including TTKSF (virulent to *Sr21*), TTKSP (virulent to *Sr31*, *Sr21*, and *Sr24*), PTKSK, PTKST, TTKSF+, were recently identified to belong to the Ug99 lineage of races (Hodson et al. 2012). In addition to its broad virulence and evolution, TTKSK may rapidly spread from Africa to other continents. Singh et al. (2006) predicted that the pathway of TTKSK might be similar to that of the yellow rust (*Puccinia striiformis* f.sp. *tritici*) *Yr9*-virulent race, which started in the high land of east Africa, and moved to the Arabian peninsula, the Middle East and South Asia with the prevailing wind. The evidence of TTKSK found in Yemen in 2006 (Jin et al., 2008a) and Iran in 2007 (Nazari et al., 2009) supported this hypothesis. Although Ug99 lineage races have not been detected in regions other than Africa and the Middle East, by following the pathway taken by the *Yr9*-virulent race, it is expected that Ug99 will eventually threaten wheat production outside Africa (Singh et al., 2011a).

Ug99-effective resistance genes

Ug99-resistance genes derived from primary gene pool

Two *Sr* genes, *Sr22* and *Sr35*, derived from the diploid wheat *T. monococcum* confer resistance to Ug99 (Singh et al., 2011a). *Sr22* is located on the long arm of chromosome 7A (The, 1973) has not been widely used in breeding because of its association with a detrimental linkage drag causing low yield and late maturity (Paull et al., 1994). *Sr35* was mapped to the long arm of chromosome 3A between markers *XBF483299* and *XCJ656351* and it is highly resistant to Ug99 lineage races (Zhang et al., 2010). This gene was recently isolated using map-based cloning (Saintenac et al., 2013). Six *Sr* genes derived from *Ae. tauschii*, including *Sr33*, *Sr45*, *Sr46*, *SrTA1662*, *SrTA10171*, and *Sr10187* are all resistant to Ug99 (Singh et al., 2011a; Olson et al., 2013a,b). *Sr33*, *Sr45* (Sambasivam et al., 2008), and *SrTA1662* (Olson et al., 2013a) were mapped on the chromosome arm 1DS and *Sr46* was mapped onto 2DS (Rouse et al., 2011). *Sr33* was recently cloned using map-based cloning (Periyannan et al., 2013). None of the *Sr* genes from *Ae. tauschii* have been deployed into wheat cultivars and they represent new resources for breeding wheat cultivars for Ug99 resistance.

Two genes, including *Sr2* and *Sr13* derived from domesticated emmer wheat (*T. turgidum* subsp. *dicoccum*), were resistant to TTKSK (Singh et al., 2011a). Among the three genes, *Sr2* with APR was originally transferred from Yaroslav emmer to the wheat cultivar Marquis (McFadden, 1930). *Sr2* has been widely used in wheat breeding worldwide and it is now present in many wheat cultivars (Roelfs, 1985). It is located on the short arm of chromosome 3B and is associated with pseudo-black chaff (PBC) (Johnson, 1984). It confers inadequate resistance to stem rust when it is present in the cultivar alone; but it may enhance the resistance level when combined with other resistance gene(s) (Singh et al., 2011a). The tightly

linked markers *gwm533* and *csSr2* are useful to detect *Sr2* in marker-assisted selection. *Sr13* located on chromosome arm 6A (Mcintosh, 1972) and derived from Khapli emmer is a major *Sr* gene that is effective against Ug99 races in modern durum cultivars. However, the race TRTTF is virulent to *Sr13* (Singh et al., 2011a), indicating that the deployment of other Ug99-resistance genes into durum wheat is necessary. Although *Sr13* was recently mapped, digonostic markers for this gene are not available (Simons et al., 2011). *Sr14* located on 1BL (Knott, 1962) is not ascertainable on resistance to Ug99 (Jin et al., 2007).

Eight genes derived from common wheat, including *Sr28, Sr29, Sr48, SrTmp, SrCad/Sr42, SrSha7, SrHuw234,* and *SrND643,* confer resistance to TTKSK (Singh et al., 2011a). *Sr28* located on chromosome 2BL (Rouse et al., 2012) has both seedling and adult plant resistance to TTKSK, but it is ineffective to most U.S. races (Rouse et al., 2012). The *Sr28* gene has not been deployed in current cultivars. A good deployment strategy for this gene is to pyramid it with other TTKSK-resistant genes with broad spectrum resistance. *Sr28* was recently mapped and targeted by two flanking markers, *wmc332* and *wPt-7004-PCR* (Rouse et al., 2012). *SrTmp* is present in some North American, African, and Asian cultivars. However, TRTTF is virulent to *SrTmp* (Jin et al., 2008; Singh et al., 2011a). *SrCad* was initially identified in the Canadian wheat cultivar 'AC Cadillac' and is now present in many Canadian wheat cultivars (Hiebert et al., 2011). *SrCad* has moderate resistance to TTKSK. It was mapped to the short arm of chromosome 6D and can be detected by a tightly-linked marker, *FSD_RSA* (Hiebert et al., 2011). *Sr42* from 'Norin 10' is considered to be allelic to *SrCad* (Hiebert et al., 2011; Ghazvini et al., 2012). The other genes, including *Sr29, Sr48, SrSha7, SrHuw234,* and *SrND643* identified from wheat cultivars or breeding lines have not been characterized.

Alien species-derived Ug99-resistance genes

T. timopheevii with an AAGG genome is a useful source of stem rust resistance. So far, three genes *Sr36*, *Sr37*, and *Sr40* were transferred from the G-genome chromosomes of *T. timopheevii* into common wheat through chromosome translocation. *Sr36* is present in many U.S. soft winter wheat cultivars and confers a high level of resistance to TTKSK. But it was broken down by race TTTSK (Jin and Singh, 2006). *Sr37* confers a high level of resistance to Ug99 in both seedlings and adult plants, however, this gene has not been deployed into wheat cultivars since this gene exhibited variable expression of resistance during its introgression to other wheat cultivars (McIntosh et al., 1995). *Sr40* is not suitable for use in wheat breeding because of its association with undesirable genes (Singh et al., 2011a).

In the *Aegilops* species, five Ug99 resistant *Sr* genes have been transferred into wheat through molecular marker-assisted chromosome engineering. Among them, three genes *Sr32*, *Sr39*, and *Sr47* on short alien chromosome segments were recently introgressed from the *Ae. speltoides* 2S chromosome into the wheat genome through *ph1b*-induced homoeologous recombination (Niu et al., 2011; Klindworth et al., 2012; Mago et al., 2013). They all have broad spectrum resistance to many races, including the Ug99 lineage races. Molecular markers linked to the three genes on the short 2S chromosome segments were also developed and can be used for marker-assisted deployment in wheat breeding. One recently designated gene *Sr51* derived from *Ae. searsii* was transferred to the wheat group-3 chromosomes (Liu et al., 2011a). Another new gene *Sr53* derived from *Ae. geniculata* was transferred to wheat chromosome 5D (Liu et al., 2011b).

Four Ug99 resistant *Sr* genes, including *Sr24*, *Sr25*, *Sr26*, and *Sr43*, were derived from tall wheatgrass *Th. ponticum* (Podp.) Z-W. Liu & R.-C. Wang. *Sr24* and *Sr26* were extensively

used in wheat breeding and they have been deployed in many wheat cultivars in the U.S. (*Sr24*) and Australia (*Sr26*), respectively (Olson et al., 2010; Dundas et al., 2007). *Sr24* has been defeated by race TTTSK, whereas *Sr26* remains highly resistant to Ug99 lineage races. *Sr25* and *Sr43* have not been used in wheat breeding since they are associated with an undesirable gene for yellow pigment in wheat flour. Niu et al. (2013) recently reduced the *Th. ponticum* chromosome segment carrying *Sr43* but has not broken the linkage with the yellow pigment gene. *Sr44* derived from *Th. intermedium* (Host) Barkworth & D. R. Dewey is an effective gene against the Ug99 lineage races. The gene was recently transferred to wheat chromosome 7D through Robertsonian translocations induced by momosomics (Liu et al., 2013).

Common rye (*Secale cereale* L.) is also an excellent source for stem rust resistance. Among the four *Sr* genes (*Sr27*, *Sr31*, *Sr50*, and $Sr1RS^{Amigo}$) derived from the rye chromosome arm 1RS (Mago et al. 2002), three were highly resistant to the Ug99 lineage races, the exception being *Sr31* which was susceptible to TTKSK. They are currently being utilized for breeding Ug99-resistant cultivars in many wheat-breeding programs worldwide. A newly designated *Sr52* located on the long arm of chromosome 6V in the species *Dasypyrum villosum* (L.) Candargy was recently transferred to the wheat chromosome 6A through a 6AS·6V#3L Robertsonian translocation. This gene is temperature sensitive, becoming susceptible over 28 ^{o}C (Qi et al., 2011).

Potential sources of novel Ug99-resistance genes

In addition to the characterization and introgression of the Ug99-resistance genes described above, extensive efforts to search for new sources of Ug99 resistance have been made by the evaluation and characterization of germplasm collections from various wheat relative

species and their derived wheat lines. Xu et al. (2009) evaluated the seedling reactions to TTKSK, TTKST, and TTTSK among 62 wheat lines derived from crosses of durum or common wheat with the species *Th. junceum*, *Th. intermedium*, *Th. bessarabicum*, *Th. elongatum*, *Th. ponticum*, *Elymus rectisetus*, *Ae. caudata*, and *Ae. speltoides*. They identified 30 lines with resistance to the three races and suggested that 12 amphiploids and four DA lines may carry novel *Sr* genes. The results from a number of recent germplasm evaluation projects demonstrated that TTKSK-resistant genotypes were abundantly present in the core collections of *Ae. tauschii*, *T. monococcum*, *T. urartu*, *T. turgidum* subsp. *dicoccoides*, *T. turgidum* subsp. *dicoccum*, *T. timopheevii*, *Ae. speltoides*, *Ae. sharonensis*, triticale, and various *Thinopyrum* species (Steffenson et al., 2007; Jin et al., 2009; Rouse et al., 2011; Olivera et al., 2012; Zheng et al., 2014). Particularly, nearly 100% of the accessions in *Ae. speltoides* and *Thinopyrum species* and up to 69.6%, 77.7%, 78.7%, and 93.0% of the accessions in *Ae. sharonensis*, triticale, *T. monococcum* and *T. urartu*, respectively, were resistant to TTKSK. These TTKSK-resistant genotypes are a useful resource for the identification and introgression of novel *Sr* genes for future wheat improvement for stem rust resistance.

Utilization of Ug99-resistance genes in wheat breeding

An effective strategy to control the Ug99 stem rust epidemic is to use resistant cultivars carrying the Ug99-resistance genes. Since 2007, the major wheat breeding programs in their targeted regions in Eastern Africa, Southern Asia, and the Middle East have been actively utilizing the available Ug99-resistance genes in their wheat breeding. In this effort, CIMMYT has played a leading role in developingUg99-resistant cultivars. From 2009 to 2010, CIMMYT, in cooperation with local breeding programs, released 14 Ug99-resistant varieties, such as

‘Koshan 09’, ‘Muqawim 09’, ‘Baghlan 09’, and ‘Chonte #1’ in Afghanistan, ‘Danda’ and ‘Kakaba’ in Ethiopia, and ‘Robin’ and ‘Eagle 10’ in Kenya, etc. (Singh et al., 2011a). These varieties provided some initial protection to the wheat crops from stem rust epidemics in the countries. However, these varieties mainly carry *Sr2* alone or a combination of *Sr2* with either *SrTmp* or *Sr25*, and they do not have an adequate diversity of resistance genes. As a short-term strategy to control TTKSK, the wheat breeding programs in Iran started to evaluate promising germplasm in Kenya in 2007 and then released 11 bread wheat varieties with acceptable levels of resistance to stem rust (Najafian et al., 2013). These varieties are being used as parents for developing new Ug99-resistant cultivars using the gene-pyramiding strategy (Najafian et al., 2013).

Although the deployment of a single *Sr* gene is a feasible short term strategy to control Ug99, pyramiding several race-specific and APR genes is the best strategy to achieve sustainable and durable resistance in the long term. Recently, more Ug99-resistant varieties with diverse combinations of race-specific and APR genes were released in Kenya, Ethiopia, and other African counties (Njau et al., 2013). As many new and/or cytogenetically improved *Sr* genes and their linked markers become available (Bowden, 2013), a large number of Ug99-resistant cultivars with diverse combinations of Ug99-resistance genes will be relentlessly developed. Based on my review, I firmly believe that humankind will again win the war with Ug99 by using resistant cultivars carrying various combinations of Ug99-resistance genes.

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CHAPTER 3. EVALUATION AND MOLECULAR CHARACTERIZATION OF WHEAT LINES AND CULTIVARS FOR STEM RUST UG99 RESISTANCE DERIVED FROM RELATIVES OF WHEAT

Abstract

Stem rust race Ug99 (TTKSK) currently poses a serious threat to world wheat production. In order to identify useful sources of Ug99 resistance, I characterized stem rust resistance in 177 durum and common wheat cultivars and lines, most of which were derived from wheat relatives. In this research, all the cultivars and lines were first evaluated for reactions to the three most virulent races TTKSK, TRTTF, and TTTTF. The genotypes with resistance to TTKSK were further evaluated for resistance to six other races (MCCFC, QTHJC, RHTSC, RKQQC, TMLKC, and TPMKC) and analyzed using molecular markers that are diagnostic or tightly linked to the known *Sr* genes. The evaluation data showed that 71 of the cultivars and lines had resistance to TTKSK and were resistant to all or most of the other races. In addition to their resistance to TTKSK, the modern durum cultivars and derived lines from North Dakota exhibited a high level of resistance (near-immunity) to TRTTF. The marker analysis showed that *Sr2*, a gene associated with adult plant resistance from domesticated emmer wheat, is present in many wheat cultivars and lines from China and the U.S. The gene *Sr24*, derived from tall wheatgrass (*Thinopyrum ponticum*), was detected in the U.S. cultivar Kulm and its derivatives. The TTKSK-resistance gene in several Chinese winter wheat cultivars is likely *Sr42*, derived from 'Norin 10'. Based on the marker analysis and race specification, I postulated that a number of the wheat cultivars and lines that were tested may have novel genes conferring resistance to TTKSK and other races, such as Chinese Spring (CS)-*Th. elongatum* chromosome 3E and 7E disomic substitution (DS) lines, CS-*Ae. speltoides* 1S(1B) and 7S(7B) DS lines, several wheat-

Th. intermedium disomic addition lines, several Chinese winter wheat lines derived from asymmetrical somatic hybrids of common wheat with *Th. ponticum*, and durum line derived from *T. turgidum* subsp. *carthlicum*. All of the durum and wheat lines and cultivars with known and novel *Sr* genes conferring resistance to TTKSK that were identified in this study will be useful resources for improving wheat resistance to TTKSK and other emerging races of stem rust.

Introduction

Stem rust, caused by *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn., is one of the most serious fungal diseases in common wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBDD) and durum wheat (*T. turgidum* L. subsp. *durum*, 2n = 4x = 28, AABB). Historically, serious epidemics of this disease occurred in many wheat-growing regions throughout the world (Leonard and Szabo, 2005). Since the serious epidemics of stem rust that occurred in North America in the 1950s, extensive efforts have been made to manage the disease using various control measures, including eradication of the alternate host (*Berberis vulgaris* L.) and deployment of effective stem rust resistance (*Sr)* genes in wheat cultivars. Particularly, widespread utilization of stem rust-resistant cultivars has effectively controlled stem rust for more than 30 years (Singh et al., 2006). However, the detection of a stem rust race Ug99 in 1999 in Uganda (Pretorius et al., 2000) caused a worldwide concern of recurrence of stem rust epidemics (Sing et al., 2006, 2011). Jin et al. (2008b) designated Ug99 as TTKSK based on the North American stem rust nomenclature system (Roelfs and Martens, 1988).

TTKSK is considered a major threat to world wheat production due to its broad virulence, rapid movement from East Africa to other wheat-growing regions, and its ability to

overcome the deployed *Sr* genes. The extensive evaluation of wheat cultivars indicated that most of current cultivars or lines are susceptible to TTKSK (Singh et al., 2011). Only 5% to 10% of the breeding lines or cultivars from 22 countries in Asia and Africa were resistant to TTKSK (Singh et al., 2011); and 16% of hard red spring wheat cultivars, 48% of hard red winter cultivars, and 28% of soft winter wheat have resistance to TTKSK among 450 U.S. wheat cultivars or advanced breeding lines (Jin and Singh, 2006). It was predicted that the spread of TTKSK most likely would follow a route from East Africa through the Middle East and West Asia and eventually to South Asia (Singh et al., 2006). Detections of TTKSK in Yemen in 2006 (Jin et al., 2008a) and Iran in 2007 (Nazari et al., 2009) may prove this prediction. In addition to TTKSK, seven other races in the Ug99 lineage, including TTKST, TTTSK, TTKSF, TTKSP, PTKSK, PTKST, and TTKSF+ have been found (Hodson et al., 2012). In addition to the Ug99 lineage races, TRTTF identified in Yemen in 2006 is considered a major threat to durum wheat because it is virulent to *Sr13* and *Sr9e*, which are the two major *Sr* genes present in North American durum cultivars (Olivera et al., 2012). Race TRTTF is also virulent to three TTKSK-effective genes (*Sr36*, *SrTmp*, and Sr^{Amigo}), which had been frequently used in US wheat cultivars (Olivera et al., 2012).

One of the most important strategies to confine the Ug99 threat is to deploy stem rust resistance genes to wheat cultivars. Among the 57 *Sr* genes identified in wheat and its relatives (McIntosh et al., 2013), 28 are effective to Ug99 and its variants (Singh et al., 2011). However, some of those genes are not reliable under different environments or they are associated with deleterious linkage drag (Singh et al., 2011). Thus, the Ug99-effective *Sr* genes that are useful for breeding are still limited. Research efforts to evaluate and characterize new and untapped wheat germplasm lines for resistance to Ug99 and other new pathotypes of stem rust are

necessary for breeding programs, which are sustainable for developing cultivars with resistance to current and continuously-emerging races. An effective approach for identifying the *Sr* genes that are present in a wheat line is to combine the phenotyping of stem rust inoculation with the genotyping of molecular markers linked to the specific *Sr* genes. Molecular markers that are closely linked or diagnostic to several *Sr* genes are now available, such as *XcsSr2-SNP* (Bernardo et al., 2013) or *XcsSr2-CAPS* (Mago et al., 2011) for *Sr2*, *XcsIH81-BM* and *XcsIH81-AG* for *Sr22* (Periyannan et al., 2011), *Xbarc51* for *Sr35* (Yu et al., 2009), *XSr24#12* and *Xbarc71*for *Sr24* (Mago et al., 2005), *XBF145935* (Ayala-Navarrete et al., 2007) and *XGb* (Prin et al., 2001) for *Sr25* (Liu et al., 2010), *XSr26#43* (Mago et al., 2005) and *XBE518379* for *Sr26* (Liu et al., 2010), *Xrwgs30* and *Xcfa2040* for *Sr43* (Niu et al., 2014), *Xbarc55* for *Sr32* (Yu et al., 2009), and *Xrwg27* (Niu et al., 2011) and *Sr39#22r* (Mago et al., 2009) for *Sr39* (Niu et al., 2011). Some of these markers have been extensively used to genotype the wheat germplasm and cultivars with resistance to Ug99 (Bernado et al., 2013; Yu et al., 2010; Olson et al., 2010a).

The wheat germplasm improvement program at USDA-ARS, Fargo, ND, recently collected or developed a number of durum and common wheat cultivars and lines. Some of the lines were wheat-alien species derivatives (i.e. chromosome addition, substitution, and translocation lines) from interspecific hybridization between wheat and its relative species such as *Thinopyrum ponticum* (Podp.) Z-W. Liu & R.-C. Wang ($2n = 10x = 70$, EEEEEEEEEE), *Th. elongatum* (Host) D.R. Dewey ($2n = 2x = 14$, EE), *Th. intermedium* (Host) Barkworth & D. R. Dewey ($2n = 6x = 42$, EEEEStSt or JJEEStSt), and *Aegilops speltoides* Tausch ($2n = 2x = 14$, SS); some lines or cultivars may contain the known *Sr* genes derived from rye (*Sr31*), *Th. ponticum* (*Sr24*), and emmer wheat (*T. turgidum* subsp. *diccocum*) (*Sr2* and *Sr13*), and others may have novel *Sr* genes. The objectives of this study are to evaluate these wheat germplasm for

their reaction to Ug99 and other major virulent races and to investigate *Sr* genes in resistant germplasm using molecular markers linked to the known genes.

Materials and Methods

Plant materials

The plant materials used in this study include 177 hexaploid and tetraploid wheat breeding lines, cytogenetic stocks (wheat-alien species chromosome addition, substitution and translocation lines), and cultivars developed from the hybrids (or their wheat derivatives) between cultivated wheat (durum and common wheat) and their relative species by several research programs in Australia, Canada, China, and United States. The identities, pedigrees or descriptions, chromosome number, and sources of these materials are listed in Table 3.1. The relative species involved in the pedigree of hexaploid materials included *Th. ponticum* (Xia et al., 2003), *Th. intermedium* (Larkin et al., 1995, He et al., 1988), *Th. elongatum* (Dvořák, 1980), *Leymus racemosus* (Chen et al., 1995), *Ae. tauschii*, and *T. turgidum* subsp. *durum* (Table 3.1). Except for the two winter wheat cultivars ‘Shanrong 1’ and ‘Shanrong 3’ and 22 breeding lines that were developed from somatic cell fusion between winter wheat ‘Jinan 177’ and *Th. ponticum* accession AESR1 (Xia et al., 2003), all other lines or cultivars were developed through conventional hybridization and selections.

The tetraploid materials included three durum cultivars (Tioga, Carpio, and Joppa) and 22 durum lines that were recently developed for improving durum wheat resistance to Fusarium head blight. The three new durum cultivars Tioga, Carpio, and Joppa were released in 2010, 2012, and 2013, respectively, by the North Dakota Agricultural Experiment Station (Elias et al., 2013). The 22 new durum lines were developed in our durum wheat germplasm enhancement

program from the crosses and backcrosses of six previously-released ND durum cultivars, including Alkabo, Ben, Divide, Grenora, Lebsock, and Mountrail, to a hexaploid wheat line PI 277012 (Chu et al., 2011), *T. turgidum* subsp. *dicoccum*, and *T. turgidum* subsp. *carthlicum*.

In addition to the genotypes with their known donors of relative species, 80 winter and spring wheat cultivars and breeding lines that have not been characterized for Ug99 resistance were included, to determine if previously-deployed Ug99-effective *Sr* genes are present. The available parental lines for each set of lines were also included for stem rust testing and marker analysis. The wheat lines LMGP6 and Chinese Spring (CS) were used as susceptible controls in the stem rust testing. The 15 wheat lines, carrying the known Ug99-effective *Sr* genes (*Sr2, Sr13, Sr22, Sr24, Sr25, Sr26, Sr28, Sr32, Sr39, Sr40, Sr42/SrCad, Sr43,* and *Sr47*) and *Sr31* derived from relative species, were used as checks in marker analysis.

Stem rust evaluation

To detect the spectrum of resistance that may be available, nine races were used in this study. The virulence and avirulence phenotype of the nine races to the major *Sr* genes are summarized in Table 3.2. All the plant materials were first tested for reactions to two African races, TTKSK (Kenya) and TRTTF (Yemen), and the U.S. race TTTTF, all with broad virulence spectra at the seedling stage, at USDA-ARS Cereal Disease Laboratory, St Paul, MN. The inoculation and scoring were conducted using the procedures as described by Jin et al. (2007). The lines with resistance to race TTKSK and their parental lines were then tested with six additional U.S. races (MCCFC, QTHJC, RHTSC, RKQQC, TMLKC, and TPMKC) at USDA-ARS Northern Crop Science laboratory, Fargo, ND.

In the second evaluation trials, four to six seeds per line were planted in two super-cell cones (Stuewe and Sons, Inc., Corvallis, OR) filled with Sunshine SB100 Mix (Sun Gro Horticulture Distribution Inc., Bellevue, WA) and fertilized with Osmocote Plus 15-19-12 (Scotts Sierra Horticultural Product Company, Marysville, OH) in a greenhouse at 20 - 23°C, with a photoperiod of 16:8 (L:D) h. At 7-10 days (first leaf is fully developed) after planting, the seedlings were inoculated using the procedure described by Williams et al. (1992). The inoculated plants were transferred to a high humidity mist chamber and kept in the dark for 22 to 24 h. Seedlings were then moved to the greenhouse with a photoperiod of 16:8 (L:D) h. The infection types (ITs) of the primary leaf of each of the seedlings were scored at 12-14 days after inoculation using the scoring system developed by Stakman et al. (1962). In this rating system, five basic levels (0, ;, 1, 2, 3, and 4) and the additional signs (- or +, smaller or larger pustules in each basic level of 1, 2, and 3) were used to represent the ITs for the inoculated seedlings (Roelfs and Martens, 1988). Infection types of 0 to 2 were considered resistant, whereas ITs of 3 and 4 were considered susceptible. For combinations of ITs, order indicates predominant types. The resistance or susceptibility of the plants having a mixture of resistant and susceptible ITs on the same leaf was determined based on the predominated IT.

Marker analysis

Twenty seven markers diagnostic or linked to the known *Sr* genes were used in this study (Table 3.3). These markers were selected for analyzing tetraploid wheat and hexaploid wheat genotypes based on Simons et al. (2011) and Bernardo et al. (2013), respectively. The DNA extraction procedure was performed as described by Niu et al. (2011). The polymerase chain reaction (PCR) was performed by following the procedures described by Röder et al. (1998) with

minor modifications. A volume of 15 µl reaction mixture included 3 µl of 5X green GoTaq buffer with 7.5 mM $MgCl_2$ (Promega Corporation, Madison, WI), 0.48 µl of 2.5 mM each dNTP, 1.2 µl of 5000 nM each forward and reverse primer, 0.2 µl of 5 unit Taq polymerase, 2 µl of template DNA (50 ng/µl), and 8.12 µl of distil water. The PCR were conducted following one cycle of 94 ^{o}C for 4 min, 35 cycles of 94 ^{o}C for 30 sec, 55 ^{o}C annealing for 45 sec, and 72 ^{o}C extension for 45 sec, and one cycle of 72 ^{o}C for 10 min for final extension. The PCR condition for FSD and RSA markers for *Sr42/SrCad* were carried out according to the description by Laroche et al. (2000). Markers *XSr26#43* and *XBE518379* for *Sr26* were combined as a co-dominant marker (Liu et al., 2010). Multiplex PCR for markers csIH81-AG and csIH81-BM was performed using the procedures as described by Periyannan et al. (2011). The PCR products were run on 6% non-denatured poly-acrylamide gel containing 0.5× TBE buffer for 90-120 min (depends on the size of the marker) using DDH-400-33 sequencer (C.B.S. Scientific Company, Inc. Del Mar, CA) under constant 60W. The gel was stained with 1× GelRed (Biotium Corporate, Hayward, CA) for 5-10 min, and then scanned with a Typhoon 9410 imager (GE Healthcare, Inc. Waukesha, WI).

Results

A total of 177 lines and cultivars were inoculated using TTKSK, TRTTF, and TTTTF in the first trial. The infection types of all the genotypes to the three races are listed in Table A1. Evaluation data shows that 71, 112, and 92 lines or cultivars (including heterogeneous lines) were resistant (IT = 2+ or less) to TTKSK, TRTTF, and TTTTF, respectively, with 45 having resistance to all three races (Table A1). Based on evaluation data, I selected 71 lines or cultivars (including some parental lines) having resistance to TTKSK and 17 negative (CS and LMPG6)

and positive checks, that carry known *Sr* genes (*Sr2, Sr13, Sr22, Sr24, Sr25, Sr26, Sr28, Sr31, Sr32, Sr39, Sr40, Sr42/SrCad, Sr43*, and *Sr47*) for the evaluation of their resistance to six local races (MCCFC, QTHJC, RHTSC, RKQQC, TMLKC, and TPMKC) in the second trial and for analysis with molecular markers linked to the known *Sr* genes (Table 3.5 and Table A2).

Stem rust resistance of the wheat-alien species chromosome disomic addition and substitution lines

In the first trial tested with three races (TTKSK, TRTTF, TTTTF), I evaluated progenies of 26 wheat-*Th. intermedium* chromosome disomic or monosomic addition lines (Z lines and TAI lines) and 30 disomic substitution (DS) lines from *Th. elongatum*, *Th. intermedium*, *Leymus racemosus*, and *Ae. speltoides*. Of these 25 wheat-*Th. intermedium* DA lines, 12, 21, and 9 lines were resistant to TTKSK, TRTTF, and TTTTF, respectively, with five lines (Z4, Z5, Z6, TAI26, and TAI27) being resistant to all three races (Table A1). Ten of 12 lines resistant to TTKSK were tested in the second trial and they were resistant to most of the six races, with three lines (Z4, Z5, and Z6) having resistance to all of the nine races (Table 3.4). In addition to the three lines Z4, Z5, and Z6 with a broad spectrum of high level of resistance, TAI27 is also an interesting addition line for its high level of resistance to TTKSK (IT ;1+) and six other races except for the races TTTTF (IT 3+) and TPMKC (IT 34) (Table 3.4).

Among the set of 19 CS-*Th. elongatum* DS lines, only the three 7E chromosome DS lines 7E(7A), 7E(7B), and 7E(7D) exhibited moderate resistance to all the nine races (Table 3.4). In addition, three 3E chromosome DS lines 3E(3A), 3E(3B), and 3E(3D) consistently showed a low level of resistance (IT 2+3) to TTKSK, but they were susceptible to the other eight races. Of the two Thatcher-*Th. ponticum* chromosome DS lines, the $7el_1$(7D) substitution line K11463 had a

moderate level of resistance to TTKSK and the other six local races, but the $7el_2$(7D) substitution line K2620 segregated in resistance to TTKSK and the other six local races, indicating that the seed of K2620 used in this study were heterogeneous. The wheat-*Th. intermedium* 2Ai#2(2D) DS line Yi 4212, which was derived from Zhong 5 (Ai et al., 1997), showed moderate resistance to TTKSK, TRTTF, and four local races.

A set of six CS-*Ae. speltoides* S(B) DS lines (Friebe et al., 2011), except for the 5S(5B) DS, were available for this study. Evaluation data showed that only the 2S(2B) DS line TA6652 had resistance to all the nine races (Table 3.4). The 1S(1B) DS line TA6651 was highly resistant (IT ;1) to TTKSK but it was susceptible to the other eight races. The 7S(7B) DS line TA6657 showed a low level of resistance (IT 2+3) to TTKSK and a moderate level of resistance (IT 212+) to QTHJC and RKQQC, and it was susceptible to the other six races (Table 3.4).

Stem rust resistance in the newly-developed hard red spring wheat lines and cultivars

Seven (Liaochun 10, Jin 199, and Jinqiang 2 through Jingqiang 6) and one (Wildcat) hard red spring wheat cultivars developed in China and Canada, respectively, 27 lines derived from the cross between cultivars Kulm and Erik and the backcrosses of cultivars Alsen and Glenn to synthetic hexaploid wheat lines W7984 (Altar 84/*Ae. tauschii* WPI 219), TA4152-19 (Dverd 2/*Ae. tauschii* WPI 221), and TA4152-60 (Scoop 1/*Ae. tauschii* WPI 358), and their available parents were evaluated for resistance to TTKSK, TRTTF, and TTTTF in the first trial (Supplementary Table 3.1). Eleven lines and their parents with resistant to TTKSK were evaluated in the second trial (Table 3.4). The results showed that among parental lines or cultivars, only five were resistant to all the nine races including TA4152-60 and its durum parent Scoop 1, W7984 and its durum parent Altar 84, and Kulm (Table 3.4). However, all the hard red

spring wheat lines derived from backcrosses of Alsen and Glenn to TA4152-60 and W7984 were susceptible to TTKSK but they were all highly resistant to TTTTF and susceptible or moderately resistant to TRTTF. Because both Alsen and Glenn were highly resistant to TTTTF and Alsen was moderately resistant to TRTTF, the *Sr* gene(s) for the high level of TTTTF resistance in all these newly developed hard red spring wheat lines should be derived from Alsen and Glenn.

Cultivar Kulm was moderately resistant (ITs 2 or 21) to TTKSK, TRTTF, and QTHJC and highly resistant (ITs ;, ;1-, and 1-1) to the other six races (Table 3.4) while Erik was susceptible to TTKSK and TTTTF, highly resistant to MCCFC and TMLKC, and moderately resistant to the remaining five races (Table 3.4). Five of the eight lines, including KE16, KE21, KE23, KE33, and KE89, derived from the cross between cultivars Kulm and Erik were resistant to all nine races. Since Erik is susceptible to TTKSK, the *Sr* gene for TTKSK resistance in the five lines must be derived from Kulm. Moreover, three lines KE21, KE33, and KE89 exhibited higher levels of resistance to TTKSK than Kulm, indicating that the interactions of a new combination of *Sr* genes may increase resistance to TTKSK.

Stem rust resistance in the uncharacterized winter wheat cultivars and breeding lines

The winter wheat materials included 23 Chinese cultivars developed using conventional breeding methods and 22 lines (X lines) and two cultivars (Shanrong 1 and Shangrong 3) derived from somatic cell fusion between winter wheat ‘Jinan 177’ and *Th. ponticum* accession AESR1 (Xia et al., 2003). Among the 23 Chinese cultivars evaluated in the first trial, seven, 17, and 13 cultivars, including a few cultivars showing segregation, had resistance to TTKSK, TRTTF, TTTTF, respectively, with four having resistance to all the three races (Table A1 and Table 3.4). The eight cultivars (Jinan17, Jimai 20, Jinnong 6, Shimai 15, Zhoumai 16, Zhoumai 25, Zhoumai

26, and Zhoumai 27) with resistance to TTKSK were also resistant to most of the six local races tested in the second trial except that Jinnong 6 was susceptible to RHTSC and Jinan 17 was susceptible to MCCFC, TMLKC, and TPMKC.

Winter wheat cultivar Jinan 177 was susceptible to TTKSK but it was resistant to all the other eight races. *Th. ponticum* accession AESR1 was highly resistant to all nine races (Table 3.4). The result from the first trial showed that among the 22 lines and two cultivars (Shanrong 1 and Shangrong 3) derived from somatic cell fusion between Jinan 177 and AESR1, nine lines, including X025, X031, X031-1, X085, X106, X138, X144, X145, and X150 had a low level of resistance to TTKSK (IT 2+), but they were susceptible to TRTTF and TTTTF except that Xl45 was moderately resistance (IT 2-) to TRTTF. On the contrary, Shanrong 1, Shanrong 3, and another 13 lines were susceptible to TTKSK but they were moderately resistant (IT 2- or 2) to both TRTTF and TTTTF. Except for X031 and X106, seven of the lines with TTKSK resistance were evaluated in the second trial (Table 3.4). Only X145 was resistant to all the six local races and the other six lines were susceptible most of the races.

Stem rust resistance in the newly-developed durum cultivars and breeding lines

The three new durum cultivars (Tioga, Carpio, and Joppa), 22 durum lines, and all the parents of the lines were first evaluated for resistance to TTKSK, TRTTF, and TTTTF (Table 3.4). Except for Divide which was susceptible to TTKSK and TTTTF, the other eight cultivars were moderately resistant (IT 2- or 2) to TTKSK and near-immune (IT fleck) to TTTTF. Race TRTTF is virulent to the *Sr* genes present in most of the U.S. durum wheat germplasm (Olivera et al., 2012). Most interestingly, we observed that all of the nine durum cultivars were either moderately resistant (e.g. Tioga and Carpio had IT 2-) or immune/near-immune (Alkabo and

Grenora had IT 0, Maier, Lebsock, Ben, and Divide had IT 0;) to TRTTF (Table 3.4). Except for Divide, the other eight cultivars were evaluated in the second trial and they all showed near-immunity or a high level of resistance to the six local races.

Among the 22 durum lines, seven (12P772, 12P633, 12P636, 12P642, 12P660, 12P798, and 12P666) had a similar level of resistance (IT 2) to TTKSK as their durum parents and one (12P645) had a high level of resistance (IT ;1) to TTKSK. Because 12P645 is a double haploid line having a pedigree Lebsock/*T. turgidum* subsp. *carthlicum* PI 61102, it should have acquired the gene for the high level of resistance from PI 61102, which had near-immunity to TTKSK. Except for four lines (12P645, 12P758, 12P770, and 12P772) having moderate resistance to TRTTF, the other 18 lines had immunity or near-immunity to TRTTF. Similar to their durum parents, all eight lines with TTKSK resistance were also resistant to TTTTF and the six local races tested in the second trials.

Molecular marker analysis and postulation of *Sr* genes in the wheat cultivars and lines resistant to TTKSK

In order to identify or predict the *Sr* genes responsible for the TTKSK resistance, 27 molecular markers (Table 3.3) associated with 14 *Sr* genes were used to genotype the wheat cultivars and lines with TTKSK resistance (Table 3.4). The wheat cultivars and lines used for marker analysis were first classified into groups based on their pedigree and resistance spectrum. Each of the groups was then genotyped with a set of markers associated with the *Sr* genes which have the same or similar origins as the *Sr* genes in the group.

Thirty-four TTKSK-resistant lines having *Th. elongatum*, *Th. intermedium*, and *Th. ponticum* in their pedigree were analyzed using eight markers linked to four *Sr* genes derived

from *Th. ponticum*, including *Sr24* (*Xbarc71* and *XSr24#12*), *Sr25* (*XBF145935* and *XGb*), *Sr26* (*XSr26#43* and *XBE518379*), and *Sr43* (*Xcfa2040* and *Xwrgs30*) (Table A2). From the marker analysis, I found that only the hard red spring wheat cultivar Kulm and its five derived lines (KE16, KE21, KE23, KE33, and KE89) were positive for the two *Sr24*-linked markers (*Xbarc71* and *XSr24#12*) (Figure 3.1A), indicating that Kulm and the five lines carry *Sr24* for TTKSK resistance. In addition, *Xbarc71* generated the 101-bp band, which is associated with *Sr24*, from the three CS-*Th. elongatum* 3E chromosome DS lines 3E(3A), 3E(3B), and 3E(3D) but *XSr24#12* didn't amplify the expected band associated with *Sr24* (Figure 3.1A), suggesting that the *Th. elongatum* chromosome 3E may carry a different allele of *Sr24* or a new *Sr* gene. The two Thatcher-*Th. ponticum* $7el_1$(7D) DS lines K11463 and $7el_2$(7D) DS line K2620 are the donors of *Sr25* (Friebe et al., 1994) and *Sr43* (Knott et al. 1977; Kibirige-Sebunya and Knott 1983). K11463 and K2620 were the only wheat lines that were positive for the markers associated with *Sr25* and *Sr43*, respectively (Figure 3.1B, Table 3.5). Among all the wheat lines analyzed with the two *Sr26*-associated markers *XSr26#43* and *XBE518379*, only wheat-*Th. intermedium* DA line TAI22 was positive, indicating that TAI22 may carry *Sr26*. In addition, *Th. ponticum* accession AESR1 was positive for all the markers associated with *Sr24* (Figure 3.1A), *Sr25* (Figure 3.1B) and *Sr26* (Figure 3.1C), suggesting that AESR1 may have all the three genes. But none of the seven TTKSK-resistant introgression lines (X025, X031-1, X085, X138, X144, X145, and X150) derived from AESR1 were positive for any of the markers associated with the three *Sr* genes.

The three CS-*Ae. speltoides* DS lines having resistance to TTKSK, including 1S(1B) DS line TA6651, 2S(2B) DS line TA6652, and 7S(7B) DS line TA6657, were analyzed with five markers associate with the three *Sr* genes *Sr32*, *Sr39*, and *Sr47* derived from *Ae. speltoides*

chromosome 2S (Table A2, Figure 3.2). Among the three lines, only the 2B(2S) DS line TA6652 was positive for the marker *XSr39#22* associated with *Sr39,* TA6652 also had similar infection types to the nine races as RWG1, which carries *Sr39,* suggesting that TA6652 might carry *Sr39*. Because TA6652 was negative for another *Sr39*-linked marker *Xrwgs27* (Figure 3.2), it is also possible that TA6652 carries a *Sr* gene that is different from *Sr39*. None of the three lines were positive for the markers associated with *Sr32* or *Sr47,* suggesting that *Sr32* and *Sr47* are not present in these lines.

Because the *Sr2* gene derived from *T. turgidum* subsp. *dicoccum* has been deployed in many cultivars worldwide (McIntosh et al., 1995), all 71 durum and wheat lines or cultivars were genotyped with marker *Xgwm533,*which is tightly-linked to *Sr2* (Spielmeyer et al., 2003). The result showed that *Xgwm533* generated the 120-bp fragment from 25 lines or cultivars as the control 'Snowmass' for *Sr2* (Figure 3.3A). The common wheat lines and cultivars that were positive for *Xgwm533* included four Chinese winter wheat cultivars (Jinan 177, Shimai 15, Zhoumai 25, and Zhoumai 26), seven wheat-*Th. intermedium* DA lines (e.g. Z2, Z4, Z5, TAI12, TAI15, TAI26, and TAI27), two Thatcher-*Th. ponticum* DS lines (K11463 and K2620), and hard red spring wheat cultivars Kulm and Erik and their derivative lines (KE16, KE21, KE22, KE33, and KE89). In durum wheat and its tetraploid relatives, only *T. turgidum* subsp. *dicoccum* accession PI 41025 and its four derived durum lines (12P633, 12P636, 12P660, and 12P798) were positive for *Xgwm533,* indicating that PI 41025 and the four durum lines carry *Sr2.*

Except for the nine DS lines in the CS background, 41 common wheat lines or cultivars (including parental lines) were analyzed with the markers associated with four previously-deployed genes including *Sr22*, *Sr28*, *Sr31*, and *Sr42/SrCad*. Marker analysis revealed that none of the 41 wheat lines or cultivars were positive for the two markers (*Xwmc633* and

XcsIH81BM/AG) linked to *Sr22* or the marker linked to *Sr28* (*Xwmc332*). But two synthetic wheat lines (TA4152-60 and W7984) and their durum parents (Scoop 1 and Altar 84) were positive to the marker *XwPt-7004-PCR* associated with *Sr28* (Figure 3.3B). Five Chinese winter wheat cultivars, including Jinan 17, Shimai 15, Zhoumai 16, Zhoumai 26, and Zhoumai 27, were positive for the *Sr42/SrCad*-linked marker *Xbarc183* (Figure 3.3C), suggesting that these five cultivars may carry *Sr42/SrCad*. But they were all negative for another marker *XFSD-RSA* associated with *Sr42/SrCad*, indicating that there is a possibility that the TTKSK resistance in these cultivars may be controlled by *Sr* gene(s) other than *Sr42/SrCad*. Two markers *Xiag95* and *Xscm9* that are diagnostic for *Sr31* located on the 1RS/1BL translocation (Saal et al., 1999) detected *Sr31* in Z6, Jinan 177 and its derived introgression line X145, and the other five Chinese winter wheat cultivars including Shimai 15, Zhoumai 16, Zhoumai 25, Zhoumai 26, and Zhoumai 27 (Figure 3.4).

Discussion

The stem rust race TTKSK and other Ug99 lineage races are currently a major threat to wheat production in Eastern Africa and they also pose a potential threat to the wheat crops in the other continents (Singh et al., 2011). The current effort to confine the Ug99 threat globally is to deploy Ug99-effective *Sr* genes into the wheat cultivars adapted to the regions where wheat production is vulnerable to stem rust. Among *Sr* genes that are resistant to TTKSK in our study, at least five, *Sr2, Sr13, Sr24, Sr26,* and *Sr42/SrCad,* have been used in durum and bread wheat breeding. Although *Sr31*, which was widely deployed in wheat cultivars, is not resistant to TTKSK and its variants, it is also an important gene for its broad spectrum of resistance to many other races. Evaluation of durum and bread wheat cultivars currently used in production and

lines for resistance to TTKSK and characterization of the *Sr* genes present in the resistant lines and cultivars are essential for identification of novel and the deployed *Sr* genes as well as for selections of parents and appropriate schemes in breeding. In this study, I identified 71 durum and common wheat cultivars and lines carrying resistance to TTKSK and other major races conferred by novel or known *Sr* genes.

Based on the molecular marker analysis, I identified 10 common wheat cultivars that may carry 1 – 2 known TTKSK-effective *Sr* genes, including hard red spring wheat cultivars Kulm (*Sr2* and *Sr24*) and Erik (*Sr2*) and Chinese winter cultivars Jinan 17 (*Sr42/SrCad*), Jinan 177 (*Sr2*), Shimai 15 (*Sr2* and *Sr42/SrCad*), Zhoumai 16 (*Sr42/SrCad*), Zhoumai 25 (*Sr2*), Zhoumai 26 (*Sr2* and *Sr42/SrCad*), and Zhoumai 27 (*Sr42/SrCad*). Because most of these wheat cultivars are still being used in production, they provide direct protection of the wheat crops from the threat of Ug99 and other stem rust races. They will also be useful germplasm for developing new cultivars with resistance to TTKSK. For deployment of *Sr* genes into new cultivars, it is widely recognized that pyramiding several TTKSK-effective *Sr* genes together is the best strategy for breeding cultivars with both effective and durable resistance (Singh et al., 2006, 2011). The wheat cultivars and breeding lines carrying 1 – 2 known TTKSK-effective *Sr* genes identified in this study will be valuable parental lines in breeding for stacking the existing *Sr* gene(s) with other potent TTKSK-effective *Sr* genes that have recently become available such as *Sr32* (Mago et al., 2013), *Sr39* (Niu et al., 2011), *Sr47* (Klindworth et al., 2012), and *Sr51* (Liu et al., 2011).

This study revealed that several wheat lines or cultivars might carry novel *Sr* genes for resistance to TTKSK and other races. *Th. ponticum* accession AESR1 was near immune to all nine races. Chinese winter wheat cultivar Jinan 177 was highly susceptible to TTKSK but it was resistant to the other eight races. Marker analysis showed that AESR1 was positive for the

markers associated with *Sr24*, *Sr25*, and *Sr26* derived from *Th. ponticum* while Jinan 177 was positive for the markers associated with *Sr2* and *Sr31*. None of the seven TTKSK-resistant introgression lines from somatic cell hybridization between AESR1 and Jinan 177 were found to carry *Sr2*, *Sr24*, *Sr25*, and *Sr26* except for one line (X145) carrying *Sr31*. Because AESR1 was negative for *Sr43* derived from *Th. ponticum*, the TTKSK resistance of the seven introgression lines should be controlled by novel alien *Sr* gene(s) from *Th. ponticum* AESR1. Chinese winter wheat cultivars Jimai 20 and Jinnong 6 were moderately resistant to TTKSK and six local races, and they were negative for all the markers tested, suggesting that they may carry novel gene(s) for stem rust resistance.

Among six CS-*Ae. speltoides* DS lines, the 2S(2B) DS line TA6652 had resistance to all the nine races; the 1S(1B) DS line TA6651 was highly resistant (IT ;1) only to TTKSK; and the 7S(7B) DS line TA6657 showed a low level of resistance (IT 2+3) to TTKSK and a moderate level of resistance (IT 212+) to QTHJC and RKQQC. So far, the stem rust resistance genes derived from *Ae. speltoides* (i.e, *Sr32*, *Sr39*, and *Sr47*) are all located on chromosome 2S, therefore the 1S(1B) and 7S(7B) DS lines should carry novel *Sr* genes. In addition, the 2S(2B) DS line TA6652 was positive for one marker (*XSr39#22*) associated to *Sr39*, but was negative to another *Sr39*-linked marker (i.e. *Xrwgs27*). Thus, although the *Sr* gene in TA6652 was postulated as *Sr39*, there is possibility that TA6652 carries a novel *Sr* gene.

In addition to *Ae. speltoides*, *Thinopyrum* species is considered to be another excellent source for resistance to TTKSK (Xu et al., 2009; Turner et al., 2013; Zheng et al., 2014). To date, four *Sr* genes (*Sr24*, *Sr25*, *Sr26*, and *Sr43*) from *Th. ponticum* and one (*Sr44*) from *Th. intermedium* have been transferred into wheat. But, no *Sr* genes have been transferred from diploid species *Th. elongatum*. In this study, I found that three CS-*Th. elongatum* 7E(7A),

7E(7B), and 7E(7D) DS lines exhibited moderate resistance to all the nine races and they were all negative for the two markers associated with *Sr25* located on the wheat-*Th. ponticum* translocation chromosome T7DS·7DL-7Ae#1L (Kim et al., 1993; Friebe et al.,1994), indicating that the *Th. elongatum* chromosome 7E may carry a novel *Sr* gene(s). In addition, three CS-*Th. elongatum* 3E chromosome DS lines 3E(3A), 3E(3B), and 3E(3D) had a low level of resistance to TTKSK and they were positive for marker *Xbarc71*, associated with *Sr24* located on the wheat-*Th. ponticum* translocation chromosome T3DS-3DL-3Ae#1L (Friebe et al.,1996). But, they were all negative for another marker, *XSr24#12*, associated with *Sr24*. Moreover, *Sr24* controls a much higher level and broader spectrum of resistance to stem rust than the three CS-*Th. elongatum* 3E chromosome DS lines (Jin et al., 2007), suggesting that the *Th. elongatum* chromosome 3E carries a different allele of *Sr24* or a new *Sr* gene.

Xu et al. (2009) identified five wheat-*Th. intermedium* amphiploids (Zhong 4 through Zhong 8) with a high level of resistance to three Ug99 lineage races (TTKSK, TTKST, and TTTSK) and five North American races. In this study, I showed that three DA lines Z4, Z5, and Z6 derived from Zhong 5 (Larkin et al., 1995) and the DA line TAI 27 derived from Zhong 3 (He et al., 1988) exhibited a high level of resistance to TTKSK and most of the other eight races except for TAI27 which is susceptible to TTTTF and TPMKC. In addition, three DA lines (TAI15, TAI22, and TAI26) were moderately resistant to TTKSK and also to most of the other eight races. The marker data showed that only TAI22 was positive for the two markers, *XSr26#43* and *XBE518379*, associated with *Sr26*. The other five DA lines were negative for all the markers associated with the four genes (*Sr24*, *Sr25*, *Sr26*, and *Sr43*) derived from *Th. ponticum*, indicating that they most likely do not carry these genes or their homoeoalleles. Because a robust PCR marker that is diagnostic or closely-linked to *Sr44* from *Th. intermedium*

is not available for our study, I cannot rule out the possibility that some of the DA lines may carry *Sr44*. Thus, if the TTKSK resistance in these DA lines were derived from *Th. intermedium*, it should be controlled by either *Sr44* or novel *Sr* genes. Recently, *Sr44* was found to be located on the short arm of *Th. intermedium* chromosome 7J (Liu et al. 2013). Any of these DA lines carrying a pair of *Th. intermedium* chromosome other than 7J most likely carries novel *Sr* gene(s) from *Th. intermedium*. The DA line Z6 was previously identified to carry a pair of *Th. intermedium* group-2 chromosomes based on the characterization of 2Ai#2(2D) DS line Yi4212 (Tang et al., 2000). The TTKSK resistance in Yi4212 and Z6 is probably controlled by a novel *Sr* gene(s) on the *Th. intermedium* chromosome 2Ai#2. The identities of the *Th. intermedium* chromosomes in other DA lines are currently being investigated using molecular markers.

The wheat-alien species DA and DS lines with novel alien *Sr* genes for a high level TTKSK resistance should be excellent bridging materials for transferring the *Sr* genes from alien chromosomes into wheat genomes through chromosome engineering. During the alien gene introgression of stem rust resistance, stem rust testing is a primary method to select the new recombinants with reduced alien segments carrying the *Sr* genes (Niu et al., 2011). If the wheat genomes in the original DA and DS lines carry other *Sr* genes, there is a possibility that the *Sr* genes other than the targeted genes from the alien species may be picked up based on the stem rust test. Therefore, knowledge of the presence of the other *Sr* genes will help mitigate the risk of selecting the wrong *Sr* gene. Based on the marker analysis, I found that four of the wheat-*Th. intermedium* DA lines including Z4, Z5, TAI26, and TAI27 probably carry *Sr2*, and Z6 carries *Sr31* in their wheat background. If these DA lines carry novel *Sr* genes for TTKSK resistance on the *Th. intermedium* chromosomes, the effect of the *Sr* genes in the wheat background should be considered when the targeted *Sr* genes are being transferred into wheat. The *Sr* genes in the

wheat background could be eliminated from progenies of the initial crosses based on molecular marker analysis or stem rust test using an appropriate race that is virulent to the *Sr* genes in the wheat background.

In durum wheat, except for Divide which is susceptible to TTKSK, all the other eight modern cultivars (i.e. Alkabo, Ben, Carpio, Grenora, Joppa, Lebsock, Tioga, and Maier) adapted to northern Great Plains in the U. S. have resistance to TTKSK and the other eight races tested in this study. It was postulated that *Sr13* and *Sr9e* are among the major genes for stem rust resistance in the North American durum cultivars and that *Sr13* is the only known gene responsible for resistance to TTKSK (Olivera et al., 2012). However, Olivera et al. (2012) recently found that when the Ug99-resistant durum lines from the U.S. were evaluated in Debre Zeit, Ethiopia, many were susceptible to stem rust. In this region, three stem rust races, including JRCQC, TRTTF, and TTKSK, were identified and both JRCQC and TRTTF have virulence to *Sr13* and *Sr9e* (Olivera et al., 2012). An interesting result discovered in this study is that most of the durum cultivars developed in North Dakota and their derived lines were immune or near immune to TRTTF. Recently, S.S. Xu and colleagues mapped the *Sr* genes in Lebsock using a double haploid population derived from the cross between Lebsock and *T. turgidum* subsp. *carthlicum* accession PI 94749 (S.S. Xu, personal communication). They identified three major quantitative trait loci (QTL) associated with chromosome regions harboring *Sr7*, *Sr8a*, and *Sr13* on chromosome arms 4AL, 6AS, and 6AL, respectively. Because *Sr8a* is resistant to TRTTF in hexaploid wheat (Olivera et al., 2012), the durum cultivars from North Dakota most likely carry *Sr8a*.

In addition to the existing *Sr* genes present in the North Dakota durum cultivars, two more *Sr* genes have likely been introduced into some of the new durum lines. Durum cultivar

Lebsock and *T. turgidum* subsp. *carthlicum* accession PI 61102 had moderate resistance (IT 2-) and near-immunity (IT 0;) to TTKSK, respectively. Because a TTKSK-resistant *Sr* gene has not been identified in *T. turgidum* subsp. *carthlicum* yet, PI 61102 may carry a novel *Sr* gene. The double haploid line 12P645 derived from the cross Lebsock/PI 61102 had a much higher level of resistance to TTKSK than Lebsock, indicating that the line may have acquired a *Sr* gene from PI 61102. The marker analysis showed that all North Dakota durum cultivars were negative to the marker *Xgwm533* linked to *Sr2*, but *T. turgidum* subsp. *dicoccum* accession PI 41025 and its derived five durum lines were positive to the marker, indicating that the five durum lines may carry *Sr2*. These new durum lines will be useful in developing new durum cultivars with an increased diversity of TTKSK-resistant *Sr* genes.

Through this study, I identified a number of new and previously-uncharacterized durum and common wheat cultivars and lines with resistance to TTKSK and other major races of stem rust. I also postulated the *Sr* genes responsible for the resistance in most of the cultivars and lines based on the marker analysis and avirulence/virulence profiles. Because marker haplotype analysis can only provide preliminary information on the *Sr* genes and gene postulations in several cases were made only based on one marker, the accurate assessments of the *Sr* gene are needed based on genetic analysis of segregation populations. Nevertheless, the data from stem rust evaluation and marker analysis provides useful guides for parental selection in wheat breeding of resistance to stem rust and for further genetic study and molecular mapping of novel *Sr* genes.

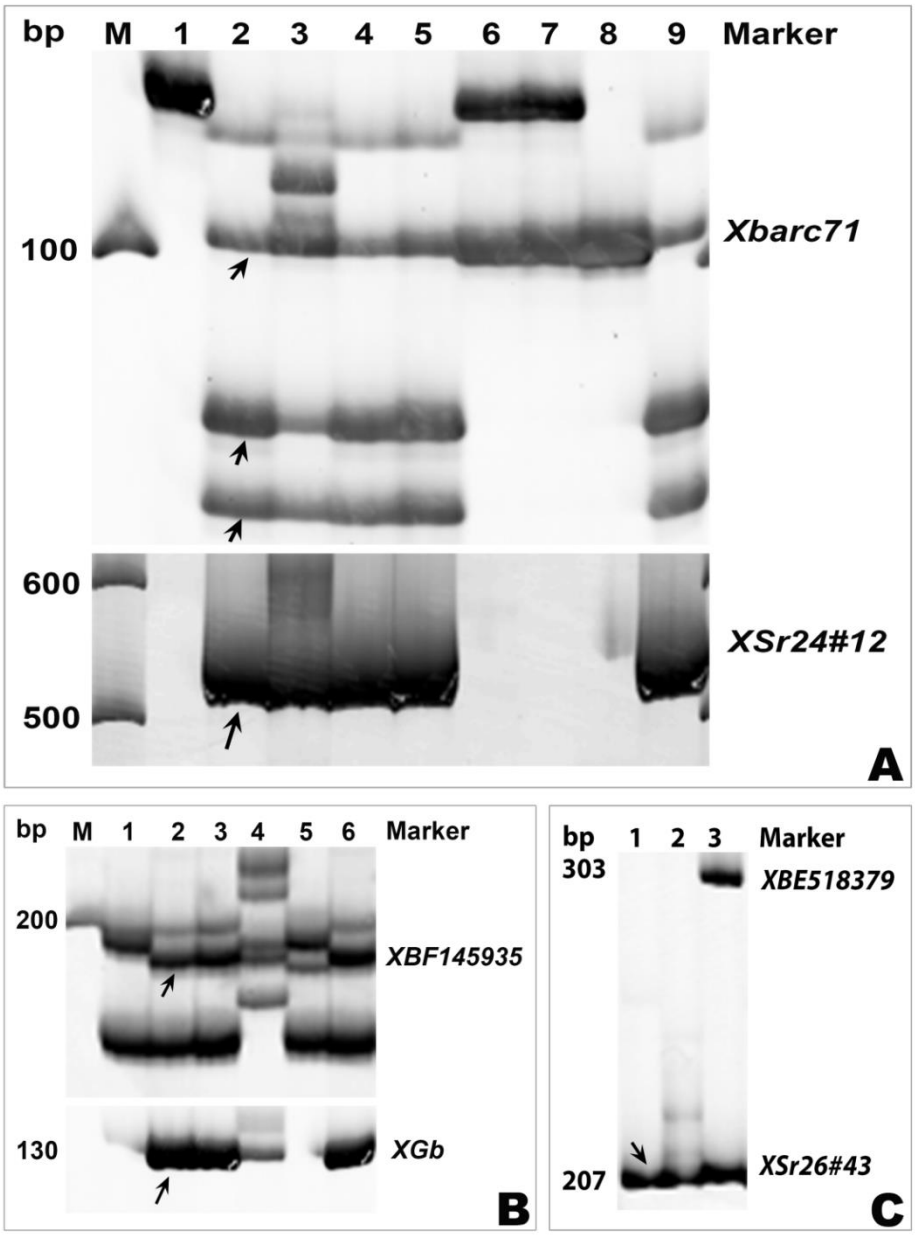

Figure 3.1. Gel images of molecular markers associated with the stem rust resistance genes *Sr24*, *Sr25*, and *Sr26* derived from *Th. ponticum*. **A)** Illustrative wheat lines and checks (lanes 1 - 9) analyzed with *Sr24*-linked markers *Xbarc71* and *XSr24#12* : (1) Chinese Spring (CS), (2) PI 520490 (*Sr24* check), (3) AESR1, (4) Kulm, (5) KE16, (6) CS-*Th. elongatum* 3E(3A) disomic substitution (DS) line, (7) CS-*Th. elongatum* 3E(3B) DS line, (8) CS-*Th. elongatum* 3E(3D) DS line, and (9) PI 520490. **B)** Illustrative wheat lines and checks (Lane 1 to lane 6) analyzed with *Sr25*-linked markers *XBF145935* and *XGb*: (1) Chinese Spring, (2) Wheatear (*Sr25* check), (3) K11463, (4) AESR1, (5) X025, and (6) Wheatear (*Sr25* check). **C)** Wheat lines and checks analyzed with *Sr26*-linked markers *XBE518379* (amplified 303 bp band) and *Sr26#43* (amplified

207 bp band): (1) WA-1 (*Sr26* check), (2) AESR1, and (3) TAI22. M = molecular weight, bp = base pair.

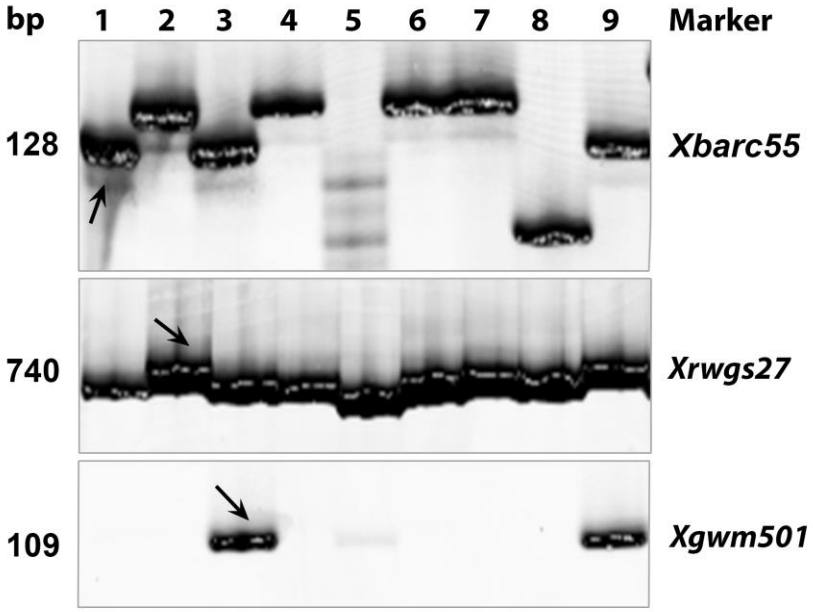

Figure 3.2. Gel images of molecular markers *Xbarc55, Xrwgs27*, and *Xgwm501* associated with the stem rust resistance genes *Sr32*, *Sr39*, and *Sr47*, respectively, derived from *Ae. speltoides*. Lanes 1 to 8 are the representative lines analyzed: (1) U5926-2-8 (*Sr32* check), (2) RWG1 (*Sr39* check), (3) RWG35 (*Sr47* check), (4) CS-*Ae. speltoides* 1S(1B) disomic substitution (DS) line, (5) CS-*Ae. speltoides* 2S(2B) DS line, (6)CS-*Ae. speltoides* 7S (7B) DS line, (7) Chinese Spring, and (8) LMPG6. Lane 9 for marker *Xbarc55* is U5926-2-8, for marker *Xrwgs27* is RWG1, for marker *Xgwm501* is RWG35. bp = base pair.

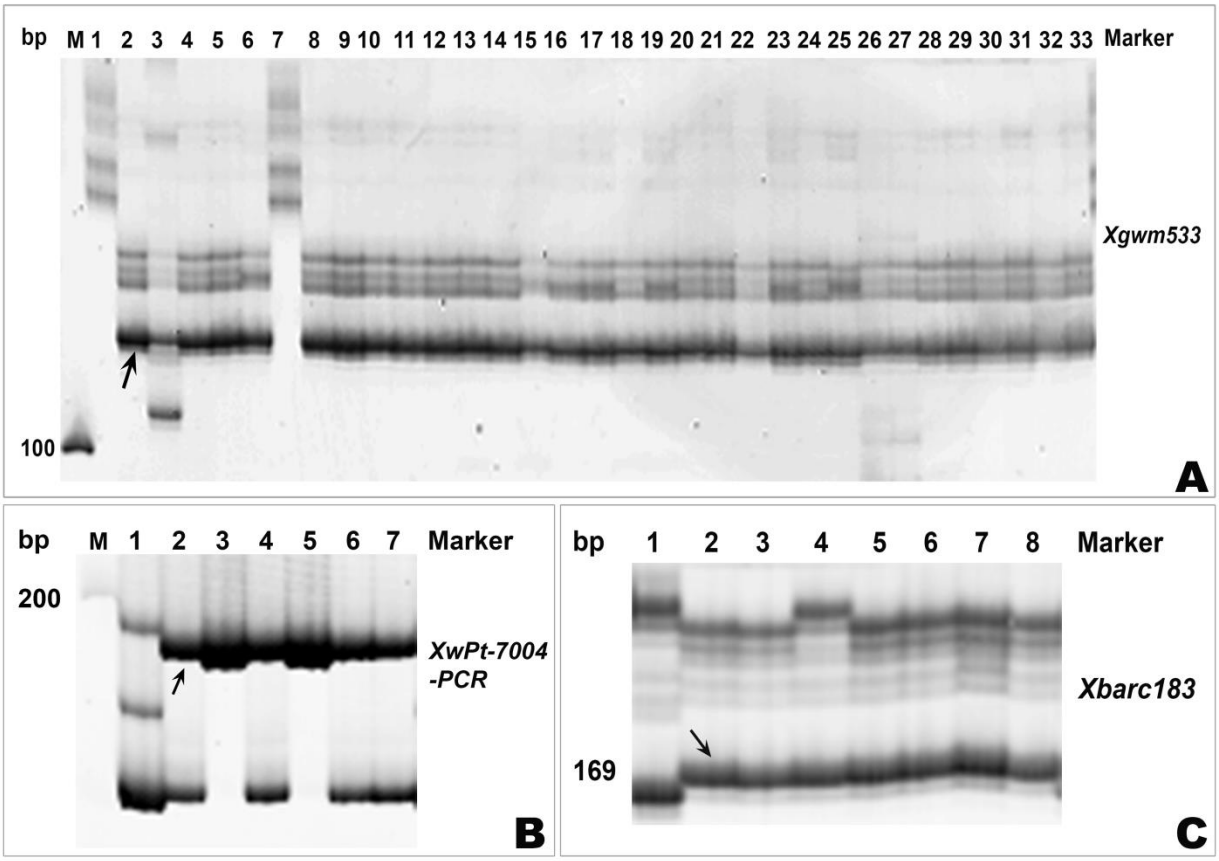

Figure 3.3. Gel images of molecular markers *Xgwm533, XwPt-7004-PCR,* and *Xbarc183* associated with the stem rust resistance genes *Sr2*, *Sr28*, and *Sr42/SrCad*, respectively. **A)** Representative wheat lines and checks analyzed with marker *Xgwm533* linked to *Sr2*: (1) Chinese Spring (CS), (2) Snowmass (*Sr2* check), (3) W2691Sr28kt (*Sr28* check), (4) Sr36-5 (*Sr36* check), (5) U5941-1-6 (*Sr40* check), (6) HY438 (*Sr42/Cad* check), (7) CS, (8) Snowmass, (9) Z2, (10) Z4, (11) Z5, (12) TAI12, (13) TAI15, (14) TAI26, (15) TAI27, (16) K11463 ($7el_1$), (17) K2620 ($7el_2$), (18) Kulm, (19) Erik, (20) KE16, (21) KE21, (22) KE22, (23) KE33, (24) KE89, (25) Shimai 15, (26) Zhoumai 25, (27) Zhoumai 26, (28) PI 41025, (29) 12P633, (30) 12P636, (31) 12P660, (32) 12P798, and (33) Snowmass. **B)** Representative wheat lines and checks analyzed with marker *XwPt-7004-PCR* linked to *Sr28*: (1) CS, (2) W2691Sr28kt (*Sr28* check), (3) TA4154-27, (4) TA4152-60, (5) TA4154-4, (6) W7984, and (7) W2691Sr28kt. **C)** Representative wheat lines and checks analyzed with marker *Xbarc183* linked to *Sr42/SrCad*: (1) LMPG6, (2) HY438 (*Sr42/SrCad check*), (3) Zhoumai 27, (4) Jinan 17, (5) Shimai 15, (6) Zhoumai 16, (7) Zhoumai 26, and (8) HY438 (*Sr42/SrCad* check). M = molecular weight, bp = base pair.

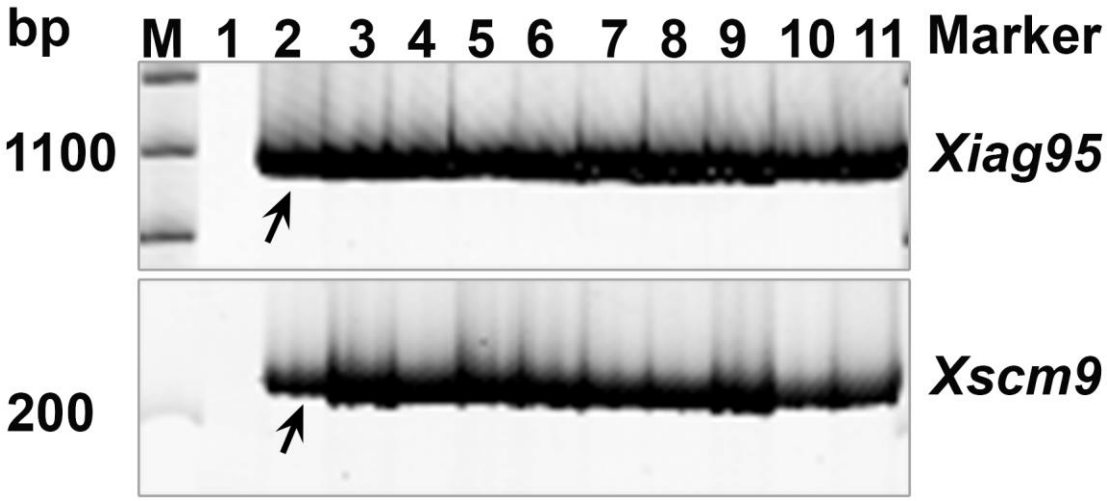

Figure 3.4. Gel image of representative wheat lines analyzed with markers *Xiag95* and *Xscm9* linked to *Sr31*. Lane 1 to lane 11 are wheat lines and cultivars: (1) Chinese Spring, (2) *Sr31*/LMPG6 (*Sr31* check), (3) Jinan177, (4) X145, (5) Z6, (6) Shimai 15, (7) Zhoumai 16, (8) Zhoumai 25, (9) Zhoumai 26, (10) Zhoumai 27, and (11) *Sr31*/LMPG6 (*Sr31* check). M = molecular weight, bp = base pair.

Table 3.1. Wheat cultivars/breeding lines and their parents characterized for their resistance to stem rust.

Category	Line name†	Pedigree or description†	Growth habit	2n‡	No.§	Sources or references
Wheat-alien species chromosome disomic addition and substitution lines						
Th. intermedium derived disomic addition (DA) lines and disomic substitution (DS) lines	Z1	Zhong 5/4/Zhong 7606 (F_3)	Spring	42', 43'+2t'	2	Larkin et al. (1995)
	Z2-Z5	Zhong 5/2-4/Wan 7107 (F_3)	Spring	42'-44'	8	Larkin et al. (1995)
	Z6	Zhong 5/4/Zhong 8423 (F_3)	Spring	44'	1	Larkin et al. (1995)
	Yi4212 (2Ai#2(2D))	77-5433/Zhong 5	Spring	42	1	Ai et al. (1997)
	TAI11, TAI12, TAI14, and TAI 15	Zhong 2 Progeny	Spring	42'-44'	6	He et al. (1988)
	TAI 22-24, TAI26-27	Zhong 3, 4, 5 Progeny	Spring	42'-44'	8	He et al. (1988)
Th. elongatum derived DS lines	XWC11-58 ~XWC11-76	Chinese Spring (CS)-*Th. elongatum* 1E(1A) to 7E(7D) DS lines (4E(4B) and 5E(5A) not available)	Spring	42	19	Dvořák (1980)
	K11463 and K2620	Thatcher-*Th. elongatum* $7el_1$(7D) and $7el_2$(7D) DS lines	Spring	42	2	Knott et al. (1977)
Leymus racemosus derived DA lines	XC04A-1030 and XC04A-1033	CS-*Leymus racemosus* DA lines	Spring	44	2	Chen et al. (1995)
Ae. speltoides derived DS lines	TA6651~TA6654 and TA6656~TA6657	CS-*Ae. speltoides* 1S(1B) to 7S(7B) DS lines (no 5S(5B) available)	Spring	42	6	Friebe et al. (2011)
Newly-developed hard red spring wheat lines and cultivars						
Canada cultivar	Wildcat	NB113/Glenlea	Spring	42	1	Clarke et al. (1994)
Chinese hard red spring wheat cultivars (HRSW)	Liaochun 10	Hybrid x Liao 70181-2	Spring	42	1	He at al. (2001)
	Jinqiang 2	Wildcat/Liaochun 10	Spring	42	1	
	Jinqiang 3-6	Liaochun 10/Wildcat	Spring	42	4	
	Jin 199			42	1	
HRSW parents and their pedigrees	Kulm	HRSW cultivar	Spring	42	1	Friesen et al. (2003)
	Erik	HRSW cultivar	Spring	42	1	
	KE6, KE14, KE16, KE17, KE21, KE22, KE33, and KE89	Kulm/Erik RIL 6	Spring	42	8	
Hard spring wheat and synthetic wheat and their pedigrees	TA4152-19	Dverd 2/*Ae.tauschii* (221)	Spring	42	1	Mujeeb et al. (2000)
	Alsen	ND674//ND2710 (PI 633976)/ND688	Spring	42	1	Frohberg et al. (2006)

Table 3.1. Wheat cultivars/breeding lines and their parents characterized for their resistance to stem rust (continued).

Category	Line name†	Pedigree or description†	Growth habit	2n‡	No.§	Sources or references
	12P738	TA4152-19/3*Alsen	Spring	42	1	
	TA4154-27	Scoop 1	Spring	28	1	Mujeeb et al. (2000)
Hard spring wheat and synthetic wheat and their pedigrees	TA2516	*Ae. tauschii* (358)	Spring	14	1	Mujeeb et al. (2000)
	TA4152-60	Scoop 1/*Ae.tauschii* (358) TA2516	Spring	42	1	Mujeeb et al. (2000)
	12P594, 12P600, and 12P726	TA4152-60/3*Alsen	Spring	42	3	
	Alsen-19 and Alsen-60	TA4152-60/6*Alsen	Spring	42	2	
	W7984	Altar 84/*Ae. tauschii* WPI 219	Spring	42	1	Mujeeb et al. (2000)
	TA4154-4	Altar 84	Spring	28	1	Mujeeb et al. (2000)
	Glenn	ND 2831/Steele-ND (PI 634981)	Spring	42	1	Mergoum et al. (2006)
	12P618, 12P729, and 12P732	Glenn*2/W7984/3/Glenn	Spring	42	3	
Uncharacterized winter wheat cultivars and breeding lines						
Th. ponticum derived lines and their parents	AESR1	*Th. ponticium*	Winter	70	1	Xia et al. (2003)
	Jinan177	*T. aestivium*	Winter	42	1	
	X004, X012, X023, X025, X027, X031, X031-1, X042, X068, X085, X090,X091, X106, X116, X138, X144, X145, X150, X159, X182, X188, X194, Shanrong 1, and Shanrong 3	Jinan177/AESR1	Winter	42	24	
Chinese cultivars	Jinnong 6, Jingdong 8, Nongda 211, Zhongmai 175, Shimai 15, Zhouheimai 1, Zhoumai series (16~27), Jinan 17, Jimai 20, Jimai 22, Zheng 9023, Yangmai 16	Chinese winter wheat	Winter	42	23	
Newly-developed durum cultivars and breeding lines and parents						
	Carpio	ND durum line	Spring	28	1	
	Joppa	ND durum line	Spring	28	1	
	Tioga	Plaza/Maier	Spring	28	1	Elias and Manthey (2013)
	Alkabo	D901247/D89263	Spring	28	1	Elias and Manthey (2007c)

Table 3.1. Wheat cultivars/breeding lines and their parents characterized for their resistance to stem rust (continued).

Category	Line name†	Pedigree or description†	Growth habit	2n‡	No.§	Sources or references
	Grenora	D901260/D901419	Spring	28	1	Elias and Manthey (2007b)
	Maier	D8193/D8335	Spring	28	1	Elias and Miller (2000)
	Lebsock	Munich/D8469	Spring	28	1	Elias et al. (2001)
	Ben	D8024/Monroe	Spring	28	1	Elias and Miller (1998)
	Divide	Ben/D901282//Belzer	Spring	28	1	Elias and Manthey (2007a)
	PI 61102, PI 94748	*T. turgidum* subsp. *carthlicum*	Spring	28	2	
	PI 41025, PI 254188, PI 254193, PI 272527	*T. turgidum* subsp. *dicoccum*	Spring	28	4	
	PI 277012	Spring wheat	Spring	42	1	Chu et al. (2011)
	12P746, 12P749, 12P754, 12P 758, 12P760, 12P762, 12P766	Lebsock/PI 277012//Lebsock	Spring	28	7	
	12P768, 12P770	Mountrail/PI 277012//Divide	Spring	28	2	
	12P772	Ben/PI 277012//Ben	Spring	28	1	
	12P776, 12P786, 12P796	Divide/PI 272527/Divide	Spring	28	3	
	12P802	Divide/PI 254193/Divide	Spring	28	1	
	12P804	Lebsock/PI 254188/Alkabo	Spring	28	1	
	12P633, 12P636	Ben/PI 41025//Maier	Spring	28	2	
	12P642	Lebstock/PI 94748//Lebstock	Spring	28	1	
	12P645	Lebsock/PI61102	Spring	28	1	
	12P660	Lebsock/08F130¶//Alkabo	Spring	28	1	
	12P666, 12P798	Grenora/08F286¶//Grenora	Spring	28	2	

† Line name and pedigree were from the literatures as indicated in the references or were provided by seed providers.
‡ 2n refer to chromosome numbers, which were based on the literatures as indicated in the references or were provided by seed providers.
§ No. indicates the number of lines or cultivars.
¶ 08F130 and 08F286 were the F_4 plants with a pedigree Ben/PI41025//Maier.

Table 3.2. Avirulence/virulence on the North America differentials for nine stem rust races used in this study.

Race	Isolate	Origin	Avirulence	Virulence
TTKSK	04KEN156/04	Kenya	*24 36 Tmp*	*5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 30 31 38 McN*
TRTTF	06YEM34-1	Yemen	*8a 24 31*	*5 6 7b 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McN Tmp*
TTTTF	01MN84A-1-2	USA	*24 31*	*5 6 7b 8a 9a 9b 9d 9e 9g 10 11 17 21 30 36 38 McN Tmp*
MCCFC	A-5	USA	*6 8a 9a 9b 9d 9e 11 21 24 31 36 38*	*5 7b 9g 10 17 30 Tmp McN*
QTHJC	64E(1) sp1	USA	*7b 9a 9e 24 30 31 36 38 Tmp*	*5 6 8a 9b 9d 9g 10 11 17 21 McN*
RHTSC	72.22	USA	*5 7b 8a 11 21 24 31 38 Tmp*	*6 9a 9b 9d 9e 9g 10 17 30 36 Mcn*
RKQQC		USA	*9e 10 11 17 24 30 31 38 Tmp*	*5 6 7b 8a 9a 9b 9d 9g 21 36 McN*
TMLKC	72-41 (sp2)	USA	*6 8a 9a 9b 17 24 30 31 38*	*5 7b 9d 9e 9g 10 11 21 36 McN Tmp*
TPMKC	TNMK	USA	*6 9a 9b 24 30 31 38*	*5 7b 8a 9d 9e 9g 10 11 17 21 36 Tmp McN*

Source: Jin et al. (2007).

Table 3.3. A list of target stem rust genes, name and type of markers, and primers sequence.

Gene			Marker		Primer sequence	References
Gene	Sources	Loc. †	Name	Type		
Sr2	*T. turgidum*	3BS	*Xgwm533*	SSR	AAGGCGAATCAAACGGAATA GTTGCTTTAGGGGAAAAGCC	Spielmeyer et al. (2003)
Sr13	*T. turgidum*	6AL	*Xbarc104b*	SSR	GCGCTTCCAAGGCTTAGAGGCT GGACCAGGCATGTCTACCCT	Simons et al. (2011)
Sr13	*T. turgidum*	6AL	*XCD926040*	EST‡	GTTGGCTTGGCTACTGCTTT AGCATTCAGCTCTGTGAGCA	Simons et al. (2011)
Sr13	*T. turgidum*	6AL	*XCK207347*	EST	TTACGGGCCACAAACAATCT AGCTCTCATCCATCCAGGAA	Simons et al. (2011)
Sr13	*T. turgidum*	6AL	*XBE403950*	EST	GGAACATGTTGACGCTGTTG AACACTGTTCCCGAAGTTGG	Simons et al. (2011)
Sr22	*T. monococcum*	7AL	*Xwmc633*	SSR	ACACCAGCGGGGATATTTGTTAC GTGCACAAGACATGAGGTGGATT	Olson et al. (2010b)
Sr22	*T. monococcum*	7AL	*XcsIH81-BM*	EST	TTCCATAAGTTCCTACAGTAC TAGACAAACAAGATTTAGCAC	Periyannan et al. (2011)
Sr22	*T. monococcum*	7AL	*XcsIH81-AG*	EST	CTACCTCTGTCAATTTGAAC GAAAAATGACTGTGATCGC	Periyannan et al. (2011)
Sr24	*Th. ponticum*	3DL	*Xbarc71*	SSR	GCGCTTGTTCCTCACCTGCTCATA GCGTATATTCTCTCGTCTTCTTGTTGGTT	Mago et al. (2005)
Sr24	*Th. ponticum*	3DL	*XSr24#12*	EST	CACCCGTGACATGCTCGTA AACAGGAAATGAGCAACGATGT	Mago et al. (2005)
Sr25	*Th. ponticum*	7DL	*XBF145935*	EST	CTTCACCTCCAAGGAGTTCCAC GCGTACCTGATCACCACCTTGAAGG	Ayala et al. (2007); Liu et al. (2010)
Sr25	*Th. ponticum*	7DL	*XGb*	EST	CATCCTTGGGGACCTC CCAGCTCGCATACATCCA	Prin et al. (2001); Liu et al. (2010)
Sr26	*Th. ponticum*	6AL	*XSr26#43*	EST	AATCGTCCACATTGGCTTCT CGCAACAAAATCATGCACTA	Mago et al. (2005)
Sr26	*Th. ponticum*	6AL	*XBE518379*	EST	AGCCGCGAAATCTACTTTGA TTAAACGGACAGAGCACACG	Liu et al. (2010)
Sr28	*T. aestivum*	2BL	*XwPt-7004-PCR*	DArT‡	CTCCCACCAAAACAGCCTAC AGATGCGAATGGGCAGTTAG	Rouse et al. (2012)
Sr28	*T. aestivum*	2BL	*Xwmc332*	SSR	CATTTACAAAGCGCATGAAGCC GAAAACTTTGGGAACAAGAGCA	Rouse et al. (2012)
Sr31	*Secale cereale*	1R	*Xiag95*	EST	CTCTGTGGATAGTTACTTGATCGA CCTAGAACATGCATGGCTGTTACA	Saal et al. (1999)
Sr31	*Secale cereale*	1R	*Xscm9*	SSR	TGACAACCCCCTTTCCCTCGT TCATCGACGCTAAGGAGGACCC	Saal et al. (1999)

Table 3.3. A list of target stem rust genes, name and type of markers, and primers sequence (continued).

Gene			Marker		Primer sequence	References
Gene	Sources	Loc. †	Name	Type		
Sr32	*Ae. speltoides*	2BS	*Xbarc55*	SSR	GCGGTCAACACACTCCACTCCTCTCTC	Yu et al. (2009)
Sr32	*Ae. speltoides*	2BS	*Xbarc55*	SSR	CGCTGCTCCCATTGCTCGCCGTTA	Yu et al. (2009)
Sr39	*Ae. speltoides*	2BS	*XSr39#22r*	EST	AGAGAAGATAAGCAGTAAACATG TGCTGTCATGAGAGGAACTCTG	Mago et al. (2009)
Sr39	*Ae. speltoides*	2BS	*Xrwgs27*	EST	GCC TTGGTGGATTTTGTGAT GCGCTTTCAGTACAGGGTTC	Niu et al. (2011)
Sr40	*T. araraticum*	2BS	*XSr39#22r*	SSR	AGAGAAGATAAGCAGTAAACATG TGCTGTCATGAGAGGAACTCTG	Bernardo et al. (2013)
SrCad	*T. aestivum*	6DS	*XFSD-RSA*	SCAR	FSD-GTTTTATCTTTTTATTTC RSA-CTCCTCCCCCCA	Laroche et al. (2000); Ghazvini et al. (2012)
SrCad	*T. aestivum*	6DS	*Xbarc183*	SSR	CCCGGGACCACCAGTAAGT GGATGGGGAATTGGAGATACAGAG	Ghazvini et al. (2012)
Sr43	*Th. ponticum*	7DL	*Xrwgs30*	EST	CTCTTGGTGCCACACTCTGA TCAGTTCCCTCCCATTCATC	Niu et al. (2013)
Sr43	*Th. ponticum*	7DL	*Xcfa2040*	SSR	TCAAATGATTTCAGGTAACCACTA TTCCTGATCCCACCAAACAT	Niu et al. (2013)
Sr47	*Ae. speltoides*	2BL	*Xgwm501*	SSR	GGCTATCTCTGGCGCTAAAA TCCACAAACAAGTAGCGCC	Faris et al. (2008)
Sr47	*Ae. speltoides*	2BL	*Xrwgs33*	EST	AGTGGCTGCAGTGGAATTG ACCGAGAACAAGGAGAAGCA	Xu et al., unpublished

† loc. indicates gene location.
‡ EST and DArT mean EST derived and DArT derived marker.

Table 3.4. Infection types of TTKSK-resistant durum and common wheat lines caused by nine races of stem rust pathogen.

Line	Pedigree or Description	Chr. No. †	Infection types to nine races‡								
			TTKSK	TRTTF	TTTTF	MCCFC	QTHJC	RHTSC	RKQQC	TMLKC	TPMKC
Chinese Spring	*T. aestivum*		-	-	-	32	32	341	32	32	34
LMPG6	*T. aestivum*		-	-	-	32	32	34	34	32	32
Snowmass (*Sr2*)	KS96HW94//Trego/CO960293		-	-	-	3-2	32	321	32	32	34
W2691Sr13 (*Sr13*)	*Sr13* control		-	-	-	21	2+2/32	321	21	21	21
St464-C1(*Sr13*)	*Sr13* control		-	-	-	21	2+2	23-/32	21	21	21
U5924-10-6 (*Sr22*)	Fuller*2//*Sr*22Tb/2*2174		-	-	-	;	;1-	;1-	;	;1-	;
PI 520490 (*Sr24*)	*Sr24* control		-	-	-	12/32	21	12	21	2+2/ 32	2/34
Wheatear (*Sr25*)	*Sr25* control		-	-	-	;	12	0;	;1-1	;1-	21
WA-1 (*Sr26*)	Eagle/Chinese Spring (CS) ph1ph1b/*6 Angas		-	-	-	;	12	12	12	;1-	;1-1
W2691/Sr28kt (*Sr28*)	*Sr28* control		-	-	-	3-2	32	321	32	-	32
Sr31/6*LMPG6 (*Sr31*)	*Sr31* control		-	-	-	2+2	2+2	231	3-2;	3-2	3-2
U5926-2-8 (*Sr32*)	Duster*2//Cns*Sr*32As/2*2174		-	-	-	;1-1	32	341	3-2	32	21/32
Sr36-5 (*Sr36*)	*Sr36* control		-	-	-	;	3/0	341	32	32	32
RWG1 (*Sr39*)	CS//CS ph1bph1b*2/RL6082(BC_2F_2)		-	-	-	12	12	12	21	12-	12
U5941-1-6 (*Sr40*)	Fuller*2//RL6088 (*Sr*40)/2*2174		-	-	-	32	32;	0;	32;	32;	34
HY438 (*Sr42/SrCad*)	HY320*6/7424-BW5B4//Kenya 321/Takahe/4/HY320*5/BW553// HY358///HY358/7915-QX76B2		-	-	-	1-1	21	0;	12-	1-1	12
RWG34 (*Sr43*)	CS//CS ph1bph1b*2/KS10-2 (BC_2F_2)		-	-	-	22+	2+23	;123	123-	2+2	32
RWG35 (*Sr47*)	Rusty/3/Rusty 5D(5B)/DAS15//47-1 5D(5B)		-	-	-	;	;	0;	;	;	;
Z2 (08Ae457)	Zhong 5/2-4/Wan 7107 (F_3)	42/41	2+	2+	4	21	2+23	;1-	3-2	2+2	32
Z3 (09Ae 9)	Zhong 5/2-4/Wan 7107 (F_3)		2+3	2-	3+	;12	2+23	;1-	2+23-	21	32
Z4	Zhong 5/2-4/Wan 7107 (F_3)	44	1+	1N	1+	;1-1	12	;1-	123-	;1-2+	;123
Z5	Zhong 5/2-4/Wan 7107 (F_3)	43-44	1+	1+	;13-	;11-	;12	;1-	;123-	;1-	;12-
Z6	Zhong 5/4/Zhong 8423 (F_3)	44	;1	;2-	2	21	;1	;1-	12	12	21
Yi4212	77-5433/Zhong 5	42	2	2	2+3			;1	21		2+23
TAI 12	Zhong 2 Progeny	42	2+3	2	22+	3-2	2+2	23-1	3-2	3-2	34

Table 3.4. Infection types of TTKSK-resistant durum and common wheat lines caused by nine races of stem rust pathogen (continued).

Line	Pedigree or Description	Chr. No. †	Infection types to nine races‡								
			TTKSK	TRTTF	TTTTF	MCCFC	QTHJC	RHTSC	RKQQC	TMLKC	TPMKC
TAI 15	Zhong 2 Progeny		2+	2	3+	-	2	-	4	-	4
TAI 22	Zhong 3, 4, 5 Progeny	43-44	2+	2+	3+	-	2+	-	3+	-	3+
TAI 26	Zhong 3, 4, 5 Progeny	42-43	2+	2+	22+	21	2+23	23-1	32	;12	21
TAI 27	Zhong 3 Progeny	44	;1+	2+	3+	12	;1-	;123-	21	-	34
XWC11-64	CS-*Th. elongatum* 3E(3A) DS		2+3	3+	2+/4	32	3-2	321	3-2	3-2	32
XWC11-65	CS-*Th. elongatum* 3E(3B) DS		2+3	2+3	3	32	3-	32	32	32	32
XWC11-66	CS-*Th. elongatum* 3E(3D) DS		2+3	3	3	32	3-2	32	3-2	32	32
XWC11-74	CS-*Th. elongatum* 7E(7A) DS		2	2	2	21	21	23-1	2+2	212+	212+
XWC11-75	CS-*Th. elongatum* 7E(7B) DS		2	2-	2	21	21	212+	21	22+1	12
XWC11-76	CS-*Th. elongatum* 7E(7D) DS		2	2	2+	213-	21	22+1	21	2+21	12
K11463	TC-*Th. ponticum* $7el_1$(7D) DS		22+	-	-	21	2+2	21	2	22+1	212+
K2620	TC-*Th. ponticum* $7el_2$(7D) DS		;1/2/2+2/3+	-	-	21/3-2	212+	21	21/3-2	22+1/ 32	21
TA6651	CS-*Ae. speltoides* 1S(1B) DS		;1	3+	4	32	34	32	32	32	34
TA6652	CS-*Ae. speltoides* 2S(2B) DS		2- LIF	2	2	;1-1	12	;12-	12	12	21
TA6657	CS-*Ae. speltoides* 7S(7B) DS		2+3	4	4	32	212+/ 3-2	321	212+	3-2	32
Kulm	HRSW cultivar		2	2	;	;	21	;	1-1	;	;1-
Erik	HRSW cultivar		2-	2-	2	;	22+/34	3-21	2+2/34	;	21
KE16	Kulm/Erik RIL 16		3	2+3	23-	;1	21	;1-	12-	;	21
KE21	Kulm/Erik RIL 21		;1 LIF	2-	0;	;1-	21	;1-	1-1	0;	12
KE23	Kulm/Erik RIL 23		2- LIF	2-	2-	;1-	21	;	1-1	;	12
KE33	Kulm/Erik RIL 33		;	2-	;2-	;1-	12	;	1-1	0;	12
KE89	Kulm/Erik RIL 89		;1	2-	;	;1-	12	;	1	;	12
TA4154-27	Scoop 1		2-	2-	;1	;1-1	;1-	;	;1-	;1-	;1-1
TA2516	*Ae. tauchii* (358)		2+	3	3	2+2	32	2++	32	2+23-	32
TA4152-60	Scoop 1/*Ae.tauschii* (358)		2+	2	2-	;12	;1-	;1-	1-	12	;12
TA4154-4	Altar 84		2	2-	1;	;1-	;1-	;1-	;	;1-1	;1-1
W7984	Altar 84/*Ae. tauschii* WPI 219		22+	2-;	2	;1-	;1-	;1-	;	;	;1-
AESR1	*Th. ponticium*		;	;/1	0;	;	0;	;1	;	;1-	0;
Jinan 177	*T. aestivium*		4	;	2	21	21	1	2	12	21
X025	Jinan 177/AESR1		2+	4	4	32	212+	321	3-2	32	32
X031-1	Jinan 177/AESR1		2+	3+	3	32	212+	321	3-2	32	32
X085	Jinan 177/AESR1		2+	4	4	321	2+2	23-	2	34	34

Table 3.4. Infection types of TTKSK-resistant durum and common wheat lines caused by nine races of stem rust pathogen (continued).

Line	Pedigree or Description	Chr. No. †	Infection types to nine races‡								
			TTKSK	TRTTF	TTTTF	MCCFC	QTHJC	RHTSC	RKQQC	TMLKC	TPMKC
X138	Jinan 177/AESR1		2+	4	4	32	2+23-	321	2+2	32	34
X144	Jinan 177/AESR1		2+	4	4	32	2+2	321	2+2	32	32
X145	Jinan 177/AESR1		2+	2-	-	12	21	21	12	21	1-1
X150	Jinan 177/AESR1		2+	4	4	3-2	2+23-	321	3-2	3-2	34
Jinnong 6	Chinese winter wheat cultivar		22+	4	4	12	21	321	2	212+	12
Shimai 15	Chinese winter wheat cultivar		2+3	2-	2	12	21	;1-1	12-	12	12
Zhoumai 16	Chinese winter wheat cultivar		0/2+	2-	2	21	21	;1-1	21	12	21
Zhoumai 25	Chinese winter wheat cultivar		0	2-	2-;	;1-	21	;1-1	1-1	;	;1-1
Zhoumai 26	Chinese winter wheat cultivar		3-	2-	2	21	12	;1	1-1	12	12
Zhoumai 27	Chinese winter wheat cultivar		3/;	2-	2	12	12	;1	1-1	12	12
Jinan 17	Chinese winter wheat cultivar		2	2+	4	32	123-	22+	2+2	32	3-2
Jimai 20	Chinese winter wheat cultivar		2	4	4	12	212+	21	21	12	12
Carpio	ND durum line		2-	2-	;	;	;	;1-	;	;	;1-
Joppa	ND durum line		2-	;/2-	;	;	;	;	;	;	;1-
Tioga	Plaza/Maier		2-	2-	;	;	;	;	;	;1-1	;1-1
Alkabo	D901247/D89263		2	0	;	;	;	0;	;	;	0;
Grenora	D901260/D901419		2	0	;	;	;	;	;	;	0;
Maier	D8193/D8335		2-	0;	;	;	;	;	;	;	0;
Lebsock	Munich/D8469		2-	-	;	;	;	;	;	;	0;
Ben	D8024/Monroe		2-	0;	;	;	;	;	;	;	;
PI 41025	*T. turgidum* subsp. *dicocum*		4	3+	4	32	32	32	32	32	34
P 61102	*T. turgidum* subsp. *carthlicum*		0;	4	3	21	21	22+1	21	21	21
P I94748	*T. turgidum* subsp. *carthlicum*		;13	3+	2+	21	21	22+1	22+	12	22+
P I277012	Spring wheat		3+	3+	4	21	212+	;12	12	32	32
12P772	Ben/PI 277012//Ben		2	2-	;1	12	12	;	1-1	;1-	;1-1
12P633	Ben/PI 41025//Maier		2	0;	2	;	;1-	;	;	;	;
12P636	Ben/PI 41025//Maier		2	0;	;1	;	;1-	;	;	0;	;
12P642	Lebstock/PI 94748//Lebstock		2	0;	2	1-1	21	;1-	;	0;	0;
12P645	Lebsock/PI 61102		;1 LIF	2+	2-	21	212+	;	12	1-1	21
12P660	Lebsock/08F130//Alkabo		2	0;	;	;	;1-	;	;	;	;
12P666	Grenora/08F286//Grenora		2	0;	;	;	;1-	;	;	;	;
12P798	Grenora/08F286//Grenora		2	0	0;	;	;1-	;	;	;	;

† 'Chr. No.' indicates chromosome number of Z lines and TAI lines.

‡ Infection types were scored using system proposed by Stakman et al. (1962). In our study, infection types of 0 to 2+ were considered resistance, whereas IT of 3 and 4 were considered susceptibility. LIF = low infection frequency; N = necrosis; – = missing data.

Table 3.5. Postulated genes in the tested lines (including positive control) associated with corresponding positive markers.

Line	Pedigree or Description	Chr. No. †	Positive markers‡	Postulated *Sr* genes‡
Snowmass (*Sr2*)	KS96HW94//Trego/CO960293		*Xgwm533*	*Sr2*
U5924-10-6 (*Sr22*)	Fuller*2//*Sr*22Tb/2*2174		*Xwmc633*, *XcsIH81-BM&AG*	*Sr22*
PI 520490 (*Sr24*)	*Sr24* control		*Xbarc71*, *XSr24#12*	*Sr24*
Wheatear (*Sr25*)	*Sr25* control		*XBF145935*, *XGb*	*Sr25*
WA-1 (*Sr26*)	Eagle/Chinese Spring (CS) ph1ph1b/*6 Angas		*XSr26#43&XBE518379*	*Sr26*
W2691/*Sr*28kt (*Sr28*)	*Sr28* control		*Xgwm533*, *XwPt-7004-PCR*, *Xwmc332*	*Sr2*, *Sr28*
*Sr*31/6*LMPG6 (*Sr31*)	*Sr31* control		*Xiag95*, *Xscm9*	*Sr31*
U5926-2-8 (*Sr32*)	Duster*2//Cns*Sr*32As/2*2174		*Xbarc55*	*Sr32*
*Sr*36-5 (*Sr36*)	*Sr36* control		*Xgwm533*	*Sr2*
RWG1 (*Sr39*)	CS//CS ph1bph1b*2/RL6082(BC_2F_2)		*XSr39#22r*, *Xrwgs27*	*Sr39*
U5941-1-6 (*Sr40*)	Fuller*2//RL6088 (*Sr*40)/2*2174		*Xgwm533*	*Sr2*
HY438 (*Sr42/SrCad*)	HY320*6/7424-BW5B4//Kenya 321/Takahe/4/HY320*5/BW553// HY358///HY358/7915-QX76B2		*Xgwm533*, *XFSD-RSA*, *Xbarc183*	*Sr2*, *Sr42/SrCad*
RWG34 (*Sr43*)	CS//CS ph1bph1b*2/KS10-2 (BC_2F_2)		*Xrwgs30*, *Xcfa2040*	*Sr43*
RWG35 (*Sr47*)	Rusty/3/Rusty 5D(5B)/DAS15//47-1 5D(5B)		*Xbarc55*, *Xcfg10*, *Xgwm501*	*Sr32*, *Sr47*
Z2 (08Ae457)	Zhong 5/2-4/Wan 7107 (F_3)	42/41	*Xgwm533*	*Sr2*
Z4	Zhong 5/2-4/Wan 7107 (F_3)	44	*Xgwm533*	*Sr2*
Z5	Zhong 5/2-4/Wan 7107 (F_3)	43-44	*Xgwm533*	*Sr2*
Z6	Zhong 5/4/Zhong 8423 (F_3)	44	*Xiag95*, *Xscm9*	*Sr31*
TAI 12	Zhong 2 Progeny	42	*Xgwm533*	*Sr2*
TAI 15	Zhong 2 Progeny		*Xgwm533*	*Sr2*
TAI 26	Zhong 3, 4, 5 Progeny	42-43	*Xgwm533*	*Sr2*
TAI 27	Zhong 3 Progeny	44	*Xgwm533*	*Sr2*
XWC11-64	CS-*Th. elongatum* 3E(3A) DS		*Xbarc71*	*Sr24*
XWC11-65	CS-*Th. elongatum* 3E(3B) DS		*Xbarc71*	*Sr24*
XWC11-66	CS-*Th. elongatum* 3E(3D) DS		*Xbarc71*	*Sr24*
K11463	TC-*Th. ponticum* $7el_1$(7D) DS		*Xgwm533*, *XBF145935*, *XGb*	*Sr2*, *Sr25*
K2620	TC-*Th. ponticum* $7el_2$(7D) DS		*Xgwm533*, *Xrwgs30*, *Xcfa2040*	*Sr2*, *Sr43*
TA6652	CS-*Ae. speltoides* 2S(2B) DS		*XSr39#22*	*Sr39*
Kulm	HRSW cultivar		*Xgwm533*, *Xbarc71*, *XSr24#12*	*Sr2*, *Sr24*
Erik	HRSW cultivar		*Xgwm533*	*Sr2*
KE16	Kulm/Erik RIL 16		*Xgwm533*, *Xbarc71*, *XSr24#12*	*Sr2*, *Sr24*

Table 3.5. Postulated genes in the tested lines (including positive control) associated with corresponding positive markers (continued).

Line	Pedigree or Description	Chr. No. †	Positive markers‡	Postulated *Sr* genes‡
KE21	Kulm/Erik RIL 21		*Xgwm533*, *Xbarc71*, *XSr24#12*	*Sr2*, *Sr24*
KE23	Kulm/Erik RIL 23		*Xgwm533*, *Xbarc71*, *XSr24#12*	*Sr2*, *Sr24*
KE33	Kulm/Erik RIL 33		*Xgwm533*, *Xbarc71*, *XSr24#12*	*Sr2*, *Sr24*
KE89	Kulm/Erik RIL 89		*Xgwm533*, *Xbarc71*, *XSr24#12*	*Sr2*, *Sr24*
TA4154-27	Scoop 1		*XwPt-7004-PCR*	*Sr28*
TA4152-60	Scoop 1/*Ae.tauschii* (358)		*XwPt-7004-PCR*	*Sr28*
TA4154-4	Altar 84		*XwPt-7004-PCR*	*Sr28*
W7984	Altar 84/*Ae. tauschii* WPI 219		*XwPt-7004-PCR*	*Sr28*
AE*SR*1	*Th. ponticium*		*Xbarc71*, *XSr24#12*, *XBF145935*, *XGb*, *XSr26#43&XBE518379*	*Sr24*, *Sr25*, *Sr26*
Jinan 177	*T. aestivium*		*Xgwm533*, *Xbarc71*, *XSr24#12*	*Sr2*, *Sr31*
X145	Jinan 177/AE*SR*1		*Xiag95*, *Xscm9*	*Sr31*
Shimai 15	Chinese winter wheat cultivar		*Xgwm533*, *Xiag95*, *Xscm9*, *Xbarc183*	*Sr2*, *Sr31*, *Sr42/SrCad*
Zhoumai 16	Chinese winter wheat cultivar		*Xiag95*, *Xscm9*, *Xbarc183*	*Sr31*, *Sr42/SrCad*
Zhoumai 25	Chinese winter wheat cultivar		*Xgwm533*, *Xiag95*, *Xscm9*	*Sr2*, *Sr31*
Zhoumai 26	Chinese winter wheat cultivar		*Xgwm533*, *Xiag95*, *Xscm9*, *Xbarc183*	*Sr2*, *Sr31*, *Sr42/SrCad*
Zhoumai 27	Chinese winter wheat cultivar		*Xiag95*, *Xscm9*, *Xbarc183*	*Sr31*, *Sr42/SrCad*
Jinan 17	Chinese winter wheat cultivar		*Xbarc183*	*Sr42/SrCad*
PI 41025	*T. turgidum* subsp. *dicocum*		*Xgwm533*	*Sr2*
12P633	Ben/PI 41025//Maier		*Xgwm533*	*Sr2*
12P636	Ben/PI 41025//Maier		*Xgwm533*	*Sr2*
12P660	Lebsock/08F130//Alkabo		*Xgwm533*	*Sr2*
12P798	Grenora/08F286//Grenora		*Xgwm533*	*Sr2*

† 'Chr. No.' indicates chromosome number of Z lines and TAI lines.

‡ 'Positive markers' indicate that markers amplifying specific band link to postulated *Sr* genes.

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CHAPTER 4. DEVELOPMENT AND CHARACTERIZATION OF SYNTHETIC HEXAPLOIDS FROM UNDER-EXPLOITED TETRAPLOIDS AS A NEW RESOURCE FOR STEM RUST UG99 RESISTANCE

Abstract

In the *Triticum* genus, tetraploid wheat (*Triticum turgidum* L.) is a useful resource for germplasm improvement of hexaploid common wheat (*T. aestivum* L.). Several recent studies demonstrated that TTKSK-resistant genotypes were abundantly present among seven tetraploid subspecies (*T. turgidum* subsp. *carthlicum*, *dicoccum*, *dicoccoides*, *durum*, *polonicum*, *turgidum*, and *turanicum*). To transfer stem rust resistance from tetraploid into hexaploid wheat, I developed 200 SHW lines by crossing 181 accessions of the seven tetraploid subspecies to 14 accessions of *Aegilops tauschii* Cosson. These new SHW lines are currently being characterized for resistance to stem rust. So far, 66 new SHW lines, 14 previously-developed SHW lines, and their parents have been evaluated for resistance to TTKSK, TRTTF, TTTTF and six other races and genotyped using molecular markers linked to known genes previously identified in *T. dicoccum* and *Ae. tauschii*. The evaluation data showed that 44, 49, and 57 SHW lines were resistant to races TTKSK, TRTTF, and TTTTF respectively, with 29 lines being resistant to all three races. Comparisons of individual SHW lines and their parents indicated that resistance expression in the SHW lines is highly dependent on their *Ae. tauschii* parents. Most of the SHW lines derived from the resistant *Ae. tauschii* accession PI 268210 had similar or slightly increased levels of resistance compared to their tetraploid parents. However, most of the SHW lines derived from susceptible *Ae. tauschii* accessions (e.g. CIae26 and RL5286) had distinctly lower levels of resistance compared to their tetraploid parents, and some of the SHW lines completely lost the resistance. Interestingly, a number of SHW lines only lost their resistance to TTKSK, suggesting

that a suppressor(s) specifically for TTKSK resistance might be present in the *Ae. tauschii* accessions. Based on the marker analysis and resistance expression, I postulated that a number of SHW lines have novel genes conferring resistance to TTKSK and other races and they represent new sources of stem rust resistance for hexaploid wheat improvement.

Introduction

In the *Triticum* genus, tetraploid wheat (*Triticum turgidum* L., $2n = 4x = 28$, AABB) and diploid *Aegilops tauschii* Coss. ($2n = 2x = 14$, DD) are useful resources for germplasm improvement of hexaploid common wheat (*Triticum aestivum* L., $2n = 6x = 42$, genome AABBDD). Since the 1930s, numerous unique genes controlling desirable characters have been transferred from *Ae. tauschii* and various tetraploid wheat subspecies into common wheat and have been utilized in wheat production (see review by Ogbonnaya et al., 2013). The transfer of genes from *Ae. tauschii* and tetraploid wheat to common wheat can be accomplished either through interploidy hybridization followed by backcrossing or by the production of synthetic hexaploid wheat (SHW) (×*Aegilotriticum* spp., $2n = 6x = 42$, AABBDD) (Mujeeb-Kazi et al., 1996; Cox, 1997; Yu et al., 2012). Compared with direct hybridization and backcrossing, SHW has the advantages of allowing for utilizing the genes from both the tetraploid and *Ae. tauschii* parents, evaluating the value of genes in combination, and performing large scale testing (Mujeeb-Kazi et al., 1996; Yu et al., 2012). In addition, traits (e.g. resistance to Fusarium head blight) which are difficult to evaluate in *Ae. tauschii* can be evaluated through SHW.

Because of the importance of SHW for wheat improvement, a large number of SHW lines have been produced since the 1940s. A recent review by Ogbonnaya et al. (2013) indicated that over 1,500 SHW lines have been developed globally since McFadden and Sears (1944)

created the first SHW line. Many of these SHW lines were identified as unique sources of genes for disease and insect resistance from *Ae. tauschii*, such as the powdery mildew-resistance gene *Pm2* (Lutz et al., 1995), greenbug-resistance genes *Gb3* (Joppa and Williams, 1982) and *Gb7* (Weng et al., 2005), cereal cyst nematode-resistance genes *Cre3* (Eastwood et al., 1994; Lagudah et al., 1997), stem rust-resistance genes *Sr33* (Saintenac et al., 2013), *Sr45* (McIntosh et al., 2013), and *Sr46* (McIntosh et al., 2013), Hessian fly-resistance genes *H26* (Wang et al., 2006) and *H32* (Sardesai et al., 2005), *Septoria tritici* blotch-resistance gene *Stb5* (Arraiano et al., 2001), rootknot nematode- resistance gene *Rkn* (Kaloshian et al., 1989), and Russian wheat aphid-resistant gene *Dn3* (Nkongolo et al., 1991). Some of the SHW lines were used as the parental materials for developing mapping populations. The most widely used wheat reference mapping populations were developed from the cross between the CIMMYT SHW line W7984 and the cultivar 'Opata 85' (Nelson et al., 1995a, b, c; Sorrells et al., 2011). The original recombinant-inbred line population (Nelson et al., 1995a, b, c) and the reconstructed SynOpDH population (Sorrells et al., 2011) have been extensively used for mapping the wheat genome and quantitative trait loci (QTL) for disease resistance and agronomically important traits (Anderson et al., 1993; Faris et al., 1997; Nelson et al., 2006; Sorrells et al., 2011). Another extensively used mapping population was developed using the SHW line TA 4152-60 (Mujeeb-Kazi et al., 2000) and the wheat line ND495. This population was used to construct a whole genome map (Chu. et al., 2008b) and to identify genes and QTL for resistance to leaf rust (Chu et al., 2009), Fusarium head blight (Zhong et al., 2011), tan spot (Chu et al., 2008a), Stagonospora nodorum blotch (Chu et al., 2010), stem rust (S.S. Xu, personal communication), and Hessian fly (S.S. Xu, personal communication)

For the practical utilization of SHW germplasm in wheat breeding, breeding programs from the International Maize and Wheat Improvement Center (CIMMYT), The International Center for Agricultural Research in the Dry Areas (ICARDA), China, Australia, the United Kingdom, and the United States are using SHW lines or their derivatives as parents to develop new wheat lines and cultivars. Ogbonnaya et al. (2013) indicated that, on average, 17% of all the entries from all nurseries in CIMMYT and ICARDA were SHW derivatives and several cultivars derived from synthetic wheat were released in China, Uruguay, and the United States for increased yield potential and pest resistance. It was reported that four high-yielding wheat cultivars the 'Chuanmai' series, which now grows on more than 100,000 ha, were developed by backcrossing CIMMYT SHW lines with adapted Chinese cultivars (Yang et al., 2009). In the United States, the greenbug-resistance gene *Gb3* from the SHW line Largo (Langdon/*Ae. tauschii* PI 286210) has been deployed in the winter wheat cultivars 'TAM 110' (Lazar et al., 1997) and 'TAM 112' (PI 643143), which provide effective protection from greenbug in the southern Great Plains (Lu et al., 2010).

Most of the previous programs for SHW development generally focused on genetic diversity in the *Ae. tauschii* collections. The tetraploid wheat parents, which are usually modern durum wheat [*T. turgidum* subsp. *durum* (Desf.) Husnot, abbreviated as *T. durum*] cultivars or lines, were mainly used as the donor of the AABB genome for SHW lines. Accordingly, most of the existing SHW lines were developed using a few durum wheat genotypes in crosses with a large number of *Ae. tauschii* accessions. For example, the Wide Hybridization Program at CIMMYT produced approximately 1,300 SHW lines using approximately 900 *Ae. tauschii* accessions (Mujeeb-Kazi and Delgado, 2001; Mujeeb-Kazi, 2003). In the 1980s, L.R. Joppa developed a number of spontaneous SHW lines by crossing the durum wheat 'Langdon'

(abbreviated as LDN) to different *Ae. tauschii* accessions (Friesen et al., 2008; Xu et al., 2010). In addition to durum wheat, other *T. turgidum* subspecies such as *T. turgidum* subsp. *carthlicum* (Nevski) Á. Löve & D. Löve, *T. turgidum* subsp. *dicoccoides* (Körn. ex Asch. & Graebner) Thell., *T. turgidum* subsp. *dicoccum* (Schrank ex Schübler) Thell., *T. turgidum* subsp. *polonicum* (L.) Thell., *T. turgidum* subsp. *turanicum* (Jakubz.) Á. Löve & D. Löve, and *T. turgidum* subsp. *turgidum* (abbreviated as *T. carthlicum*, *T. polonicum*, *T. turgidum*, *T. dicoccum*, and *T. dicoccoides*, respectively) are also useful for developing SHW lines for hexaploid wheat improvement. However, most of the previous SHW production programs have not targeted the genetic diversity in these tetraploid subspecies.

Several unique disease resistance genes were identified from *T. dicoccoides*, these include *Pm16* (Reader and Miller, 1991), *Pm30* (Liu et al., 2002), and *pm42* (Hua et al., 2009) for resistance to powdery mildew, *Lr23* (McIntosh and Dyck, 1975) for resistance to leaf rust, and *Yr15* (Grama and Gerechter-Amitai, 1974) and *YrH52* (Peng et al., 1999) for resistance to stripe rust, while the genes *Sr2* (Knott, 1968), *Sr13* (Knott, 1962), and *Sr14* (Knott, 1962) for resistance to stem rust and *Hdic* (Brown-Guedira et al., 2005) for resistance to Hessian fly were identified in *T. dicoccum*. The results from a number of recent germplasm evaluation projects demonstrated that the six tetraploid subspecies (*T. carthlicum*, *T. polonicum*, *T. turgidum*, *T. dicoccum*, and *T. dicoccoides*) were good sources of resistance to Fusarium head blight, tan spot, and Stagonospora nodorum blotch (Oliver et al., 2008; Chu et al., 2008a,b). For stem rust resistance, Olivera et al. (2011, 2012) evaluated 1,882 accessions of the six tetraploid subspecies with TTKSK and other races with broad virulence and identified 395 (21%) accessions with seedling resistance to TTKSK. Thus, tetraploid wheat accessions with resistance to the major

diseases represent an untapped and rich source of new genes for disease resistance in wheat improvement.

The objectives of this study were: to develop new SHW lines by using the unique tetraploid wheat genotypes; to evaluate the stem rust resistance in the new SHW lines; to characterize the expression of stem rust resistance in the hexaploid level, and to determine the novelty of the *Sr* genes in the TTKSK-resistant SHW lines using molecular markers linked to the known *Sr* genes derived from *T. dicoccum* and *Ae. tauschii*.

Materials and Methods

Plant materials

Based on previous studies on the characterization of a large number of accessions (Oliver et al., 2008; Olivera et al., 2012) belonging to six tetraploid subspecies, I selected 181 unique tetraploid genotypes from the six subspecies, including 46 *T. carthlicum*, 116 *T. dicoccum*, 1 *T. dicoccoides*, 13 *T. polonicum*, 2 *T. turanicum*, and 3 *T. turgidum* accessions, and 9 durum cultivars or lines, to cross with 14 *Ae. tauschii* accessions in order to develop new SHW lines (Table 4.1 and Table 4.2). Fourteen spontaneous SHW lines that were previously developed from crosses between LDN and 14 *Ae. tauschii* accessions (Xu et al., 2010) were included in the stem rust test. The common wheat cultivar 'Snowmass' (Haley et al., 2011) and *Aegilops tauschii* accessions TA1600 (RL5288), TA1662, TA1599 and RL5289, and CIae25 carrying the known genes *Sr2* (Haley et al., 2011), *Sr33* (Olson et al., 2013), *SrTA1662* (Olson et al., 2013), *Sr45* (Olson et al., 2013), and *Sr46* (McIntosh et al., 2013) were used as the checks in the marker analysis.

Synthetic hexaploid wheat development

New SHW development was performed using the procedure as described by Xu and Joppa (1995) with modification. The 181 tetraploid wheat accessions were used as female parents in crosses with the 14 *Ae. tauschii* accessions. Parental plants were planted as single plants in 6-inch clay pots in a greenhouse at 22–25 °C with a 16-h photoperiod. All the pots used in this study were filled with Sunshine SB100 Mix (Sun Gro Horticulture Distribution Inc., Bellevue, WA) and fertilized with Osmocote Plus 15–19–12 (Scotts Sierra Horticultural Product Company, Marysville, OH). All of the tetraploid wheat accessions used in this study are spring type, whereas the *Ae. tauschii* accessions are winter type and were vernalized for 8 to 10 weeks at 4-6 °C in a vernalization chamber. The spikes of the tetraploid wheat accessions were emasculated by hand before anthesis and pollinated 3-4 days after emasculation. At 14-16 days after pollination, hybrid embryos were aseptically isolated and cultured on MS basal medium with sucrose and agar (pH = 5.8) (Sigma-Aldrich Inc., St. Louis, MO) in the Petri dishes.

The cultured embryos were initially kept in the dark for 5-7 days and then provided with approximately 12 h light at room temperature. The seedlings at 1-3 cm in length were transferred to 25 mm diameter tubes containing ½ MS medium (pH = 5.8) with additional agar (4 g/l) under 10 h light conditions. The young hybrid seedlings at 5 – 7 cm in length were transplanted into 3-inch clay pots in a growth chamber at 16 °C under a 16 h photoperiod. The seedlings with 3-4 tillers were removed from the pots and treated with a colchicine solution [colchicine (0.40-0.45 g/l), GA3 (100 mg/l), DMSO (20 ml/l), and Tween 80 (0.3 ml/l)] with air flowing for 6 h in the dark at room temperature (Chu et al. 2008b). After the colchicine treatment, the seedlings were planted in 3-inch pots and maintained in the growth chamber at 16 °C with 16 h photoperiod for 14 days. After they recovered from the colchicine treatment, the seedlings were transplanted to

6-inch pots in the greenhouse. All spikes from each F_1 plant were bagged before flowering and harvested for artificially-synthesized hexaploid wheat seed at maturity.

Stem rust evaluation

The new SHW lines with adequate seed samples, 14 LDN SHW lines, and their parents were evaluated for their seedling reactions to the nine stem rust races that were used in Chapter III. The evaluation experiment with the three most virulent races, TTKSK, TRTTF, and TTTTF, was conducted at the USDA-ARS Cereal Disease Laboratory, St Paul, MN, whereas evaluation with races MCCFC, QTHJC, RHTSC, RKQQC, TMLKC, and TPMKC was performed at the USDA-ARS Northern Crop Science laboratory, Fargo, ND. The procedure for inoculation was described in Chapter III. For disease scoring, the infection types (ITs) of the primary leaf of each of the inoculated seedlings were recorded at 12-14 days after inoculation using the rating system developed by Stakman et al. (1962), where five basic levels (0, ;, 1, 2, 3, and 4) and the additional signs (- or +, smaller or larger pustules in each basic level of 1, 2, and 3) were used to represent the ITs for the inoculated seedlings (Roelfs and Martens, 1988). For simplifying analysis in this study, I used the letters "R" and "S" to represent the resistant (IT ≤ 2++) and susceptible (IT ≥ 3-) genotypes to each race, respectively. A formula "tetraploid wheat reaction × *Ae. tauschii* reaction = SHW reaction" was used to compare the reactions of a SHW line with its two parents. Thus, the reaction of a SHW line and its two parents to a race can be represented using one of eight types including R × R = R, R × R = S, R × S = R, R × S = S, S × R = R, S × R = S, S × S = R, and S × S = S.

Marker analysis

To predict the *Sr* genes present in the TTKSK-resistant SHW lines, eight molecular markers (Table 4.3) linked to the two genes, *Sr2* and *Sr13*, from *T. dicoccum* and three genes, *Sr33*, *SrTA1662*, and *Sr45*, from *Ae. tauschii* were used to genotype the SHW lines with resistance to TTKSK and their parents. These markers include *Xgwm533* for *Sr2* (Spielmeyer et al., 2003), *Xbarc104b*, *XCD926040*, *XCK207347*, and *XBE403950* for *Sr13* (Simons et al., 2011), *Xwmc222*, *Xwmc336*, and *Xwmc432* for *SrTA1662*, *Sr33*, and *Sr45* (Olson et al., 2013), respectively. Genomic DNA extraction was performed using the procedure described by Niu et al. (2011). The procedures and conditions of the polymerase chain reaction (PCR) followed Röder et al. (1998) with modification. A volume of 15 µl reaction mixture contained 100 ng template DNA, 1 unit Taq polymerase, 1× green GoTaq buffer with 1.5 mM $MgCl_2$ (Promega Corporation, Madison, WI), 0.08 mM each dNTP, and 400 nM each forward and reverse primer. PCR was performed using one cycle of 4 min at 94 ^{o}C, 35 cycles of 30 sec at 94 ^{o}C, 45 sec annealing at 55 ^{o}C, and 45 sec extension at 72 ^{o}C, and one cycle of 10 min at 72 ^{o}C for final extension. The PCR products were run on 6% non-denatured poly-acrylamide gel with 0.5× TBE buffer on a DDH-400-33 sequencer (C.B.S. Scientific Company, Inc., Del Mar, CA) at constant 60W for 90-120 min. The gel was stained using 1× GelRed (Biotium Corporate, Hayward, CA) for 5-10 min, and then scanned using a Typhoon 9410 imager (GE Healthcare, Inc. Waukesha, WI).

Results

Development of synthetic hexaploid wheat

Approximately 500 cross combinations were initially made by crossing 181 unique genotypes from the six tetraploid subspecies and nine durum cultivars or lines with 14 *Ae. tauschii* accessions to develop new SHW lines. Due to the low crossability or incompatibility in certain cross combinations, I produced hybrid embryos from approximately 350 cross combinations. The F_1 hybrid seedlings from a large number of the crosses had severe hybrid weakness such as grassiness, dwarfness, and necrotic and chlorotic dysgenesis and most of them died at the seedling stage. Eventually, the 200 new SHW lines were produced (Table 4.1 and Table 4.2). Of these SHW lines, 61, 1, 97, 22, 12, 2, and 5 lines were derived from *T. carthlicum, T. dicoccoides, T. dicoccum, T. durum, T. polonicum, T. turanicum,* and *T. turgidum,* respectively. Except for nine lines with *Ae. tauschii* AL8/78 as the parent showing moderate hybrid chlorosis, most of the SHW lines had normal growth and fertility.

Table 4.1. The number of synthetic hexaploid wheat (SHW) lines derived from crosses between six tetraploid wheat subspecies (*Triticum turgidum* subsp.) and *Aegiliops tauschii.*

T. turgidum subsp.	No of accessions *T. turgidum* subsp.	No of *Ae. tauschii* accessions	No of SHW lines
T. carthlicum	35	5	61
T. dicoccoides	1	1	1
T. dicoccum	47	4	97
T. durum	9	13	22
T. polonicum	10	2	12
T. turanicum	2	2	2
T. turgidum	3	3	5
Total†	107	14	200

†Total number of unique parental accessions and SHW lines.

Reactions of SHW lines and their parents to stem rust

Among the 200 new SHW lines, only 66 lines had adequate seed samples for stem rust testing in this study. The 66 new SHW lines, 14 previously-developed SHW lines, and their parents were evaluated with nine stem rust races and investigated for possible *Sr* genes in all the lines using molecular markers (Table 4.3). The infection types (ITs) to five races (TTKSK, TRTTF, TTTTF, RHTSC, and TMLKC) are listed in Table 4.4, and the ITs to the other four races are listed in Table A3. Based on the stem rust reactions of the parental lines that were involved in multiple cross combinations, the 80 SHW lines can be classified into four groups, which were derived from the crosses: 1) the resistant durum LDN crossed with resistant and susceptible *Ae. tauschii* accessions, 2) the susceptible durum Rusty crossed with the resistant and susceptible *Ae. tauschii* accessions, 3) the resistant and susceptible *T. dicoccum* accessions crossed with the resistant *Ae. tauschii* accession PI 268210, and 4) the resistant and susceptible *T. carthlicum*, *T. dicoccoides*, *T. dicoccum*, and *T. durum* accessions crossed with three susceptible *Ae. tauschii* accessions (Table 4.4 and Table 4.5), respectively.

The first group consists of 18 LDN SHW lines derived from the hybrids of durum LDN with 18 *Ae. tauschii* accessions (Table 4.4). The durum wheat parent LDN was moderately resistant to TTKSK, TTTTF, and TRTTF and highly resistant to the other six local races. Among the 18 *Ae. tauschii* parents, seven accessions (CIae17, CIae22, CIae25, PI 268210, TA1465, TA2377, and TA2474) were resistant to TTKSK and most of other eight races, and the other 11 accessions were susceptible to most of the nine races (Table 4.4 and Table A3). Six and four SHW lines from seven R × R and 11 R × S crosses, respectively, were resistant to TTKSK, whereas all the SHW lines were resistant to the other eight races except for a few lines with heterogeneous reactions. Most interestingly, seven SHW lines from R × S crosses of LDN with

TTKSK-susceptible *Ae. tauschii* accessions CIae26, H80-101-4, PI 476874, RL5214, RL5263, RL5286, and TA2450 were susceptible to TTKSK (ITs 3 to 3+), but they were resistant to most of the other eight races. It is known that LDN has *Sr13* for TTKSK resistance (Simmons et al., 2013) and it may also carry another gene conferring resistance to TRTTF that is virulent to *Sr13*. Therefore, these *Ae. tauschii* accessions may carry suppressor(s), which specifically suppress the expression of *Sr13* in the SHW lines. In addition, one SHW line (LDN/TA1645) had an R × R = S reactions to TTKSK, but it exhibited low infection frequency (Table 4.4).

The second group consists of seven Rusty SHW lines (Table 4.4). Rusty is a durum line that is near universally susceptible to stem rust (Klindworth et al., 2006) and it was susceptible to all nine races (Table 4.4 and Table A3). Among the seven *Ae. tauschii* accessions, four (CIae17, CIae22, CIae25, and PI 268210) were highly resistant to TTKSK, TRTTF, and most of the other seven races, two (CIae26 and RL5286) were susceptible to all nine races, and one (CIae19) was susceptible to TTKSK and RHTSC but resistant to other seven races. The four SHW lines from the crosses (S × R) of Rusty with the four resistant *Ae. tauschii* accessions (CIae17, CIae22, CIae25, and PI 268210) all had resistance to TTKSK and TMLKC (i.e. S × R = R) with a decreased resistance level, but they were susceptible (i.e. S × R = S) to at least one of the other seven races. For example, three *Ae. tauschii* accessions CIae17, CIae22, and PI 268210 were highly resistant to TRTTF, but their SHW lines with Rusty were susceptible to the race. The two SHW lines from the crosses of Rusty with two susceptible *Ae. tauschii* accessions CIae26 and RL5286, as expected, were susceptible to all the nine races. However, although *Ae. tauschii* CIae19 was susceptible to TTKSK (IT 32) and RHTSC (IT 3-2), its SHW line with Rusty were moderately resistant to the two races (ITs 22+ and 2+2).

The third group has 37 SHW lines, of which 26, nine, and two lines were developed respectively from *Ae. tauschii* CIae26 crossed to three *T. durum* lines (8815-B1, 8815-B2, and Iumillo) and 23 *T. dicoccum* accessions, *Ae. tauschii* RL5286 to *T. carthlicum* PS5 and eight *T. dicoccum* accessions, and *Ae. tauschii* PI 476874 to *T. carthlicum* PI 283888 and *T. dicoccoides* PI 481521 (Table 4.5 and Table A3). For the parental accessions, the three *Ae. tauschii* accessions were susceptible to all nine races, whereas most of tetraploid wheat accessions were resistant to all or most of the races, except for *T. dicoccoides* PI 481521 which was susceptible to all nine races. Evaluation data showed that most SHW lines from the crosses between tetraploid wheat accessions with resistance to a specific race and the three *Ae. tauschii* accessions had either decreased levels of resistance or were susceptible to the race compared with their tetraploid parents (Table 4.5 and Table A3).

The three *T. durum* lines (8815-B1, 8815-B2, and Iumillo) were highly or moderately resistant to all the nine races except that 8815-B1 was susceptible to TTKSK and TTTTF and Iumillo was susceptible to RKQQC. The SHW line from the cross 8815-B2/CIae26 was resistant to all nine races, but The SHW line from the cross 8815-B1/CIae26 was susceptible to TRTTF, RHTSC, and MCCFC, and the SHW line from the cross Iumillo/CIae26 was susceptible to TRTTF, TTTTF, and TPMKC. Among the 23 *T. dicoccum* accessions that were crossed to *Ae. tauschii* CIae26, 14, 15, and 18 were highly or moderately resistant to TTKSK, TRTTF and TTTTF, respectively, but nine, eight, and five of the SHW lines derived from these resistant *T. dicoccum* accessions were susceptible to the three races, respectively. For resistance to the other six races, the susceptible SHW lines derived from the resistant *T. dicoccum* accessions were less common.

T. carthlicum PS5 and its SHW line with *Ae. tauschii* RL5286 were susceptible to TRTTF and TTTTF and they were highly or moderately resistant to TTKSK and the other six races except that the SHW line was susceptible to TPMKC. Similarly to the SHW lines derived from crossing the *T. dicoccum* accessions to CIae26, two, two, and three SHW lines derived from resistant *T. dicoccum* accessions crossed to RL5286 were susceptible to TTKSK, TRTTF and TTTTF, respectively. For resistance to the other six races, susceptible SHW lines derived from the resistant *T. dicoccum* accessions with RL5286 were rare. Among the two SHW lines from *Ae. tauschii* PI 476874, the line from the cross *T. dicoccoides* PI 481521/PI 476874 was susceptible to all races like its parents. *T. carthlicum* PI 283888 was susceptible to TTKSK and TRTTF and it was highly or moderately resistant to the other seven races, but its SHW line with PI 476874 was susceptible to most of the races except for MCCFC.

The forth group contains 18 SHW lines derived from the crosses of *Ae. tauschii* PI 268210 to the 18 *T. dicoccum* accessions with either resistant or susceptible reactions to the nine races (Table 4.5 and Table A3). *Ae. tauschii* PI 268210 was highly resistant to all nine races, whereas the 18 *T. dicoccum* accessions had various levels of resistance to all or some of the races (Table 4.4 and Table A3). Most of the SHW lines in this group were resistant to all nine races (i.e. R × R = R or S × R = R) except for a few lines that were susceptible to some races (i.e. R × R = S or S × R = S). For example, *T. dicoccum* accessions PI 94616-1 and CItr 7687 were susceptible to TTKSK and TRTTF, respectively, and their SHW lines with PI 268210 were also susceptible to the two races, respectively. The *T. dicoccum* accessions PI 377655-1 and PI 94616-1 were moderately resistant to RHTSC (IT 21) and TPMKC (IT 22+1), respectively, but their SHW lines with PI 268210 were susceptible to the two races (IT 3-2), respectively (Table 4.5 and Table A3).

Molecular marker analysis

The 33 tetraploid wheat accessions and 18 *Ae. tauschii* accessions used as the parents for the 80 SHW lines were genotyped using five markers associated with *Sr2* and *Sr13* from *T. dicoccum* and three markers linked to *Sr33*, *Sr45*, and *SrTA1662* on the chromosome arm 1DS from *Ae. tauschii*. The marker analysis showed that the four markers *Xbarc104b*, *XCD926040*, *XCK207347*, and *XBE403950* that were associated with *Sr13* were not diagnostic for the gene in the 33 tetraploid wheat accessions. The *Sr2*-linked marker *Xgwm533* amplified the targeted 120-bp fragment from 16 tetraploid wheat accessions (Iumillo, CItr 7687-1, PI 94616-1, PI 94625-1, PI 94626-1, PI 94627-1, PI 94638-1, PI 94675-1, PI 94738-1, PI 225332-1, PI 254167-1, PI 254189-1, PI 254190-1, PI 349043-1, PI 349046-1, and PI 377655-1) and their derived SHW lines (Figure 4.1, Table 4.4, and Table 4.5), indicating that *Sr2* is commonly present in the *T. dicoccum* accessions with resistance to stem rust.

The marker *Xwmc336* linked to the three genes *Sr33/Sr45/SrTA1662* amplified a 91 bp band from five *Ae. tauschii* accessions susceptible to TTKSK (CIae26, RL5271, RL5272, RL5286, and TA2450) and five *Ae. tauschii* accessions used as the positive controls, including TA1600 (*Sr33*), TA1662 (*SrTA1662*), RL5289 and TA1599 (*Sr45*), and CIae25 (*Sr46*). Thus, the marker is not diagnostic for the three genes in *Ae. tauschii*. The markers *Xwmc222* and *Xwmc432* linked to *Sr33* produced the targeted 160-bp and 202-bp bands (Figure 4.2), respectively, from CIae17, its two SHW lines (LDN/CIae17 and Rusty/CIae17), and TA 1600 (*Sr33* check) (Olson et al., 2013), indicating that CIae17 may carry *Sr33*. CIae17 may also carry other resistance genes since CIae17 was near immune to TTKSK (IT 0;) and highly resistant to the other eight races, while TA1600 with *Sr33* had an intermediate level of resistance to TTKSK and the other races (Periyannan et al., 2013; Olson et al., 2013). The *Xwmc432* also produced a 174-bp band

from TA1662 (*SrTA1662* control) (Figure 4.2) (Olson et al., 2013) and a 210-bp and 230-bp bands from CIae25 carrying *Sr46* (S.S. Xu, personal communication), RL5272, and their SHW lines (Rusty/CIae25, LDN/CIae25, and LDN/RL5272) (Figure 4.2). Because CIae25 was highly or moderately resistant to all nine races (Table 4.4) and RL5272 was susceptible to TTKSK, TTTTF, MCCFC, and RKQQC, RL5272 should carry a different gene than *Sr46*.

Discussion

Synthetic hexaploid wheat is useful for the discovery and utilization of desirable genes from both tetraploid wheat and *Ae. tauschii* for hexaploid wheat improvement. However, most previous efforts for the development, characterization and utilization of SHW lines have been focused on the useful genes from *Ae. tauschii* germplasm collections (Ogbonnaya et al., 2013). In the current study, I developed 200 new SHW lines from crosses between 14 *Ae. tauschii* accessions and 107 tetraploid wheat accessions belonging to seven subspecies *T. carthlicum, T. dicoccoides, T. dicoccum, T. durum, T. polonicum, T. turanicum,* and *T. turgidum*. Because these tetraploid wheat accessions were selected as the parents for the SHW lines based on their resistances to several major wheat diseases such as Fusarium head blight, tan spot, Stagonospora nodorum blotch, and stem rust (Oliver et al., 2008; Chu et al., 2008a,b; Olivera et al., 2011, 2012), the SHW lines developed from these tetraploid wheat accessions in this study represent a new resource for the improvement of disease resistance in hexaploid wheat. The evaluation and characterization of these new SHW lines for resistance to major diseases and for other traits is currently underway. In this study, 66 of the new SHW lines, 14 previously-developed LDN derived SHW lines, and their tetraploid and *Ae. tauschii* parents were evaluated with nine races of the stem rust pathogen.

Stem rust evaluation showed that 44, 49, and 57 of the 80 SHW lines had resistance to the three most virulent races TTKSK, TTTTF, and TRTTF, respectively, with 29 lines being resistant to all three races. In addition, most of the SHW lines were resistant to the other six North American races tested. Thus, the SHW lines developed in this study should be a useful source of genes specifically for resistance to stem rust. Among the 33 tetraploid wheat genotypes used as parents, 16, 18, and 21 accessions were resistant to TTKSK, TTTTF, and TRTTF, respectively. Among the *Sr* genes derived from tetraploid wheat, only *Sr2* and *Sr13* derived from *T. dicoccum* were resistant to TTKSK (Jin et al., 2007). *Sr2* has been deployed in many wheat cultivars worldwide while *Sr13* is commonly present in U.S. durum cultivars (Mago et al., 2011; Simons et al., 2011). The molecular marker analysis indicated that *Sr2* may be present in the durum Iumillo and 15 *T. dicoccum* accessions. Because *Sr2* is effective only at the adult stage (Mago et al., 2011) and *Sr13* confers only a moderate level of resistance, the undescribed or novel *Sr* genes for the high level of resistance to TTKSK and other races should be present in the two durum lines (8155-B2 and Iumillo), *T. carthlicum* accession PS5 (Xu and Dong, 1992), and several *T. dicoccum* accessions such as CItr 14133-1, PI 74108-1, PI 94626-1, PI 94675-1, PI 94738-1, and PI 254190-1. Among 18 *Ae. tauschii* accessions, six (CIae17, CIae22, CIae25, PI 268210, TA1645, and TA2474) were highly resistant to TTKSK and one (TA2377) was moderately resistant to the race. A recent mapping study showed that CIae25 carries *Sr46* (Yu et al., unpublished data). The molecular marker analysis indicated that CIae17 may have *Sr33* but the other five *Ae. tauschii* accessions with resistance to TTKSK may carry novel *Sr* genes. Thus, the SHW lines developed from these *Ae. tauschii* accessions and the tetraploid wheat accessions with high levels of resistance to TTKSK are a potential source of novel *Sr* genes.

Comparisons of individual SHW lines and their tetraploid wheat and *Ae. tauschii* parents show that most SHW lines exhibited distinctly lower levels of resistance than one of their parents. Many SHW lines derived from R × S or S × R crosses were susceptible to a specific race. The decrease or disappearance of the stem rust resistance in the SHW lines is a common phenomenon and has been extensively investigated in several studies (Kerber and Dyck, 1979; Bai and Knott, 1992; Assefa and Fehrmann, 2004). It has been suggested that this phenomenon can be attributed to genome dilution and chromosome instability of the SHW lines, gene losses from DNA elimination during the polyploidization, environment factors such as temperature, and presence of suppressor genes in the parental genomes. Kerber and Dyck (1979) indicated that the resistance of SHW to stem rust became lower than their parents because effect of a resistance gene in tetraploid or diploid background was diluted in hexaploid background (Rouse et al., 2011). I believe that genome dilution in the SHW lines, in most cases, probably causes only slight decrease (e.g. from IT 1 to 2 and from 2+ to 3-) of the resistance level. Although environment factors such as temperature can affect the expression of the resistance, they should not considerably change the resistance levels of a SHW line from its parents because the evaluation experiments in this study were performed under controlled greenhouse conditions.

Regarding to chromosome instability, occurrence of aneuploidy progenies with lost ($2n < 42$) or added ($2n > 42$) chromosomes in the newly-developed SHW lines is common and has been well documented in the literatures (Joppa and Williams, 1982; Zhang et al., 2013). During the development of SHW lines in this study, I found aneuploidy with chromosome loss occurred much more frequently than that with chromosome gain. In addition, a progeny plant having $2n = 42$ from SHW lines could lose one chromosome but gain another (Zhang et al., 2013). If a progeny plant from a SHW line loses a chromosome carrying a *Sr* gene conditioning incomplete

resistance, the plant would become susceptible. Because the SHW seed samples used in this study were mostly derived from plants having 2n = 42, a small number of aneuploid plants, if existed, should not affect the expression of the resistance in a SHW line but it may result in mixed (resistant vs. susceptible) reactions. For example, the SHW line from the cross 8815-B2/CIae26 was resistant to eight races but it had mixed reactions only to QTHJC. A few susceptible plants in this line may be the aneuploids that lost a chromosome carrying the *Sr* gene.

The complete losses of high level of stem rust resistance from the parents in the SHW lines may be related to the genome changes during the amphiploidization. Feldman and Levy (2009) indicated that natural allopolyploids and synthetic allopolyploids reduced approximately 2%-10% DNA than the sum of their parents. Thus, a SHW line would become susceptible if the DNA sequence containing a *Sr* gene from its parents was eliminated during the amphiploidization. I believe that gene losses from DNA elimination during the polyploidization may be a random event and the chances for eliminating DNA sequence containing a specific *Sr* gene is probably rare. Therefore, gene losses from DNA elimination should not be a major cause for loss of stem resistance from the parents in the SHW lines in this study.

By comparing the individual SHW lines to their tetraploid wheat and *Ae. tauschii* parents, I observed that expression of stem rust resistance in the SHW lines is highly dependent on the *Ae. tauschii* and tetraploid wheat parents. *Ae. tauschii* PI 268210 was highly resistant to all the races tested. Although most SHW lines derived from PI 268210 had lower levels of resistance than PI 268210, most of them had similar or slightly increased levels of resistance to their tetraploid wheat parents. However, most of the SHW lines derived from susceptible *Ae. tauschii* accessions (e.g. CIae26 and RL5286) had distinctly lower levels of resistance than their tetraploid wheat parents. Particularly, a number of tetraploid wheat accessions, such as *T.*

dicoccum PI 74108-1, PI 94621-1, PI 94675-1, PI 94738-1 and PI 254190-1 were highly resistant to TTKSK or TRTTF, but their SHW lines with CIae 26 were susceptible to one of two races. Most interestingly, seven SHW lines from R × S crosses of LDN with CIae26 and other six susceptible *Ae. tauschii* accessions (H80-101-4, PI 476874, RL5214, RL5263, RL5286, and TA2450) were susceptible to TTKSK, but they were all resistant to most of the other eight races as LDN. These *Ae. tauschii* accessions most likely carried a suppressor that specifically suppressed *Sr13* for TTKSK resistance but had no effect on other *Sr* genes in LDN.

The suppression of stem rust resistance was previously studied in common wheat. Kerber and Green (1980) identified a suppressor gene on the long arm of chromosome 7D in the wheat cultivar Canthatch, Williams et al. (1992) inferred that the suppressor may inhibit three recessive genes on the A and/or B genomes. Although several previous studies indicated that suppressors might be present on the A and/or B and D genomes in some tetraploid wheat and *Ae. tauschii* accessions (Assefa and Fehrmann, 2004; Innes and Kerber, 1994), they have not been identified yet. In this study, I found that *Ae. tauschii* accessions CIae26 and RL5286 consistently suppress the resistance to TTKSK from a number of tetraploid genotypes. They and their SHW lines should be useful for identification and characterization of suppressors in *Ae. tauschii*. In addition, I found that several SHW lines derived from 8815-B2, Iumillo, CItr 14133-1 PI 94626-1, PI 94648-1, PI 94666-1, PI 349046-1, and PI 352548-1 crossed to CIae26 or RL5286 were still resistant to TTKSK, indicating that the *Sr* genes in the tetraploid accessions should be different from *Sr13*. Thus, the differences in the stem rust reactions of the SHW lines derived from crossing different tetraploid accessions to CIae26 or a similar type of *Ae. tauschii* may provide prediction of the novelty of the *Sr* genes form the tetraploid accessions.

In summary, a set of 200 new SHW lines derived from under-exploited AB genome tetraploids were developed in this study. The new SHW lines carrying unique genes for disease resistance and other traits from the tetraploid accessions represent a new resource for hexaploid wheat improvement. Extensive evaluation and characterization of all the SHW lines and their parents for resistance to the major wheat diseases is currently in progress. Because these SHW lines were produced recently, their tetraploid wheat and *Ae. tauschii* parents have been well maintained. Therefore, this set of SHW lines is also invaluable for investigating polyploidization, genome evolution, and intergenomic interactions in wheat.

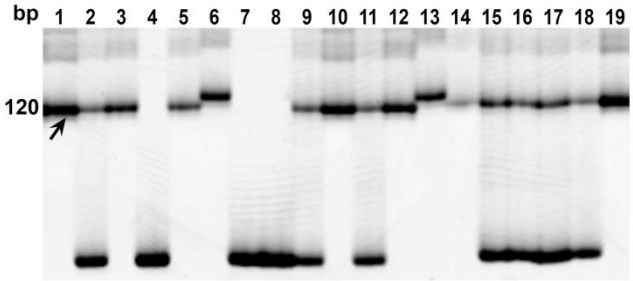

Figure 4.1. Gel image of molecular marker *Xgwm533* associated to the stem rust resistance gene *Sr2*. Representative wheat lines and checks: (1) Snowmass (*Sr2* check), (2) PI 94626-1, (3) PI 94627-1, (4) PI 94635-1, (5) PI 94638-1, (6) PI 94648-1, (7) PI 94666-1, (8) PI 94673-1, (9) PI 94675-1, (10) Snowmass, (11) PI 94738-1, (12) PI 225332-1, (13) PI 254165-1, (14) PI 254167-1, (15) PI 254189-1, (16) PI 254190-1, (17) PI 349043-1, (18) PI 349046-1, and (19) Snowmass. bp = base pair.

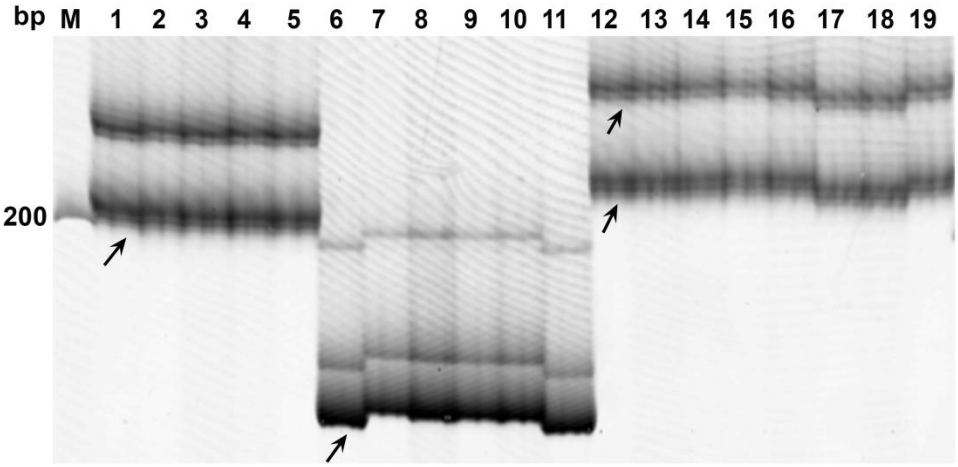

Figure 4.2. Gel image of molecular marker *Xwmc432* associated to the stem rust resistance genes *Sr33*. Representative wheat lines and checks: (1) TA1600 (*Sr33* check), (2) CIae17, (3) Rusty/CIae17, (4) LDN/CIae17, (5) TA1600 (*Sr33* check), (6) TA1662 (*SrTA1662* ckeck), (7) RL5271, (8) LDN/RL5271, (9) TA2377, (10) LDN/TA2377, (11) TA1662 (*SrTA1662* ckeck), (12) CIae25 (*Sr46* check), (13) Rusty/CIae25, (14) LDN/CIae25, (15) RL5272, (16) LDN/RL5272, (17) TA2474, (18) LDN/TA2474, and (19) CIae25. M = molecular weight. bp = base pair.

Table 4.2. Pedigrees of 200 synthetic wheat derived from 7 tetraploid species and 14 diploid species *Ae. tauschii*.

Entry	Pedigrees
1	*T. carthlicum* PS5/*Ae. tauschii* RL 5286
2	*T. carthlicum* PI 61102/*Ae. tauschii* CIae 26
3	*T. carthlicum* PI 61102/*Ae. tauschii* PI 268210
4	*T. carthlicum* PI 78812/*Ae. tauschii* CIae 26
5	*T. carthlicum* PI 94748/*Ae. tauschii* CIae 26
6	*T. carthlicum* PI 94748/*Ae. tauschii* PI 268210
7	*T. carthlicum* PI 94750/*Ae. tauschii* CIae 26
8	*T. carthlicum* PI 94750/*Ae. tauschii* PI 268210
9	*T. carthlicum* PI 94751/*Ae. tauschii* CIae 26
10	*T. carthlicum* PI 94751/*Ae. tauschii* RL 5286
11	*T. carthlicum* PI 94751/*Ae. tauschii* PI 268210
12	*T. carthlicum* PI 94752/*Ae. tauschii* CIae 26
13	*T. carthlicum* PI 94752/*Ae. tauschii* PI 268210
14	*T. carthlicum* PI 94752/*Ae. tauschii* AL8/78
15	*T. carthlicum* PI 94753/*Ae. tauschii* CIae 26
16	*T. carthlicum* PI 94753/*Ae. tauschii* PI 268210
17	*T. carthlicum* PI 94754/*Ae. tauschii* CIae 26
18	*T. carthlicum* PI 94754/*Ae. tauschii* PI 268210
19	*T. carthlicum* PI 94755/*Ae. tauschii* CIae 26
20	*T. carthlicum* PI 115816/*Ae. tauschii* CIae 26
21	*T. carthlicum* PI 115816/*Ae. tauschii* RL 5286
22	*T. carthlicum* PI 115816/*Ae. tauschii* PI 268210
23	*T. carthlicum* PI 182471/*Ae. tauschii* CIae 26
24	*T. carthlicum* PI 182471/*Ae. tauschii* RL 5286
25	*T. carthlicum* PI 182471/*Ae. tauschii* PI 268210
26	*T. carthlicum* PI 251914/*Ae. tauschii* CIae 26
27	*T. carthlicum* PI 283888/*Ae. tauschii* CIae 26
28	*T. carthlicum* PI 283888/*Ae. tauschii* PI 476874
29	*T. carthlicum* PI 283889/*Ae. tauschii* CIae 26
30	*T. carthlicum* PI 283889/*Ae. tauschii* RL 5286
31	*T. carthlicum* PI 283890/*Ae. tauschii* CIae 26
32	*T. carthlicum* PI 283890/*Ae. tauschii* PI 268210
33	*T. carthlicum* PI 286071/*Ae. tauschii* CIae 26
34	*T. carthlicum* PI 352278/*Ae. tauschii* CIae 26
35	*T. carthlicum* PI 352280/*Ae. tauschii* CIae 26
36	*T. carthlicum* PI 352281/*Ae. tauschii* CIae 26
37	*T. carthlicum* PI 352281/*Ae. tauschii* PI 268210
38	*T. carthlicum* PI 532489/*Ae. tauschii* CIae 26
39	*T. carthlicum* PI 532489/*Ae. tauschii* PI 268210
40	*T. carthlicum* PI 532491/*Ae. tauschii* CIae 26
41	*T. carthlicum* PI 532491/*Ae. tauschii* PI 268210
42	*T. carthlicum* PI 532495/*Ae. tauschii* CIae 26
43	*T. carthlicum* PI 532506/*Ae. tauschii* CIae 26
44	*T. carthlicum* PI 532507/*Ae. tauschii* CIae 26
45	*T. carthlicum* PI 532509/*Ae. tauschii* CIae 26
46	*T. carthlicum* PI 532509/*Ae. tauschii* PI 268210
47	*T. carthlicum* PI 532514/*Ae. tauschii* CIae 26
48	*T. carthlicum* PI 532516/*Ae. tauschii* CIae 26
49	*T. carthlicum* PI 532516/*Ae. tauschii* PI 268210
50	*T. carthlicum* PI 532517/*Ae. tauschii* CIae 26
51	*T. carthlicum* PI 532518/*Ae. tauschii* CIae 26
52	*T. carthlicum* PI 573181/*Ae. tauschii* CIae 26

Table 4.2. Pedigrees of 200 synthetic wheat derived from 7 tetraploid species and 14 diploid species *Ae. tauschii* (continued).

Entry	Pedigrees
53	*T. carthlicum* PI 573182/*Ae. tauschii* CIae 26
54	*T. carthlicum* PI 573182/*Ae. tauschii* PI 268210
55	*T. carthlicum* PI 585017/*Ae. tauschii* CIae 26
56	*T. carthlicum* PI 585017/*Ae. tauschii* PI 268210
57	*T. carthlicum* PI 585018/*Ae. tauschii* CIae 26
58	*T. carthlicum* Blackbird/*Ae. tauschii* CIae 26
59	*T. carthlicum* Blackbird/*Ae. tauschii* RL 5286
60	*T. carthlicum* Blackbird/*Ae. tauschii* PI 268210
61	*T. carthlicum* Blackbird/*Ae. tauschii* TA 1675
62	*T. dicoccoides* PI 481521/*Ae. tauschii* PI 476874
63	*T. dicoccum* CItr 7687-1/*Ae. tauschii* CIae 26
64	*T. dicoccum* CItr 7687-1/*Ae. tauschii* PI 268210
65	*T. dicoccum* CItr 14133-1/*Ae. tauschii* CIae 26
66	*T. dicoccum* CItr 14133-1/*Ae. tauschii* RL 5286
67	*T. dicoccum* CItr 14133-1/*Ae. tauschii* PI 268210
68	*T. dicoccum* CItr 14133-1/*Ae. tauschii* AL8/78
69	*T. dicoccum* PI 74108-1/*Ae. tauschii* CIae 26
70	*T. dicoccum* PI 74108-1/*Ae. tauschii* PI 268210
71	*T. dicoccum* PI 94616-1/*Ae. tauschii* CIae 26
72	*T. dicoccum* PI 94616-1/*Ae. tauschii* RL 5286
73	*T. dicoccum* PI 94616-1/*Ae. tauschii* PI 268210
74	*T. dicoccum* PI 94621-1/*Ae. tauschii* CIae 26
75	*T. dicoccum* PI 94621-1/*Ae. tauschii* RL 5286
76	*T. dicoccum* PI 94621-1/*Ae. tauschii* PI 268210
77	*T. dicoccum* PI 94625-1/*Ae. tauschii* CIae 26
78	*T. dicoccum* PI 94625-1/*Ae. tauschii* RL 5286
79	*T. dicoccum* PI 94625-1/*Ae. tauschii* PI 268210
80	*T. dicoccum* PI 94626-1/*Ae. tauschii* CIae 26
81	*T. dicoccum* PI 94626-1/*Ae. tauschii* RL 5258
82	*T. dicoccum* PI 94626-1/*Ae. tauschii* PI 268210
83	*T. dicoccum* PI 94627-1/*Ae. tauschii* CIae 26
84	*T. dicoccum* PI 94627-1/*Ae. tauschii* RL 5286
85	*T. dicoccum* PI 94627-1/*Ae. tauschii* PI 268210
86	*T. dicoccum* PI 94635-1/*Ae. tauschii* CIae 26
87	*T. dicoccum* PI 94635-1/*Ae. tauschii* PI 268210
88	*T. dicoccum* PI 94638-1/*Ae. tauschii* CIae 26
89	*T. dicoccum* PI 94648-1/*Ae. tauschii* CIae 26
90	*T. dicoccum* PI 94648-1/*Ae. tauschii* PI 268210
91	*T. dicoccum* PI 94666-1/*Ae. tauschii* CIae 26
92	*T. dicoccum* PI 94666-1/*Ae. tauschii* PI 268210
93	*T. dicoccum* PI 94673-1/*Ae. tauschii* CIae 26
94	*T. dicoccum* PI 94673-1/*Ae. tauschii* RL 5286
95	*T. dicoccum* PI 94673-1/*Ae. tauschii* PI 268210
96	*T. dicoccum* PI 94675-1/*Ae. tauschii* CIae 26
97	*T. dicoccum* PI 94675-1/*Ae. tauschii* PI 268210
98	*T. dicoccum* PI 94738-1/*Ae. tauschii* CIae 26
99	*T. dicoccum* PI 94738-1/*Ae. tauschii* PI 268210
100	*T. dicoccum* PI 197493-1/*Ae. tauschii* CIae 26
101	*T. dicoccum* PI 225332-1/*Ae. tauschii* CIae 26
102	*T. dicoccum* PI 225332-1/*Ae. tauschii* RL 5286
103	*T. dicoccum* PI 225332-1/*Ae. tauschii* PI 268210
104	*T. dicoccum* PI 254165-1/*Ae. tauschii* CIae 26

Table 4.2. Pedigrees of 200 synthetic wheat derived from 7 tetraploid species and 14 diploid species *Ae. tauschii* (continued).

Entry	Pedigrees
105	*T. dicoccum* PI 254165-1/*Ae. tauschii* RL 5286
106	*T. dicoccum* PI 254165-1/*Ae. tauschii* PI 268210
107	*T. dicoccum* PI 254167-1/*Ae. tauschii* CIae 26
108	*T. dicoccum* PI 254167-1/*Ae. tauschii* RL 5286
109	*T. dicoccum* PI 254189-1/*Ae. tauschii* CIae 26
110	*T. dicoccum* PI 254189-1/*Ae. tauschii* RL 5286
111	*T. dicoccum* PI 254190-1/*Ae. tauschii* CIae 26
112	*T. dicoccum* PI 254190-1/*Ae. tauschii* AL8/78
113	*T. dicoccum* PI 349043-1/*Ae. tauschii* RL 5258
114	*T. dicoccum* PI 349043-1/*Ae. tauschii* PI 268210
115	*T. dicoccum* PI 349046-1/*Ae. tauschii* CIae 26
116	*T. dicoccum* PI 349046-1/*Ae. tauschii* RL 5286
117	*T. dicoccum* PI 349046-1/*Ae. tauschii* PI 268210
118	*T. dicoccum* PI 352548-1/*Ae. tauschii* CIae 26
119	*T. dicoccum* PI 352548-1/*Ae. tauschii* RL 5286
120	*T. dicoccum* PI 355507-1/*Ae. tauschii* CIae 26
121	*T. dicoccum* PI 355507-1/*Ae. tauschii* RL 5286
122	*T. dicoccum* PI 377655-1/*Ae. tauschii* CIae 26
123	*T. dicoccum* PI 377655-1/*Ae. tauschii* PI 268210
124	*T. dicoccum* CI 3686/*Ae. tauschii* RL 5286
125	*T. dicoccum* CI 7685/*Ae. tauschii* AL8/78
126	*T. dicoccum* CI 7687/*Ae. tauschii* PI 268210
127	*T. dicoccum* CI 7779/*Ae. tauschii* CIae 26
128	*T. dicoccum* CI 7779/*Ae. tauschii* PI 268210
129	*T. dicoccum* CI 14085/*Ae. tauschii* CIae 26
130	*T. dicoccum* CI 14085/*Ae. tauschii* PI 268210
131	*T. dicoccum* CI 14086/*Ae. tauschii* CIae 26
132	*T. dicoccum* CI 14086/*Ae. tauschii* PI 268210
133	*T. dicoccum* CI 14135/*Ae. tauschii* RL 5286
134	*T. dicoccum* CI 14972/*Ae. tauschii* CIae 26
135	*T. dicoccum* PI 41025/*Ae. tauschii* CIae 26
136	*T. dicoccum* PI 41025/*Ae. tauschii* PI 268210
137	*T. dicoccum* PI 41025/*Ae. tauschii* TA 1675
138	*T. dicoccum* PI 79899/*Ae. tauschii* CIae 26
139	*T. dicoccum* PI 94614/*Ae. tauschii* CIae 26
140	*T. dicoccum* PI 94618/*Ae. tauschii* CIae 26
141	*T. dicoccum* PI 94618/*Ae. tauschii* PI 268210
142	*T. dicoccum* PI 94668/*Ae. tauschii* PI 268210
143	*T. dicoccum* PI 94668/*Ae. tauschii* AL8/78
144	*T. dicoccum* PI 94669/*Ae. tauschii* CIae 26
145	*T. dicoccum* PI 94669/*Ae. tauschii* PI 268210
146	*T. dicoccum* PI 94673/*Ae. tauschii* RL 5286
147	*T. dicoccum* PI 94680/*Ae. tauschii* RL 5286
148	*T. dicoccum* PI 94681/*Ae. tauschii* CIae 26
149	*T. dicoccum* PI 94681/*Ae. tauschii* RL 5286
150	*T. dicoccum* PI 94681/*Ae. tauschii* PI 268210
151	*T. dicoccum* PI 94681/*Ae. tauschii* AL8/78
152	*T. dicoccum* PI 94738/*Ae. tauschii* PI 268210
153	*T. dicoccum* PI 190926/*Ae. tauschii* CIae 26
154	*T. dicoccum* PI 191091/*Ae. tauschii* CIae 26
155	*T. dicoccum* PI 191091/*Ae. tauschii* AL8/78
156	*T. dicoccum* PI 191390/*Ae. tauschii* CIae 26

Table 4.2. Pedigrees of 200 synthetic wheat derived from 7 tetraploid species and 14 diploid species *Ae. tauschii* (continued).

Entry	Pedigrees
157	*T. dicoccum* PI 191390/*Ae. tauschii* PI 268210
158	*T. dicoccum* PI 272527/*Ae. tauschii* CIae 26
159	*T. dicoccum* PI 272527/*Ae. tauschii* RL 5286
160	*T. durum* Ben/*Ae. tauschii* RL5286
161	*T. durum* Ben/*Ae. tauschii* TA 1645
162	*T. durum* Ben/*Ae. tauschii* TA 2377
163	*T. durum* Ben/*Ae. tauschii* TA 2450
164	*T. durum* Lebsock/*Ae. tauschii* AL8/78
165	*T. durum* Lebsock/*Ae. tauschii* RL5286
166	*T. durum* Langdon 16/*Ae. tauschii* TA 1645
167	*T. durum* Langdon 16/*Ae. tauschii* TA 2377
168	*T. durum* Langdon 16/*Ae. tauschii* TA 2450
169	*T. durum* Langdon 16/*Ae. tauschii* TA 2474
170	*T. durum* Langdon 16 (GB-2A)/*Ae. tauschii* AL8/78
171	*T. durum* Langdon 16 (ISA 2A)/*Ae. tauschii* AL8/78
172	*T. durum* Rusty/*Ae. tauschii* CIae 17
173	*T. durum* Rusty/*Ae. tauschii* CIae 19
174	*T. durum* Rusty/*Ae. tauschii* CIae 22
175	*T. durum* Rusty/*Ae. tauschii* CIae 25
176	*T. durum* Rusty/*Ae. tauschii* CIae 26
177	*T. durum* Rusty/*Ae. tauschii* RL 5286
178	*T. durum* Rusty/*Ae. tauschii* PI 268210
179	*T. durum* Iumillo/*Ae. tauschii* CIae 26
180	*T. durum* 8155-B1/*Ae. tauschii* CIae 26
181	*T. durum* 8155-B2/*Ae. tauschii* CIae 26
182	*T. polonicum* PI 223171/*Ae. tauschii* CIae 26
183	*T. polonicum* PI 225335/*Ae. tauschii* CIae 26
184	*T. polonicum* PI 254215/*Ae. tauschii* CIae 26
185	*T. polonicum* PI 272564/*Ae. tauschii* CIae 26
186	*T. polonicum* PI 272567/*Ae. tauschii* CIae 26
187	*T. polonicum* PI 272569/*Ae. tauschii* CIae 26
188	*T. polonicum* PI 272572/*Ae. tauschii* PI 268210
189	*T. polonicum* PI 290512/*Ae. tauschii* CIae 26
190	*T. polonicum* PI 290512/*Ae. tauschii* PI 268210
191	*T. polonicum* PI 349051/*Ae. tauschii* CIae 26
192	*T. polonicum* PI 349051/*Ae. tauschii* PI 268210
193	*T. polonicum* PI 349052/*Ae. tauschii* CIae 26
194	*T. turanicum* CI 11390/*Ae. tauschii* CIae 26
195	*T. turanicum* PI 185192/*Ae. tauschii* PI 268210
196	*T. turgidum* CItr 7772/*Ae. tauschii* CIae 26
197	*T. turgidum* CI 7863/*Ae. tauschii* CIae 26
198	*T. turgidum* CI 8115/*Ae. tauschii* CIae 26
199	*T. turgidum* CI 8115/*Ae. tauschii* PI 268210
200	*T. turgidum* CI 8115/*Ae. tauschii* AL8/78

Table 4.3. A list of target stem rust genes, name and type of markers, and primer sequence.

Gene			Marker		Primer sequence	References
Gene	Sources	Loc. †	Name	Type		
Sr2	*T. turgidum*	3BS	*Xgwm533*	SSR	AAGGCGAATCAAACGGAATA GTTGCTTTAGGGGAAAAGCC	Spielmeyer et al. (2003)
Sr13	*T. turgidum*	6AL	*Xbarc104b*	SSR	GCGCTTCCAAGGCTTAGAGGCT GGACCAGGCATGTCTACCCT	Simons et al. (2011)
Sr13	*T. turgidum*	6AL	*XCD926040*	EST‡	GTTGGCTTGGCTACTGCTTT AGCATTCAGCTCTGTGAGCA	Simons et al. (2011)
Sr13	*T. turgidum*	6AL	*XCK207347*	EST	TTACGGGCCACAAACAATCT AGCTCTCATCCATCCAGGAA	Simons et al. (2011)
Sr13	*T. turgidum*	6AL	*XBE403950*	EST	GGAACATGTTGACGCTGTTG AACACTGTTCCCGAAGTTGG	Simons et al. (2011)
Sr33/ Sr45/ SrTA 1662§	*Ae. tauschii*	1DS	*Xwmc222*¶	SSR	AAAGGTGCGTTCATAGAAAATTAGA AGAGGTGTTTGAGACTAATTTGGTA	Olson et al. (2013)
	Ae. tauschii	1DS	*Xwmc336*¶	SSR	GTCTTACCCCGCGATCTGC GCGGCCTGAGCTTCTTGAG	Olson et al. (2013)
	Ae. tauschii	1DS	*Xwmc432*¶	SSR	ATGACACCAGATCTAGCAC AATATTGGCATGATTACACA	Olson et al. (2013)

† loc. indicates gene location.
‡ EST means EST derived and DArT derived marker.
§ Positive control of *Sr33, SrTA1662, Sr45,* and *Sr46* are TA1600 (RL5288), TA1662, TA1599 and RL5289, and CIae25, respectively.
¶ *Xwmc222* produces a 160 bp band from TA1600 (RL5288) (*Sr33* positive control), CIae17, and two synthetic wheat (LDN/CIae17 and Rusty/CIae17); *Xwmc336* amplifies a 91 bp band from TA1600 (RL5288) (*Sr33* positive control), TA1662 (*SrTA1662* positvie control), TA1599 and RL5289 (*Sr45* positive control), and CIae25 (*Sr46* positive control), indicating that this marker may not differential *Sr33, Sr45, SrTA1662, and Sr46*; *Xwmc432* produce a 202 band for *Sr33* (CIae17 and its derived SHW), and a 174 band for *SrTA1662*, indicating that this marker is diagnostic.

Table 4.4. The infection types of 18 Langdon (LDN) and seven Rusty derived synthetic wheat to five races of stem rust pathogen.

Pedigree	TTKSK†		TRTTF†		TTTTF†		RHTSC†		TMLKC†	
	D‡	ABD‡	D	ABD	D	ABD	D	ABD	D	ABD
LDN/AL 8/78	3	2+3	3+	2	3+	2	32	;1-	3-2/1	21
LDN/CIae 17§	0;	2	;1	2-	;1	2+	;1	;1-	1-1	21
LDN/CIae 19	32	22+	11+	2	1+2	2+	3-2	;1-	1-1	12
LDN/CIae 22	1	22+	11+3	2	23-	2/3+	3-2	;1-	12	21
LDN/CIae 25	1;	2	;1+	2-	23	2+	21	;1-	12-	21
LDN/CIae 26	3+	33+	3+	2	3+	2/3	32	;1-	32	21
LDN/H80-101-4	3	3	3+	2	3+	2	32	1-1	32	21
LDN/PI 268210	1	2	0;1	2	0;	2	;1	;1-	12-	21
LDN/PI 476874	32+	3+	3+	2	3+	2+	32	;1	32	21
LDN/RL 5214	3+	33+	33+	2	3	2/3+	2+2	;1	32	21
LDN/RL 5263	33+	3+	3	2	3-	22+	2+2	;1	32	21
LDN/RL 5271§	33+	2+	;13LIF	2	3-1;	2	2+2	;1	22+	21
LDN/RL 5272	31	12-	;13	1;	3+	2	2+2/32	;1	12-	;1-1
LDN/RL 5286	3+	3+	3	2	3+	22+	32	;1-	34	21
LDN/TA 1645	1+	3 LIF	0/23	2-	23	22+	3-2	;1-	22+	21
LDN/TA 2377§	22-	2+	1	2	2	3/2	12	;1-	12	12
LDN/TA 2450	33+	3+	0/3-	2	3+	2+	2+2	;1-	32	21
LDN/TA 2474	;	2	1	2-	2-	2	12	;1-	;1-	12-
Rusty/CIae 17§	0;	2	;1	3	;1	3+	;1	21	1-1	21
Rusty/CIae 19	32	22+	11+	2+3	1+2	3	3-2	2+2	1-1	2+2
Rusty/CIae 22	1	22+	11+3	3	23-	3+	3-2	2+2	12	2+2
Rusty/CIae 25	1;	2	;1+	2+	23	4	21	2+2	12-	2+2
Rusty/CIae 26	3+	4	3+	3	3+	4	32	34	32	32
Rusty/PI 268210	1	2+	0;1	3	0;	22+	;1	12	12-	212+
Rusty/RL 5286	3+	4	3	4	3+	3+	32	32	34	34

Durum parents	TTKSK	TRTTF	TTTTF	RHTSC	TMLKC
Langdon (LDN)	2+	;2	;2-	;1-	12-
Rusty	3+	3+	4	34	34

† Infection type of plants to each race were scored according to description of Stackman et al. (1962); '-' = missing data; 'LIF' = low infection frequency; '/' = heterogeneous, the predominant type given first.

‡ D and ABD indicate *Ae. tauschii* parents and synthetic hexaploid wheat, respectively.

§ The fragments amplified by markers of *Sr33* or *SrTA1662* indicate the SHW and its *Ae. tauschii* parents may carry one of *Sr33* or *SrTA1662*.

Table 4.5. The infection types of CIae26, RL 5286, PI 476874, and PI 268210 derived SHW to five races.

Pedigree	TTKSK†		TRTTF†		TTTTF†		RHTSC†		TMLKC†	
	AB‡	ABD‡	AB	ABD	AB	ABD	AB	ABD	AB	ABD
8815-B1/CIae 26	3	4	;	3+;	3+	4	0;	3-2	0;	;23-
8815-B2/CIae 26	11+	2+	2	2+	2	2+	0	2+2	12	21
Iumillo/CIae 26§	0;	2+	;13-	3+	;1	4	;1	23-	;	32
CItr 14133-1/CIae 26	0;	;12	3+	4	3+	4		32	32	32
PI 74108-1/CIae 26	1	3+	2+	2+	;	2	;	;1-	;	12-
PI 94616-1/CIae 26§	33+	3+	2	22+	;	;	;	;1-	;	;12-
PI 94621-1/CIae 26	11+	3	2-	-	2	-	2+2	3-2	;1-	2+2
PI 94625-1/CIae 26§	-	3+	3+;	3	;	3	;	;12	21	3-2
PI 94626-1/CIae 26§	;1	2	2	2+	2-;	2-	;	;1	;	21
PI 94627-1/CIae 26§	3+	3	2	2+	;	;	;	;1-	;	;12
PI 94638-1/CIae 26§	3	3	2	22+	;	;	;	;1-	;	;12
PI 94648-1/CIae 26	2+	2+3	3+	3+	2+	2	1	;1-1	2+2	32
PI 94666-1/CIae 26	2-	2+3	2	3	3+	3	3-2	3-2	;1-	21
PI 94673-1/CIae 26	23	3+	2	2+3	;3	2+3	;12	;23-	;1-	2+2
PI 94675-1/CIae 26§	1+;	3	2	3+	;	2	;	;1-	;	21
PI 94738-1/CIae 26§	1+;	3	2	3	;	2-	;	;1-	;	21
PI 197493-1?/CIae 26	-	3+	-	3	-	2	-	;1-	-	21
PI 225332-1/CIae 26§	3	3+	3	3	;	3	;2	;12	21	3-2
PI 254165-1/CIae 26	2+3;	3+	3;	3	;	;1+	;1	;1	2+23-	3-2
PI 254167-1/CIae 26§	23	3	23	3-	;	;13-	;	;122+	21	3-2
PI 254189-1/CIae 26§	22+	3	2	3	;2+	3	21	22+	12-	21
PI 254190-1/CIae 26§	1+	3	2	3	;	2-	;	;1-	;1-1	21
PI 349046-1/CIae 26§	2-	2+	2-	2+3	;1+	3	;12	213-/32	;1-	21
PI 352548-1/CIae 26	2-;	2+	2	2+	2	2+	21	23-	1-1	21
PI 355507-1/CIae 26	3+	3+	3-	3	;	2-	;1	;1-1	;	;12
PI 377655-1/CIae 26§	3+	3+	3+	3+	3	3+	21	23-/32	;	;23
PS5/RL 5286	0;	;1-	3+	4	3	4	21/3-2	3-2	212+	2+2
PI 94616-1/RL 5286§	33+	3	2	2+3	;	;	;	;1-	;	;1-
PI 94621-1/RL 5286	11+	22+	2-	3	2	4	2+2	2+2	;1-	2+2
PI 94673-1/RL 5286	23	3	2	2+3	;3	2+3	;12	2+2	;1-	21
PI 225332-1/RL 5286§	3	3+	3	3+	;	3+	;2	123-	21	2+3-2
PI 254165-1/RL 5286	2+3;	3+	3;	2+3	;	2+3	;1	;122+	2+23-	2+23-
PI 349046-1/RL 5286§	2-	2+	2-	3	;1+	3	;12	2+21	;1-	21
PI 352548-1/RL 5286	2-;	2+	2	2+	2	2+	21	23-	1-1	21
PI 355507-1/RL 5286	3+	4	3-	3+	;	2-	;1	12	;	;
PI 283888/PI 476874	32	3+	4	3+	2+3	4	2+2	321	21	3-2
PI 481521/PI 476874	3+	3+	4	4	3+	4	32	34	32	34

Table 4.5. The infection types of CIae26, RL 5286, PI 476874, and PI 268210 derived SHW to five races (continued).

Pedigree	TTKSK†		TRTTF†		TTTTF†		RHTSC†		TMLKC†	
	AB‡	ABD‡	AB	ABD	AB	ABD	AB	ABD	AB	ABD
CItr 7687-1/PI 268210§	3;	2-	3;	3	;	2-	;	;1	21	21
CItr 14133-1/PI 268210	0;	;1	3+	2+	3+	2		12	32	12
PI 74108-1/PI 268210	1	2	2+	2	;	2-	;	;1-	;	1-1
PI 94616-1/PI 268210§	33+	3+	2	2+	;	;	;	;1-	;	;12
PI 94621-1/PI 268210	11+	2	2-	22+	2	2+	2+2	12	;1-	21
PI 94625-1/PI 268210§	-	22+	3+;	23-	;	;1	;	;1	21	12
PI 94626-1/PI 268210§	;1	2-	2	2+	2-;	2	;	1-1	;	12
PI 94627-1/PI 268210§	3+	2	2	2	;	;	;	;	;	;12
PI 94635-1/PI 268210	2+3	22+	3+	2+3	;	2-	;	;1-	;1-1	21
PI 94666-1/PI 268210	2-	2	2	2+	3+	2	3-2	21	;1-	21
PI 94673-1/PI 268210	23	2	2	22+	;3	2-	;12	;1	;1-	21
PI 94675-1/PI 268210	1+;	2	2	2+	;	2-	;	;1-	;	21
PI 94738-1/PI 268210§	1+;	2	2	2+	;	2-	;	;1-	;	21
PI 254165-1/PI 268210	2+3;	22+	3;	3-	;	;	;1	;1-	2+23-	22+
PI 254189-1/PI 268210§	22+	2	2	2	;2+	2-	21	;12	12-	21
PI 349043-1/PI 268210	2	2	2	22+	1;	2-;	;21	;1-	;	12
PI 349046-1/PI 268210§	2-	2	2-	22+	;1+	2	;12	;1-1	;1-	21
PI 377655-1/PI 268210§	3+	2+	3+	3	3	2	21	3-2	;	;12

Ae. tauschii parents	TTKSK	TRTTF	TTTTF	RHTSC	TMLKC
CIae 26	3+	3+	3+	32	32
RL 5286	3+	3	3+	32	34
PI 476874	32+	3+	3+	32	32
PI 268210	1	0;1	0;	;1	12-

† Infection type of plants to each race were scored according to description Stackman et al. (1962); '-' = missing data; 'LIF' = low infection frequency; '/' = heterogeneous, the predominant type given first.

‡ AB and ABD indicate tetraploid wheat parents and synthetic hexaploid wheat, respectively.

§ A 120 bp fragment amplified by *Xgwm533* indicates that the SHW and its tetraploid parents may carry *Sr2*.

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APPENDIX

Table A1. Seedling infection types (ITs) to three stem rust races TTKSK, TRTTF, and TTTTF of 177 wheat cultivars and breeding lines.

Line	Pedigree or description	2n[†]	Gen[‡]	Infection types[§]		
				TTKSK	TRTTF	TTTTF
Z1 (09Ae 1)	Zhong 5/4/Zhong 7606 (F_3)	42		4	3+	4
Z1 (09Ae 26)	Zhong 5/4/Zhong 7606 (F_3)	43+2t		4	3+	4
Z2 (09Ae 3-4)	Zhong 5/2-4/Wan 7107 (F_3)	42		4	2+	-
Z2 (08Ae 455)	Zhong 5/2-4/Wan 7107 (F_3)			4	2+	4
Z2 (08Ae 456)	Zhong 5/2-4/Wan 7107 (F_3)			2+3	2	4
Z2 (08Ae 457)	Zhong 5/2-4/Wan 7107 (F_3)	42/41		2+	2+	4
Z3 (09Ae 9)	Zhong 5/2-4/Wan 7107 (F_3)			2+3	2-	3+
Z3 (09Ae 6-7)	Zhong 5/2-4/Wan 7107 (F_3)	44		3	2	4
Z4	Zhong 5/2-4/Wan 7107 (F_3)	44		1+	1N	1+
Z5	Zhong 5/2-4/Wan 7107 (F_3)	43-44		1+	1+	;13-
Z6	Zhong 5/4/Zhong 8423 (F_3)	44		;1	;2-	2
Yi4212	77-5433/Zhong 5	42		2	2	2+3
TAI11 (08Ae 671)	Zhong 2 Progeny	42		4	2	-
TAI11 (08Ae 674-675)	Zhong 2 Progeny	44		4	2	2+3
TAI12 (08Ae 676-677)	Zhong 2 Progeny	42		2+3	2	22+
TAI12 (09Ae 28)	Zhong 2 Progeny	43		3	2+	22+
TAI14	Zhong 2 Progeny	42+2t		4	3-	4
TAI15	Zhong 2 Progeny			2+	2	3+
TAI22	Zhong 3, 4, 5 Progeny	43-44		2+	2+	3+
TAI23 (08Ae 701)	Zhong 3, 4, 5 Progeny			3+	2+	3+
TAI23 (08Ae 702-703)	Zhong 3, 4, 5 Progeny	43		3+	3	-
TAI24 (08Ae 705)	Zhong 3, 4, 5 Progeny			3+	2	22+
TAI24 (08Ae 706)	Zhong 3, 4, 5 Progeny			3+	2	2+3
TAI26 (08Ae 709)	Zhong 3, 4, 5 Progeny			2+	2+	22+
TAI26 (08Ae 711)	Zhong 3, 4, 5 Progeny			2+	2+	22+
TAI27	Zhong 3 Progeny	44		;1+	2+	3+
XWC11-58	CS-*Th. elongatum* 1E(1A) DS			4	3	4
XWC11-59	CS-*Th. elongatum* 1E(1B) DS			4	3	3+
XWC11-60	CS-*Th. elongatum* 1E(1D) DS			4	4	4
XWC11-61	CS-*Th. elongatum* 2E(2A) DS			4	3+	3
XWC11-62	CS-*Th. elongatum* 2E(2B) DS			4	3+	3
XWC11-63	CS-*Th. elongatum* 2E(2D) DS			4	3+	3
XWC11-64	CS-*Th. elongatum* 3E(3A) DS			2+3	3+	2+/4
XWC11-65	CS-*Th. elongatum* 3E(3B) DS			2+3	2+3	3

Table A1. Seedling infection types (ITs) to three stem rust races TTKSK, TRTTF, and TTTTF of 177 wheat cultivars and breeding lines (Continued).

Line	Pedigree or description	2n[†]	Gen[‡]	Infection types[§]		
				TTKSK	TRTTF	TTTTF
XWC11-66	CS-*Th. elongatum* 3E(3D) DS			2+3	3	3
XWC11-67	CS-*Th. elongatum* 4E(4A) DS			3+	3+	4
XWC11-68	CS-*Th. elongatum* 4E(4D) DS			3+	3+	4
XWC11-69	CS-*Th. elongatum* 5E(5B) DS			3	4	4
XWC11-70	CS-*Th. elongatum* 5E(5D) DS			3	3	22+
XWC11-71	CS-*Th. elongatum* 6E(6A) DS			3+	3+	4
XWC11-72	CS-*Th. elongatum* 6E(6B) DS			3+	3+	4
XWC11-73	CS-*Th. elongatum* 6E(6D) DS			3+	3+	4
XWC11-74	CS-*Th. elongatum* 7E(7A) DS			2	2	2
XWC11-75	CS-*Th. elongatum* 7E(7B) DS			2	2-	2
XWC11-76	CS-*Th. elongatum* 7E(7D) DS			2	2	2+
K11463	TC-*Th. ponticum* DS $7el_1$(7D)			22+	-	-
K2620	TC-*Th. ponticum* DS $7el_2$(7D)			;1/2/2+2/3+	-	-
XC04A-1030	CS-*Leymus racemosus* DA			4	3+	4
XC04A-1033	CS-*Leymus racemosus* DA			3+	3+	3
TA6651	CS-*Ae. speltoides* 1S(1B) DS			;1	3+	4
TA6652	CS-*Ae. speltoides* 2S(2B) DS			2- LIF	2	2
TA6653	CS-*Ae. speltoides* 3S(3B) DS			3+	4	3
TA6654	CS-*Ae. speltoides* 4S(4B) DS			4	4	4
TA6656	CS-*Ae. speltoides* 6S(6B) DS			4	4	4
TA6657	CS-*Ae. speltoides* 7S(7B) DS			2+3	4	4
Wildcat	NB113/Glenlea			3+	3	3+
Liaochun 10	Hybrid X Liao 70181-2			3+	3+	3+
Jinqiang 2	Wildcat/Liaochun 10			4	3+	3
Jinqiang 3	Liaochun 10/Wildcat			4	2+/4	3/2+
Jinqiang 4	Liaochun 10/Wildcat			4	2+	3-
Jinqiang 5	Liaochun 10/Wildcat			4	2+/4	4
Jinqiang 6	Liaochun 10/Wildcat			3+	22+	2+3/4
Jin 199				3+	2	2
Kulm	HRSW cultivar			2	2	;
Erik	HRSW cultivar			3+	2+3	3
KE6	Kulm/Erik RIL 6			3+	3	2+
KE14	Kulm/Erik RIL 14			3+	3	2+
KE16	Kulm/Erik RIL 16			2-	2-	2
KE17	Kulm/Erik RIL 17			3	2+3	23-

Table A1. Seedling infection types (ITs) to three stem rust races TTKSK, TRTTF, and TTTTF of 177 wheat cultivars and breeding lines (continued).

Line	Pedigree or description	2n[†]	Gen[‡]	Infection types[§]		
				TTKSK	TRTTF	TTTTF
KE21	Kulm/Erik RIL 21			;1 LIF	2-	0;
KE23	Kulm/Erik RIL 23			2- LIF	2-	2-
KE33	Kulm/Erik RIL 33			;	2-	;2-
KE89	Kulm/Erik RIL 89			;1	2-	;
TA4152-19	DVERD 2/*Ae.tauschii* (221)			3+	23	4
Alsen	ND674//ND2710/ND688			3+	2+	;1
12P 738	TA4152-19/3*Alsen		BC_2F_4	3+	3+	;1
TA4154-27	Scoop 1			2-	2-	;1
TA2516	*Ae. tauschii*			2+	3	3
TA4152-60	Scoop 1/*Ae.tauschii* (358) TA2516			2+	2	2-
12P594	TA4152-60/3*Alsen		BC_2F_4	3+	2	13-
12P600	TA4152-60/3*Alsen		BC_2F_4	4	2+	;1+
12P726	TA4152-60/3*Alsen		BC_2F_4	3+	3	;1
Alsen-19	TA4152-19/6*Alsen			4	3	0;
Alsen-60	TA4152-60/6*Alsen			3+	3	0;
W7984	Altar 84/*Ae. tauschii* WPI 219			22+	2-;	2
TA4154-4	Altar 84			2	2-	1;
Glenn	ND 2831/Steele-ND			3+	3	;13
12P618	Glenn*2/W7984/3/Glenn			3+	3	1+;
12P729	Glenn*2/W7984/3/Glenn			3+	2+3	;1+
12P732	Glenn*2/W7984/3/Glenn			4	2+	;13
AESR1	*Th. ponticium*			;	;/1	0;
Jinan177	*T. aestivium*			4	;	2
X004	Jinan177-AESR1			3	2-;	2-2
X012	Jinan177-AESR1			4	2-	2
X023	Jinan177-AESR1			4	2-;	22+
X025	Jinan177-AESR1			2+	4	4
X027	Jinan177-AESR1			4	2+	2
X031	Jinan177-AESR1			2+	3+	4
X031-1	Jinan177-AESR1			2+	3+	3
X042	Jinan177-AESR1			4	2-	2
X068	Jinan177-AESR1			3	4	4
X085	Jinan177-AESR1			2+	4	4
X090	Jinan177-AESR1			4	2-	2
X091	Jinan177-AESR1			4	2-;	2

Table A1. Seedling infection types (ITs) to three stem rust races TTKSK, TRTTF, and TTTTF of 177 wheat cultivars and breeding lines (continued).

Line	Pedigree or description	2n[†]	Gen[‡]	Infection types[§]		
				TTKSK	TRTTF	TTTTF
X106	Jinan177-AESR1			2+	4	-
X116	Jinan177-AESR1			3+	2-	2-2
X138	Jinan177-AESR1			2+	4	4
X144	Jinan177-AESR1			2+	4	4
X145	Jinan177-AESR1			2+	2-	-
X150	Jinan177-AESR1			2+	4	4
X159	Jinan177-AESR1			4	4	4
X182	Jinan177-AESR1			4	4	4
X188	Jinan177-AESR1			4	2	2
X194	Jinan177-AESR1			4	2	2-
ShanRong 1	Jinan177-AESR1			3+	2	2
ShanRong 3	Jinan177-AESR1			2+/4	2	2
Jinnong 6	Chinese winter wheat cultivar			22+	4	4
Jingdong 8	Chinese winter wheat cultivar			3+	2-	2
Nongda 211	Chinese winter wheat cultivar			3+	2-	2-
Zhongmai 175	Chinese winter wheat cultivar			3+	3+	4/2
Shimai 15	Chinese winter wheat cultivar			2+3	2-	2
Zhouheimai 1	Chinese winter wheat cultivar			3+	2-	2-
Zhoumai 16	Chinese winter wheat cultivar			0/2+	2-	2
Zhoumai 17	Chinese winter wheat cultivar			3	2-	2
Zhoumai 18	Chinese winter wheat cultivar			3 LIF	2-	2
Zhoumai 19	Chinese winter wheat cultivar			3	2	4
Zhoumai 20	Chinese winter wheat cultivar			3	2	4
Zhoumai 21	Chinese winter wheat cultivar			3	2+	3
Zhoumai 22	Chinese winter wheat cultivar			3+	2-	2
Zhoumai 23	Chinese winter wheat cultivar			4	4	4
Zhoumai 24	Chinese winter wheat cultivar			3	2-	2
Zhoumai 25	Chinese winter wheat cultivar			0	2-	2-;
Zhoumai 26	Chinese winter wheat cultivar			3-	2-	2
Zhoumai 27	Chinese winter wheat cultivar			3/;	2-	2
Jinan 17	Chinese winter wheat cultivar			2	2+	4
Jimai 20	Chinese winter wheat cultivar			2	4	4
Jimai 22	Chinese winter wheat cultivar			2+/3+	3+	4
Yangmai 16	Chinese winter wheat cultivar			3+	2+	4
Zheng 9023	Chinese winter wheat cultivar			4	2+	3

Table A1. Seedling infection types (ITs) to three stem rust races TTKSK, TRTTF, and TTTTF of 177 wheat cultivars and breeding lines (continued).

Line	Pedigree or description	2n[†]	Gen[‡]	Infection types[§]		
				TTKSK	TRTTF	TTTTF
Carpio	ND durum line			2-	2-	;
Joppa	ND durum line			2-	;/2-	;
Tioga	Plaza/Maier			2-	2-	;
Alkabo	D901247/D89263			2	0	;
Grenora	D901260/D901419			2	0	;
Maier	D8193/D8335			2-	0;	;
Lebsock	Munich/D8469			2-	-	;
Ben	D8024/Monroe			2-	0;	;
Divide	Ben/D901282//Belzer			4	0;	3-
PI 61102	*T. turgidum* subsp. *carthlicum*			0;	4	3
PI 94748	*T. turgidum* subsp. *carthlicum*			;13	3+	2+
PI 41025	*T. turgidum* subsp. *dicocum*			4	3+	4
PI 254188[¶]	*T. turgidum* subsp. *dicocum*			3+	33+	33+
PI 254193[¶]	*T. turgidum* subsp. *dicocum*			3+	3+	3
PI 272527[¶]	*T. turgidum* subsp. *dicocum*			33+	3+3;	3+;
PI 277012	Spring wheat			3+	3+	4
12P746	Lebsock/PI277012//Lebsock		F_7	3+	0;	3-
12P749	Lebsock/PI 277012//Lebsock		F_7	33+	0;	11+
12P754	Lebsock/PI 277012//Lebsock		BC_1F_7	3+	0	3+
12P758	Lebsock/PI 277012//Lebsock		BC_1F_7	3+	2	3
12P760	Lebsock/PI 277012//Lebsock		BC_1F_7	3+	0	2+3
12P762	Lebsock/PI 277012//Lebsock		BC_1F_6	3+	0	;1
12P766	Lebsock/PI 277012//Lebsock		BC_1F_7	3	0	3
12P768	Mountrail/PI 277012//Divide		BC_1F_6	4	0	3+
12P770	Mountrail/PI 277012//Divide		BC_1F_7	3+	2	4
12P772	Ben/PI 277012//Ben		BC_1F_7	2	2-	;1
12P776	Divide/PI 272527/Divide		BC_1F_7	3+	0;	;
12P786	Divide/PI 272527/Divide		BC_1F_8	3+	0	;
12P796	Divide/PI 272527/Divide		BC_1F_8	3+	0;	;
12P802	Divide/PI 254193/Divide		BC_1F_7	3+	0;	4
12P804	Lebsock/PI 254188/Alkabo		BC_1F_8	3	0;	3+
12P633	Ben/PI 41025//Maier		BC_1F_{10}	2	0;	2
12P636	Ben/PI 41025//Maier		BC_1F_{10}	2	0;	;1
12P642	Lebstock/PI 94748//Lebstock		BC_1F_{10}	2	0;	2
12P645	Lebsock/PI 61102		DH[‡]	;1 LIF	2+	2-

Table A1. Seedling infection types (ITs) to three stem rust races TTKSK, TRTTF, and TTTTF of 177 wheat cultivars and breeding lines (continued).

Line	Pedigree or description	2n†	Gen‡	Infection types§		
				TTKSK	TRTTF	TTTTF
12P660	Lebsock/08F130//Alkabo		BC_1F_6	2	0;	;
12P666	Grenora/08F286//Grenora		BC_1F_8	2	0;	;
12P798	Grenora/08F286//Grenora		BC_1F_8	2	0	0;

† ‘2n’ indicates chromosome number of Z lines and T lines.
‡ ‘Gen.’ indicates generation; DH = double haploid.
§ Infection types were scored using system proposed by Stakman et al. (1962). In our study, infection types of 0 to 2+ were considered resistance, whereas IT of 3 and 4 were considered susceptibility. LIF = low infection frequency; N = necrosis; – = missing data.
¶ The data for PI 254188, PI 254193, and PI 272527 were based on Olivera et al. (2012).
# Durum lines 08F130 and 08F286 were the F_4 plants with a pedigree Ben/PI 41025//Maier.

Table A2. Marker haplotypes of wheat cultivars and lines with resistance to TTKSK.

Line name	*Sr2-Xgwm533*	*Sr22-Xwmc633*	*Sr22-XcslH81-BM&cslH81-AG*	*Sr28-XwPt-7004-PCR*	*Sr28-Xwmc332*	*Sr31-Xiag95*	*Sr31-Xscm9*	*Sr42-Xbarc183*	*Sr42-XFSD-RSA*	*Sr24-Xbarc71*	*Sr24-XSr24#12*	*Sr25-XBF145935*	*Sr25-XGb*	*Sr26-Sr26-#43&BE518379*	*Sr43-cfa2040*	*Sr43-Xrwgs30*	*Sr32-Xbarc55*	*Sr39-Sr39-#22*	*Sr39-Xrwgs27*	*Sr47-Xrwgs33*	*Sr47-Xgwm501*
CS	-†	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMPG6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Snowmass (*Sr2*)	+†	-	-	-	-	-	-	-	-												
W2691Sr13 (*Sr13*)																					
St464-C1 (*Sr13*)																					
U5924-10-6 (*Sr22*)	-	+	+	-	-	-	-	-	-												
PI 520490 (*Sr24*)										+	+	-	-	-	-	-					
Wheatear (*Sr25*)										-	-	+	+	-	-	-					
WA-1 (*Sr26*)										-	-	-	-	+	-	-					
W2691/Sr28kt (*Sr28*)	+	-	-	+	+	-	-	-	-												
Sr31/6*LMPG6 (*Sr31*)	-	-	-	-	-	+	+	-	-												
U5926-2-8 (*Sr32*)																	+	-	-	-	-
Sr36-5 (*Sr36*)	+	-	-	-	-	-	-	-	-												
RWG1 (BC2F3) (*Sr39*)																	-	+	+	-	-
U5941-1-6 (*Sr40*)	+	-	-	-	-	-	-	-	-												
HY438 (*Sr42/Cad*)	+	-	-	-	-	-	-	+	+												
RWG34 (*Sr43*)										-	-	-	-	-	+	+					
RWG35 (*Sr47*)																	+	-	-	+	+
Z2	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
Z3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
Z4	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
Z5	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
Z6	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-					
Yi4212	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
TAI12	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
TAI15	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
TAI22	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-					
TAI26	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
TAI27	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					

Table A2. Marker haplotypes of wheat cultivars and lines with resistance to TTKSK (continued).

Line name	*Sr2-Xgwm533*	*Sr22-Xwmc633*	*Sr22-XcsIH81-BM&csIH81-AG*	*Sr28-XwPt-7004-PCR*	*Sr28-Xwmc332*	*Sr31-Xiag95*	*Sr31-Xscm9*	*Sr42-Xbarc183*	*Sr42-XFSD-RSA*	*Sr24-Xbarc71*	*Sr24-XSr24#12*	*Sr25-XBF145935*	*Sr25-XGb*	*Sr26-Sr26-#43&BE518379*	*Sr43-cfa2040*	*Sr43-Xrwgs30*	*Sr32-Xbarc55*	*Sr39-Sr39-#22*	*Sr39-Xrwgs27*	*Sr47-Xrwgs33*	*Sr47-Xgwm501*
XWC11-64										+	-	-	-	-	-	-					
XWC11-65										+	-	-	-	-	-	-					
XWC11-66										+	-	-	-	-	-	-					
XWC11-74										-	-	-	-	-	-	-					
XWC11-75										-	-	-	-	-	-	-					
XWC11-76										-	-	-	-	-	-	-					
K11463	+	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-					
K2620	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+					
TA6651																	-	-	-	-	-
TA6652																	-	+	-	-	-
TA6657																	-	-	-	-	-
Kulm	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-					
Erik	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
KE16	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-					
KE21	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-					
KE22	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-					
KE33	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-					
KE89	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-					
TA4154-27	-	-	-	+	-	-	-	-	-												
TA2516	-	-	-	-	-	-	-	-	-												
TA4152-60	-	-	-	+	-	-	-	-	-												
TA4154-4	-	-	-	+	-	-	-	-	-												
W7984	-	-	-	+	-	-	-	-	-												
AESR1										+	+	+	+	+	-	-					
Jinan177	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-					
X025	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
X031-1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
X085	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
X138	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
X144	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
X145	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-					
X150	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					

Table A2. Marker haplotypes of wheat cultivars and lines with resistance to TTKSK (continued).

Line name	*Sr2-Xgwm533*	*Sr22-Xwmc633*	*Sr22-XcsIH81-BM&csIH81-AG*	*Sr28-XwPt-7004-PCR*	*Sr28-Xwmc332*	*Sr31-Xiag95*	*Sr31-Xscm9*	*Sr42-Xbarc183*	*Sr42-XFSD-RSA*	*Sr24-Xbarc71*	*Sr24-XSr24#12*	*Sr25-XBF145935*	*Sr25-XGb*	*Sr26-Sr26-#43&BE518379*	*Sr43-cfa2040*	*Sr43-Xrwgs30*	*Sr32-Xbarc55*	*Sr39-Sr39-#22*	*Sr39-Xrwgs27*	*Sr47-Xrwgs33*	*Sr47-Xgwm501*
Jinnong 6	-	-	-	-	-	-	-	-	-												
Shimai 15	+	-	-	-	-	+	+	+	-												
Zhoumai 16	-	-	-	-	-	+	+	+	-												
Zhoumai 25	+	-	-	-	-	+	+	-	-												
Zhoumai 26	+	-	-	-	-	+	+	+	-												
Zhoumai 27	-	-	-	-	-	+	+	+	-												
Jinan 17	-	-	-	-	-	-	-	+	-												
Jimai 20	-	-	-	-	-	-	-	-	-												
Carpio	-																				
Joppa	-																				
Tioga	-																				
Alkabo	-																				
Grenora	-																				
Maier	-																				
Lebsock	-																				
Ben	-																				
LDN 16	-																				
PI 41025	+																				
PI 61102	-																				
PI 94748	-																				
PI 277012	-																				
12P772	-																				
12P633	+																				
12P636	+																				
12P642	-																				
12P645	-																				
12P660	+																				
12P798	+																				
12P666	-																				

† - / + indicates negative/positive.

Table A3. The infection types of 80 synthetic wheat and their parents to four local races.

Pedigree	MCCFC†			QTHJC†			RKQQC†			TPMKC†		
	AB‡	D‡	ABD‡	AB	D	ABD	AB	D	ABD	AB	D	ABD
LDN/AL8/78	12	32	;1-1	1-1	32	12	;1-	3-2	1-1	12	34	12
LDN/CIae 17§		1-1	1-1		1	12		;1-1	1-1		12	12
LDN/CIae 19		23-	1-1		12	12		2+2	1-1		12	21
LDN/CIae 22		2+2	1-1		12	12		22+	1-1		12	21
LDN/CIae 25		22+	;1-1		12	21		22+	1-1		12	21
LDN/CIae 26		3-2	1-1		3-2	12		3-2	1-1		34	21
LDN/H80-101-4		32	;1-1		32	12		32	1-1		32	12
LDN/PI 268210		12	1-1		;1	12		12	1-1		12	21
LDN/PI 476874		32	1-1		32	12		32	1-1		3-2	21
LDN/RL5214		32	1		32	21		32	1-1		3-2	21
LDN/RL5263		32	1-1		2+2	12		3-2	1		21	21
LDN/RL5271§		21	1-1		21	12		2+2	1		12	21
LDN/RL5272		3-2	;1-1		22+	12		3-2	1-1		12	12
LDN/RL 5286		3-2	1-1		32	12		32	1-1		34	21
LDN/TA 1645		3-2	12		21	12		2+2	1-1		12	21
LDN/TA 2377§		2+2	1-1		21/3-2	21		21	1-1		12	12
LDN/TA 2450		3-2	1-1		32	12		3-2	1-1		21	212+
LDN/TA 2474		2+2	;1-1		21	12		12	;1-		;1-	12
Rusty/CIae 17§	32	1-1	12	34	1	21	32	;1-1	21	32	12	21
Rusty/CIae 19		23-	23-		12	21		2+2	2+23		12	3-2
Rusty/CIae 22		2+2	23-		12	2+2		22+	32		12	3-2
Rusty/CIae 25		22+	3-2		12	3-2		22+	2+23-		12	2+23-
Rusty/CIae 26		3-2	3-2		3-2	3-2		3-2	34		34	32
Rusty/PI 268210		12	12		;1	21		12	34		12	23
Rusty/RL 5286		3-2	32		32	32		32	34		34	32
8815-B1/CIae 26	;12	3-2	3-2	0;	3-2	3-2	;	3-2	;23-	0;	34	;23-
8815-B2/CIae 26	12		2+2	2+2		2+2/34	12		1	;1-		212+
Iumillo/CIae 26¶	;1-		;123-	;		3-2	32		32	;32		32
CItr 14133-1/CIae 26	;		32	32		34	32		32	3-2		32
PI 74108-1/CIae 26	;12		12	21		2+2	;1-1		21	;1		21
PI 94616-1/CIae 26¶	;1-		;1-	12		21	;		;1	22+1		32
PI 94621-1/CIae 26	3-21		3-2	3-2		32	12		21	;1-		12
PI 94625-1/CIae 26¶	2+2		3-2	3-2		2+2	2+2		3-2	2+3		32
PI 94626-1/CIae 26¶	;		12	12		23-	;1-		21	;1-		22+
PI 94627-1/CIae 26¶	;		;1-	21		12	;		;1-	2+23		3-2
PI 94638-1/CIae 26¶	;1-		;1-1	21		12	;		;1-	2+23		2+2

Table A3. The infection types of 80 synthetic wheat and their parents to four local races (continued).

Pedigree	MCCFC†			QTHJC†			RKQQC†			TPMKC†		
	AB‡	D‡	ABD‡	AB	D	ABD	AB	D	ABD	AB	D	ABD
PI 94648-1/CIae 26	12	3-2	12	12	3-2	12	122+	3-2	21	22+	34	3-2
PI 94666-1/CIae 26	3-2		3-2	2+2		2+2	1-1		21	;1-		21
PI 94673-1/CIae 26	2+2		2+2	3-2		3-2	1-1		21	;1-		213-
PI 94675-1/CIae 26¶	;1-1		21	2+2		32	;1-		12	;1-		12
PI 94738-1/CIae 26¶	;1-		12	21		3-2	1-1		21	;1-		12
PI 197493-1?/CIae 26			21			23-			2-1			12
PI 225332-1/CIae 26¶	2+2		3-2	32		2+2	122+		2+2	2+23		3-2
PI 254165-1/CIae 26	21		2+2	3-2		2+2	12		3-2	2+23		2+2
PI 254167-1/CIae 26¶	21		21	2+2		2+2	12		2+23-	2+23		2+2
PI 254189-1/CIae 26¶	3-2		34	3-2		23-	1-1		21	12		12
PI 254190-1/CIae 26¶	;1-		21	21		2+2/32	;1-		1	1-1		12
PI 349046-1/CIae 26¶	3-2		3-2	3-2		3-2	;1-		2	1-1		12
PI 352548-1/CIae 26	12		2+2	21		2+2	1-1		2-1	1-1		12
PI 355507-1/CIae 26	;1		;12	12		22+	;		;1-1	0;		2+23
PI 377655-1/CIae 26¶	2+2		32	12		2+2	21		212+	32		3-2
PS5/RL 5286	12	3-2	12	21	32	2+2	21	32	22+	21	34	3-2
PI 94616-1/RL 5286¶	;1-		1-1	12		21	;		1-1	22+1		2+2
PI 94621-1/RL 5286	3-21		32	3-2		3-2	12		21	;1-		21
PI 94673-1/RL 5286	2+2		2+2	3-2		3-2	1-1		12	;1-		21
PI 225332-1/RL 5286¶	2+2		3-2	32		21	122+		2+2	2+23		3-2
PI 254165-1/RL 5286	21		2+2	3-2		21	12		2+23-	2+23		3-2
PI 349046-1/RL 5286¶	3-2		3-2	3-2		23-	;1-		1-1	1-1		12
PI 352548-1/RL 5286	12		2+2	21		212+	1-1		1-1	1-1		12
PI 355507-1/RL 5286	;1		21	12		212+	;		12-	0;		32
PI 283888/PI 476874	12	32	2+2	21	32	32	21	32	32/2+2	12	3-2	32
PI 481521/PI 476874	34		32	32		32	32		32	321		32
CItr 7687-1/PI 268210¶	21	12	21	2+2	;1	22+	21	12	212+	32	12	2+12
CItr 14133-1/PI 268210	;		;1-	32		;12	32		2+21;	3-2		213-
PI 74108-1/PI 268210	;12		12	21		21	;1-1		12	;1		21
PI 94616-1/PI 268210¶	;1-		;1-1	12		;12	;		;1-	22+1		3-2
PI 94621-1/PI 268210	3-21		21	3-2		21	12		21	;1-		21
PI 94625-1/PI 268210¶	2+2		21	3-2		21	2+2		22+	2+3		2+23-
PI 94626-1/PI 268210¶	;		12	12		21	;1-		21	;1-		12
PI 94627-1/PI 268210¶	;		12	21		12	;		1-1	2+23		21
PI 94635-1/PI 268210	;1		12	21		12	1-1		21	12		21
PI 94666-1/PI 268210	3-2		21	2+2		2+2	1-1		21	;1-		21

Table A3. The infection types of 80 synthetic wheat and their parents to four local races (continued).

Pedigree	MCCFC†			QTHJC†			RKQQC†			TPMKC†		
	AB‡	D‡	ABD‡	AB	D	ABD	AB	D	ABD	AB	D	ABD
PI 94673-1/PI 268210	2+2	12	12	3-2	;1	21	1-1	12	12	;1-	12	12
PI 94675-1/PI 268210	;1-1		21	2+2		21	;1-		12	;1-		21
PI 94738-1/PI 268210¶	;1-		21	21		2+2	1-1		21	;1-		12
PI 254165-1/PI 268210	21		21	3-2		21	12		22+	2+23		21
PI 254189-1/PI 268210¶	3-2		21	3-2		21	1-1		1-1	12		12
PI 349043-1/PI 268210	3-2		21	2+2		21	1-1		21	;1		2
PI 349046-1/PI 268210¶	3-2		21	3-2		122+	;1-		2-1	1-1		12
PI 377655-1/PI 268210¶	2+2		;12/3-2	12		212+	21		21	32		2+213-

† Infection type of plants to each race were scored according to description Stackman et al. (1962); - = data not available;
‡ AB, D, and ABD indicate tetraploid wheat parents, *Ae. tauschii* parents, and synthetic hexaploid wheat, respectively.
§ The SHW and its *Ae. tauschii* parents amplified marker band linked to one of *Sr33* or *SrTA1662*.
¶ The SHW and its tetraploid parents amplified a 120 bp marker band linked to *Sr2*.