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Molecular cytogenetic characterization of four partial wheat-*Thinopyrum ponticum* amphiploids and their reactions to *Fusarium* head blight, tan spot, and *Stagonospora nodorum* blotch

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Abstract Four wheat (*Triticum aestivum* L.)-*Thinopyrum ponticum* derivatives SS5 (PI604926), SS156 (PI604947), SS363 (PI604970), and SS660 (PI604879), were identified as resistant to *Fusarium* head blight (FHB), a serious fungal disease of wheat worldwide. Seedling reactions to tan spot and *Stagonospora nodorum* blotch (SNB), two important foliar diseases of wheat, suggest that these four derivatives are resistant to tan spot and two of them (SS5 and SS156) are resistant to SNB. Fluorescent genomic in situ hybridization (FGISH) patterns of mitotic chromosomes indicate that these four derivatives are partial wheat-*Th. ponticum* amphiploids, each with a total of 56 chromosomes, though with different amounts of *Th. ponticum* chromatin. These four amphiploids were hybridized with each other to determine homology between the *Th. ponticum* genomes in each of the amphiploids. Analysis of chromosome pairing in the F_1 hybrids using FGISH suggests that each amphiploid carries a similar set of *Th. ponticum* chromosomes. These wheat-*Th. ponticum* amphiploids represent a potential novel source of resistance to FHB, tan spot, and SNB for wheat breeding.

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Introduction

Common wheat (*Triticum aestivum* L., $2n = 6\times = 42$, AABBDD genomes) is represented by a narrow germplasm base, which causes vulnerability to biotic and abiotic stresses (Sears 1981; Jiang et al. 1994; Friebe et al. 1996). This narrow gene pool minimizes opportunities for developing genetic resistance to diseases; however, relatives of wheat constitute a valuable reservoir of genes for cultivar improvement (Zeller and Hsam 1983; Gale and Miller 1987; Jiang et al. 1994; Jones et al. 1995; Friebe et al. 1996; Wang et al. 2003). *Thinopyrum ponticum* (Podp.) Barkworth and D. R. Dewey ($2n = 10\times = 70$) [syn. *Agropyron elongatum* (Host) Beauv., *Elytrigia pontica* (Podp.) Holub., *Lophopyrum ponticum* (Podp.) Á. Löve] is an important relative of wheat, due to its high crossability with many *Triticum* species and harboring of desirable genes in its genomes. *Thinopyrum ponticum* has been used to develop wheat germplasm lines with improved resistance to various pests and tolerance to abiotic stresses (Dewey 1984; Cai et al. 1998, 2001; Cox 1998; McIntosh et al. 1998; Li et al. 2003; Chen et al. 2004). One of the objectives in this study was to investigate the reaction of four wheat-*Th. ponticum* derivatives to three important diseases of wheat, *Fusarium* head blight (FHB), tan spot, and *Stagonospora nodorum* blotch (SNB).

Fusarium head blight, caused mainly by *Fusarium graminearum* Schwabe [teleomorph *Gibberella zeae* (Schw.) Petch], is a destructive disease of wheat and poses a serious threat to the health of consumers of wheat products (McMullen et al. 1997; Stack 2003; Bai and Shaner 2004). In the United States, cumulative economic

losses due to FHB in wheat have been estimated at $4.8 billion from 1991 through 1997 (Johnson et al. 2003). Extensive efforts have been made to utilize host resistance for managing this disease. However, progress has been limited because of a lack of effective sources of resistance, and the complex inheritance patterns of currently identified sources of partial resistance. Therefore, there is a need to identify novel sources of resistance to FHB.

Resistance to FHB has been identified in a number of relatives of wheat and wheat germplasm lines derived from the crosses between wheat and its relatives in previous studies (Oliver et al. 2005; Cai et al. 2005). The present study evaluated four wheat-*Th. ponticum* derivatives for resistance to the spread of infection within the spike. This type of resistance has been termed 'Type II resistance' (Schroeder and Christensen 1963; Wang and Miller 1988; Mesterhazy 1995).

Tan spot and SNB, caused by *Pyrenophora tritici-repentis* (Died.) Drechs. [anamorph: *Drechslera tritici-repentis* (Died.) Shoem.] and *Phaeosphaeria nodorum* (E.Mull.) Hedjar. [anamorph: *Stagonospora nodorum* (Berk.) Castell & Germano], respectively, are both important foliar diseases of cultivated wheat. These two diseases have been an increasing problem in recent years due to reduced tillage practices and lack of resistant cultivars in wheat growing regions of the world. They could cause significant yield losses in wheat (Rees and Platz 1983; King et al. 1983; Fried and Meister 1987; Riede et al. 1996). Sources of resistance to these diseases are limited, which has hindered development of wheat cultivars with satisfactory levels of resistance. Identification of novel resistance genes is vital for the development of wheat cultivars with robust and durable disease resistance.

Four wheat-*Th. ponticum* derivatives involved in this study were previously developed by W. J. Sando in 1930s; however, their chromosome compositions and potential usefulness for wheat improvement have not been investigated. Cytogenetic characterization of these wheat-*Th. ponticum* derivatives, as well as knowledge of their reaction to multiple diseases, facilitates their utilization in wheat breeding. Fluorescent genomic in situ hybridization (FGISH) has been successfully used to detect alien chromatin integrated into the wheat genomes and to investigate genomic relationships between wheat and its relatives (Heslop-Harrison et al. 1990; Jauhar 1995; Cai and Jones 1997; Fedak et al. 2000; Cai et al. 2001; Chen et al. 2002). The present study was initiated to evaluate four wheat-*Th. ponticum* derivatives for resistance to FHB, tan spot, and SNB and to characterize their chromosome constitutions.

Materials and methods

Plant materials

The four wheat-*Th. ponticum* derivatives, SS5 (PI604926), SS156 (PI604947), SS363 (PI604970), and SS660 (PI604879), were originally developed by W. J. Sando, USDA-ARS, University of California at Davis. Seeds of these four derivatives were obtained from the Sando Selections maintained at the National Small Grains Collection in Aberdeen, ID, USA. For FHB screening, Sumai 3, a Chinese common wheat cultivar widely used as a source of FHB resistance in breeding, was adopted as a resistant control. Susceptible controls included 'Russ', a spring wheat cultivar released by the South Dakota Agricultural Experiment Station, and a synthetic hexaploid wheat line SW55 developed by L. R. Joppa, Northern Crop Science Laboratory, USDA-ARS, Fargo, ND. SW55 was derived from the cross of the durum wheat cultivar Langdon [*T. turgidum* L. ssp. *durum* (Desf.) Husn., $2n = 4\times = 28$, AABB genome] and *T. tauschii* ($2n = 2\times = 14$, DD genome). A CIMMYT hexaploid synthetic wheat line W-7976 (Cando/R143//Mexi 'S'/3/*T. tauschii* C122) and a spring common wheat cultivar Grandin, released by the North Dakota Agricultural Experiment Station, were used as resistant and susceptible controls for the evaluation of reactions to tan spot and SNB, respectively.

Evaluation of reaction to FHB

Evaluation for Type II FHB resistance was conducted over three seasons in a greenhouse with a controlled environment. Plants were arranged in a randomized complete block design with two replicates in the first season and three replicates in the second and third seasons. In each season, approximately 20 spikes were evaluated in each replicate. Inoculation was performed following the methods described by Stack et al. (2002). Inoculum was prepared from three strains of pathogenic *F. graminearum* by flooding the fungal cultures with sterile distilled water and straining the resulting suspension through sterile cheesecloth. The final conidiospore suspension was adjusted to a concentration of 50,000 spores ml^{-1}. Ten microliter of the suspension was injected into a single central spikelet of a spike at anthesis. High relative humidity was maintained for 72 h post-inoculation by covering each spike with a plastic bag and misting at least once daily. Reaction to FHB was evaluated based on resistance to the spread of infection within the spike. Disease was visually scored as the number of diseased spikelets per spike at 21 days post-inoculation. Total spikelet numbers in each of the inoculated spikes were also recorded.

Evaluation of reaction to tan spot

Seedling reactions to tan spot were evaluated following the methods of Xu et al. (2004). Plants were grown in cones, with two to three plants per cone and three cones in each of three replications. Plants at the three-leaf stage were inoculated with a *P. tritici-repentis* race 1 conidial suspension concentrated to 3,000 spores ml^{-1}

and kept in a chamber at 100% relative humidity at 21°C for 24 h following inoculation, then transferred to a growth chamber at 21°C and a 12 h photoperiod. Evaluation was conducted at 7 days post-inoculation. Disease lesions were scored on a 1–5 scale, according to the rating system developed by Lamari and Bernier (1989), with 1 being resistant and 5 being highly susceptible. Lines with an equal amount of two lesion types were assigned an intermediate score.

Evaluation of reaction to SNB

Evaluation of seedling reaction to SNB was conducted using the same conditions and experimental design as described for tan spot. Inoculation with *P. nodorum* was performed at the two-to-three-leaf stage, using the field isolate, Sn2000. The spore suspension was adjusted to a concentration of 1×10^6 conidia ml^{-1}, and evaluation was conducted at 10 days post-inoculation. Disease was scored on a 1–5 scale, according to Xu et al. (2004). A Type 1 reaction (resistant) exhibited minimal necrotic and/or dark spots; a Type 5 reaction (highly susceptible) exhibited extensive, coalescing lesions.

Statistical analysis

Analysis of variance (ANOVA) was performed using the Statistical Analysis System version 8.2 (SAS Institute 1999). Fisher's protected least significant difference (FLSD) was used for mean separation between genotypes (Steel et al. 1997).

Molecular cytogenetic analysis

The four wheat-*Th. ponticum* derivatives were crossed to each other using conventional hybridization techniques. FGISH was performed on mitotic chromosomes of the four wheat-*Th. ponticum* derivatives, and on meiotic chromosomes of the F_1 hybrids between the derivatives, as described by Cai et al. (1998). Mitotic chromosomes were prepared from root tips, and meiotic chromosomes at metaphase I (MI) were prepared from pollen mother cells (PMCs), following the procedures described by Cai et al. (1996). Total genomic DNA of *Th. ponticum* was labeled with Biotin-16-dUTP via nick translation (Diagnostics Nick Translation Kit, Enzo Diagnostics, Inc., NY, USA) and used as a probe for FGISH. Total genomic DNA of *T. aestivum* L. cv. Chinese Spring (CS) was sheared by boiling in 0.4 M NaOH for 40–50 min, and used as blocking DNA for FGISH. Fluorescein isothiocyanate (FITC)-conjugated avidin (Vector Laboratories, Inc., CA, USA) was used to detect hybridization of the biotin-labeled probe with *Th. ponticum* chromatin (yellow-green fluorescence). Wheat chromatin was counterstained with propidium-iodide (red fluorescence). Slides were mounted in VECTASHIELD antifading medium (Vector Laboratories, Inc.) containing 1 μg ml^{-1} propidium iodide for counterstaining. Fluorescein isothiocyanate-conjugated avidin and propidium iodide were excited at 450–490 nm. Photographs were taken with a CCD camera (SPOT RT, Diagnostic Instruments, Inc., MI, USA) under an Olympus BX-51 phase/fluorescence microscope.

Results

Fusarium head blight resistance

The four wheat-*Th. ponticum* derivatives evaluated in this study exhibited FHB resistance comparable to Sumai 3 (Table 1). The disease was limited to the spikelet inoculated in most of the spikes evaluated in these four derivatives. In each season, ANOVA indicated that the

Table 1 Mean FHB severity of four partial wheat-*Th. ponticum* amphiploids and resistant and susceptible controls

Genotype	Pedigree	Season 1		Season 2		Season 3	
		NIS[a]	PIS[b]	NIS	PIS	NIS	PIS
Sumai 3	*T. aestivum* cultivar (PI 481542)[c]	1.0	5.5	1.0	8.5	1.2	7.7
Russ	*T. aestivum* cultivar (PI 592785)[d]	10.0	57.5	–	–	7.7	51.8
SW55	*T. turgidum* cv. Langdon/*T. tauschii* (RL5257) synthetic hexaploid wheat line[d]	8.1	50.0	9.2	67.7	–	–
SS5	Chinese Spring/*Thinopyrum ponticum*// Arlando/Leapland/Comet 125	1.4	8.5	0.7	6.2	2.2	17.5
SS156	Chinese Spring/*Th. ponticum*// Federation/Kinney/Prelude	1.1	7.1	0.9	7.3	1.3	9.2
SS363	Chinese Spring/*Th. ponticum*// Federation/Kinney/Prelude//Carala*2	0.9	5.9	1.0	8.0	1.2	8.5
SS660	Unknown	1.3	7.1	0.9	6.2	1.1	7.4
$LSD_{0.05}$		2.3	15.4	1.4	10.7	1.4	9.4

[a]Average number of infected spikelets at 3 weeks post-inoculation
[b]Average percent infection at 3 weeks post-inoculation. Percent infection was calculated as the number of diseased spikelets divided by the total number of spikelets
[c]Resistant control
[d]Susceptible control

Table 2 Average reactions of four wheat-*Th. ponticum* derivatives to tan spot and *Stagonospora nodorum* blotch

Genotype	Tan spot	SNB
W-7976[a]	2.2	2.0
Grandin[b]	4.0	3.8
SS5	1.5	1.3
SS156	3.0	2.5
SS363	2.7	2.8
SS660	3.0	3.8
$LSD_{0.05}$	1.0	0.8

[a]Resistant control. W-7976 is a CIMMYT synthetic wheat line with pedigree of Cando/R143//Mexi 'S'/3/*Aegilops tauschii*
[b]Susceptible control; *Triticum aestivum* cultivar

mean FHB severity of the derivatives was significantly lower than the susceptible controls in terms of number of infected spikelets per spike and percentage of infected spikelets. There was no significant difference in mean FHB severity between the derivatives and the resistant control (Table 1).

Tan spot and SNB resistance

Mean reaction data to tan spot showed that one wheat-*Th. ponticum* derivative, SS5, was resistant (1.5) and three (SS156, SS363, and SS660) were moderately resistant (2.7–3.0) (Table 2). Resistance levels in these derivatives were significantly higher than the susceptible control, and none of the derivatives differed significantly from the resistant control (Table 2).

Mean SNB reactions of the four derivatives ranged from 1.3 to 3.8 (Table 2). Two derivatives (SS5 and SS156) exhibited resistance comparable to W-7976, the resistant control. One derivative (SS363) showed intermediate resistance, which was significantly different from both the resistant and susceptible controls. The fourth derivative (SS660) was susceptible to SNB.

Molecular cytogenetic analysis

Chromosome constitutions of the four wheat-*Th. ponticum* derivatives were analyzed using FGISH. The FGISH patterns of mitotic chromosomes indicated that these four derivatives are partial wheat-*Th. ponticum* amphiploids, each with 56 chromosomes. Two of these amphiploids, SS5 and SS156, carry 14 *Th. ponticum* chromosomes and 42 wheat chromosomes (Fig. 1a, b); one amphiploid, SS660, carries 16 *Th. ponticum* chromosomes and 40 wheat chromosomes (Fig. 1c); and the fourth amphiploid, SS363, carries 14 *Th. ponticum*

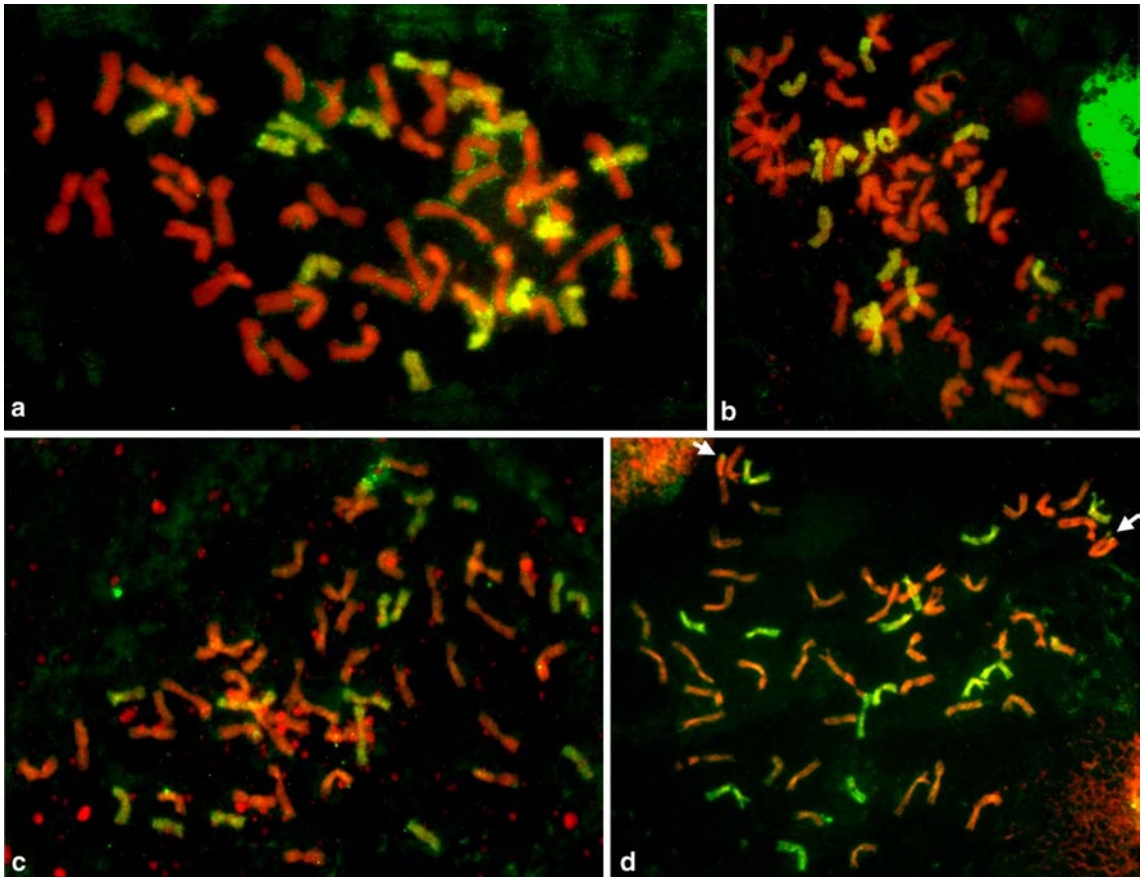

Fig. 1 Fluorescent genomic in situ hybridization patterns of mitotic chromosomes. **a** SS5, **b** SS156, **c** SS660, and **d** SS363. *Arrows* indicate translocated chromosomes. *Thinopyrum ponticum* chromatin fluoresces *green*; wheat chromatin fluoresces *red*

chromosomes, 40 wheat chromosomes, and two wheat-*Th. ponticum* translocated chromosomes. Only a small piece of *Th. ponticum* chromatin was detected at one end of the translocated chromosome (Fig. 1d). The wheat chromosome involved in this translocation could not be determined based on the FGISH pattern.

These four partial wheat-*Th. ponticum* amphiploids were hybridized with each other and six F_1 hybrids were obtained. Wheat chromatin was distinguished from *Th. ponticum* chromatin in PMCs at MI of the F_1 hybrids using FGISH. Chromosome pairing configurations were analyzed in five of the six hybrids. All five of these F_1 hybrids showed high frequencies of pairing between wheat chromosomes and between *Th. ponticum* chromosomes even though univalents were observed for both wheat and *Th. ponticum* chromosomes (Fig. 2, Table 3). An average of 5.57 and 6.83 *Th. ponticum* chromosome bivalents were observed in the hybrids of SS363 with SS5 and SS156, respectively (Table 3). The wheat-*Th. ponticum* translocated chromosome in SS363 normally paired with a corresponding wheat chromosome from SS5 and SS156 (Fig. 2d, e). The F_1 hybrids of SS660 with SS156 and SS363 showed 5.88 and 6.42 *Th. ponticum* chromosome bivalents, respectively (Table 3). In the hybrid between SS5 and SS6605.73 *Th. ponticum* chromosome bivalents were observed. The F_1 hybrid between SS5 and SS156 was not involved in this experiment because chromosome pairing results from the five hybrids allowed us to determine homology between *Th. ponticum* genomes in these four amphiploids.

Increased frequencies of unpaired wheat chromosomes (1.62–2.37) or *Th. ponticum* chromosomes and multivalents, including trivalents and quadrivalents, formed by *Th. ponticum* chromosomes were observed in the hybrids of SS660 with SS5, SS156, and SS363 (Table 3, Fig. 2a). Quadrivalents formed by wheat chromosomes were observed in all five hybrids and trivalents in the hybrids SS5 × SS363, SS5 × SS660, and SS156 × SS363 (Table 3, Fig. 2b). Pairing between wheat and *Th. ponticum* chromosomes was not found in any of the five hybrids.

Discussion

Extensive hybridization of *Th. ponticum* with wheat and chromosome manipulation have led to introgression of genes conditioning various pest resistance and tolerance to abiotic stresses from this wild species into wheat genomes (Sharma and Knott 1966; Zhong et al. 1994; Zhang 1996; Cai et al. 1998; McIntosh et al. 1998; Li et al. 2003, 2004; Chen et al. 2004). In the present study, four wheat-*Th. ponticum* derivatives were identified as resistant to the spread of FHB infection within a spike

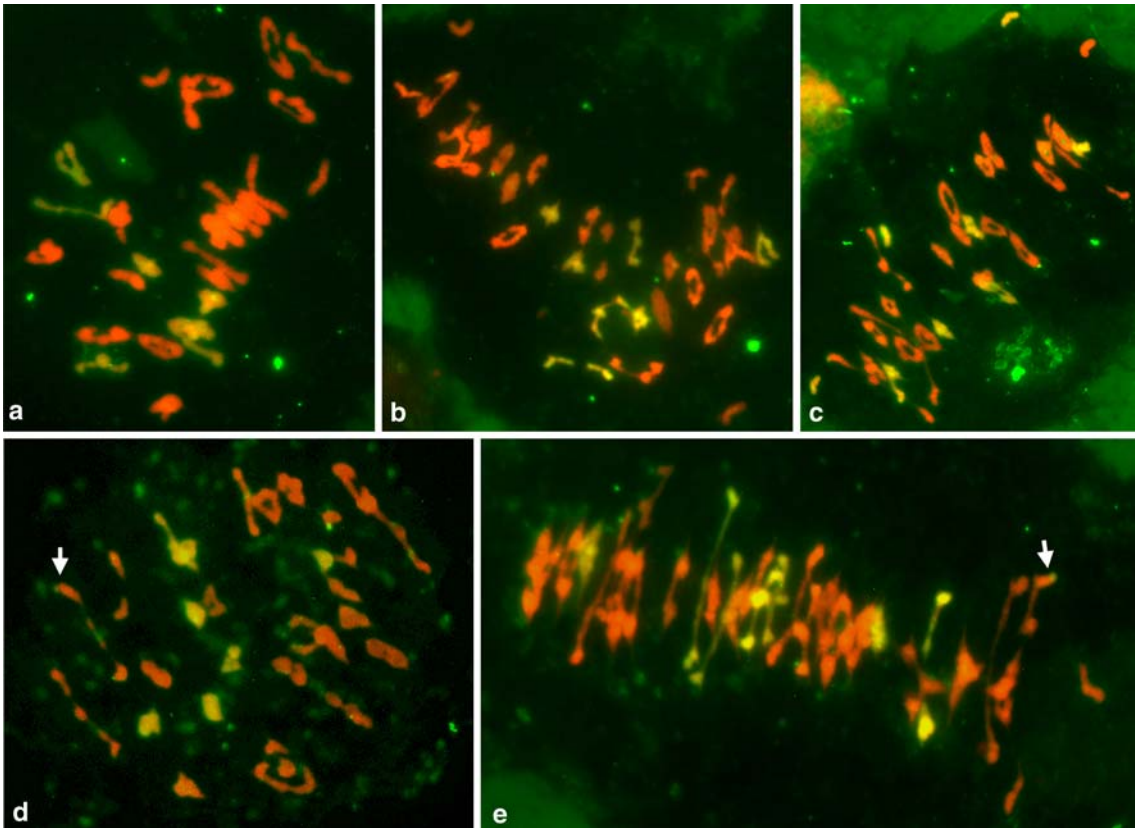

Fig. 2 Fluorescent genomic in situ hybridization patterns of meiotic chromosomes. **a** SS156 × SS660, **b** SS5 × SS660, **c** SS363 × SS660, **d** SS156 × SS363, and **e** SS5 × SS363. *Arrows* indicate translocated chromosomes

Table 3 Mean wheat and *Thinopyrum* chromosome pairing in hybrids of partial wheat-*Th. ponticum* amphiploids

	Hybrid	No. of plants	No. of cells	Wheat chromosomes				*Thinopyrum* chromosomes				
				I	II	III	IV	I	II		III	IV
									Ring	Rod		
1.	SS5 × SS363	12	109	0.73 (0–6)	20.29 (16–21)	0.09 (0–1)	0.10 (0–2)	2.84 (0–8)	3.51 (1–7)	2.06 (0–4)	0.00	0.00
2.	SS5 × SS660	10	63	2.16 (0–5)	17.78 (15–20)	0.38 (0–2)	0.52 (0–1)	1.87 (0–5)	3.38 (0–7)	2.35 (0–5)	0.37 (0–2)	0.14 (0–1)
3.	SS156 × SS363	14	46	0.83 (0–4)	19.04 (16–21)	0.04 (0–1)	0.74 (0–2)	0.35 (0–4)	5.09 (1–7)	1.74 (0–5)	0.00	0.00
4.	SS156 × SS660	9	35	2.37 (1–7)	19.23 (17–20)	0.00	0.03 (0–1)	1.40 (0–3)	4.51 (2–6)	1.37 (0–5)	0.34 (0–2)	0.20 (0–1)
5.	SS363 × SS660	11	45	1.62 (1–5)	19.16 (17–20)	0.00	0.27 (0–1)	1.80 (0–5)	4.73 (3–6)	1.69 (0–4)	0.09 (0–1)	0.02 (0–1)

Ranges are given in parentheses

(Type II resistance). These four derivatives exhibited similar levels of resistance as the Chinese common wheat cultivar Sumai 3, a widely used source of resistance in wheat breeding (Table 1). The wheat parents of the derivatives showed susceptibility to FHB (data not shown), suggesting that FHB resistance is most likely conferred by the *Th. ponticum* chromatin or wheat-*Th. ponticum* gene interactions in these derivatives. All four wheat-*Th. ponticum* derivatives exhibited similar levels of resistance to tan spot. The reactions to SNB, however, differed, suggesting genetic differences among the four derivatives (Table 2). Since the SNB reaction of the wheat parents is not known, these genetic differences may be due to either the wheat or the *Thinopyrum* parents.

FGISH identified these four wheat-*Th. ponticum* derivatives as partial wheat-*Th. ponticum* amphiploids with 56 chromosomes. They combine the genomes from wheat and *Th. ponticum* and contain large amounts of *Th. ponticum* chromatin (Fig. 1). Chromosome pairing analysis in the F_1 hybrids between these four amphiploids demonstrated that each carries a similar set of *Th. ponticum* chromosomes. High frequency of *Th. ponticum* chromosome bivalents in the hybrid between SS156 and SS363 suggested that these two amphiploids carry the same set of 14 *Th. ponticum* chromosomes and differ from SS5 in one pair of *Th. ponticum* chromosomes (Table 3). Increased frequency of wheat and *Th. ponticum* univalents in the hybrids involving SS660 might result from the chromosome constitution of SS660, which contained 40 wheat chromosomes and 16 *Th. ponticum* chromosomes (Fig. 1c). Appearance of quadrivalents and trivalents formed by wheat chromosomes and by *Th. ponticum* chromosomes in the F_1 hybrids suggested the existence of translocations between wheat chromosomes and between *Th. ponticum* chromosomes, respectively, in some of these amphiploids (Table 3, Fig. 2). It is unknown whether the same accession of *Th. ponticum* was used in the development of each of these four amphiploids. However, even if *Thinopyrum* chromatin in all four derivatives was derived from the same accession of *Th. ponticum*, they may carry different alleles at these disease resistance gene loci because *Th. ponticum* has been suggested to be an auto-allo-decaploid (Cai and Jones 1997; Chen et al. 1998a, b). Thus, these four amphiploids might have different sets of resistance genes, even though they contain a common *Th. ponticum* genome.

These four partial wheat-*Th. ponticum* amphiploids represent a potential gene source useful in breeding for resistance to FHB, tan spot, and SNB. High cross-compatibility with wheat makes these amphiploids desirable "bridge" materials for transferring the disease resistance genes from *Th. ponticum* to wheat. Results from this study will facilitate utilization of these resistance sources in breeding. Based on the chromosome constitution of these amphiploids, we have been manipulating *Thinopyrum* chromosomes in these amphiploids to eliminate unwanted *Thinopyrum* chromatin and introgress the resistance genes into wheat genomes. The resistance genes from *Th. ponticum* could be pyramided with currently identified resistance genes in wheat to enhance genetic diversity and provide more durable resistance of wheat to these diseases.

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