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Molecular Identification of a New Wheat-*Thinopyrum intermedium* ssp. *trichophorum* Addition Line for Resistance to Stripe Rust

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Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici,* was one of the most disaster foliar diseases for wheat-growing areas of the world. *Thinopyrum intermedium* has provided novel resistance genes to multi-fungal disease, and new wheat-*Th. intermedium* derivatives for stripe rust resistance still need to develop for wheat breeding. Wheat line X484-3 was selected from a cross between wheat line MY11 and wheat-*Th. intermedium* ssp. *trichophorum* partial amphiploid TE-1508, and was characterized by genomic *in situ* hybridization (GISH) and functional molecular markers. Chromosome counting revealed that the X484-3 was 2n = 44 and GISH analysis using *Pseudoroegneria spicata* genomic DNA as a probe demonstrated that X484-3 contained a pair of St-chromosomes from *Th. intermedium* donor parents. The functional molecular markers confirmed that introduced St-chromosomes belonging to linkage group 7, indicating that line X484-3 was a 7St addition line. The resistance observation displayed that the introduced *Th. intermedium* ssp. *trichophorum* derived chromosomes 7St were responsible for the stripe rust resistances at adult plant. The identified wheat-*Th. intermedium* chromosome 7St addition line X484-3 can be used as a donor in wheat breeding for stripe rust resistance.

Keywords: *in situ* hybridization, stripe rust resistance, *Thinopyrum intermedium* ssp. *trichophorum,* wheat

Introduction

Stripe rust caused by *Puccinia striiformis* f. sp. *tritici,* was a major worldwide diseases in common wheat (*Triticum aestivum* L.), which often gave rise to great wheat yield loss of in many regions including caused over 20 to 30% loss in wheat production each year in China (Roelfs et al. 1992; Kang et al. 2010). Breeding new cultivars resistant to these diseases is a cost effective and environmentally friend way to reduce the stripe rust damage. Over 40 resistance genes loci to stripe rust have been assigned to specific wheat chromo-

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somes (McIntosh et al. 2010). However, newly emerged virulent stripe rust races appeared to break down the resistance genes in released wheat cultivars (Wellings 2011). To maintain sustained genetic control of the stripe rust is dependent upon continuous utilization of new resistance gene resources. Wide cross and alien gene transfer is a valuable mean for increasing the genetic diversity including multi-resistances available to wheat breeders (Jiang et al. 1994).

Thinopyrum intermedium subspecies was hybridized extensively with wheat and proved to be a valuable source of improving wheat disease resistance and yield potential (Li and Wang 2009). Some wheat rust resistance genes were investigated in *Th. intermedium* (Cauderon et al. 1973; Tang et al. 2000), but different *Thinopyrum* sources still worthwhile to explore for novel resistance genes transfer. We produced a wheat-*Th. intermedium* ssp. *trichophorum* partial amphiploid and found that it displayed high resistance to several foliar diseases including stripe rust (Yang et al. 2006). With aim to introduce novel resistance genes from the *Th. intermedium* ssp. *trichophorum* to wheat, we started program for production of wheat-*Thinopyrum* chromosome addition, substitution and translocation lines by crossing and backcrossing the partial amphiploid with common wheat (Yang et al. 2006; Hu et al. 2011). The genomic *in situ* hybridization (GISH) was widely used for identifying the alien chromosomes in addition and substitution lines (Friebe et al. 1996; Georgieva et al. 2011). Moreover, new functional molecular markers were also effective to determine the linkage group of transferred alien chromatin in wheat (Hu et al. 2012). These cytological and molecular markers targeting alien chromosomes with novel disease resistance genes will be useful for molecular assisted selection (MAS) in wheat breeding programs (Chen 2005; Kong et al. 2009). In the present study, we developed new wheat-*Thinopyrum* addition lines with novel stripe rust resistance and determined the genomic constitution of the *Thinopyrum* chromosomes using GISH in combined with molecular marker analysis.

Materials and Methods

Plant materials

Th. intermedium ssp. *trichophorum* accession PI440125 (genome $JJ^{s}St$, 2n = 6x = 42) and *Pseudoroegneria spicata* (Pursh) A. Love (genome St, 2n = 2x = 14) accession PI 232131were obtained from the USA National Small Grains Collection at Aberdeen, Idaho. The wheat-*Th. intermedium* ssp. *trichophorum* partial amphiploid, TE-1508 was developed with identical pedigree of TE-3 by Yang et al. (2006), and wheat cultivar Mianyang 11 (MY11) and Chinese Spring (CS) are maintained at the Sichuan Agricultural University, China.

Genomic in situ *hybridization (GISH)*

Seedling root tips were collected and pretreated in water at 0°C for 24 h and fixed in ethanol-acetic acid (3:1) for 1 week. Root-tip squashes were stained using the conventional Feulgen method for chromosome counting. For GISH analysis, total genomic DNA from

Ps. spicata was labeled with digoxigenin-11-dUTP by nick translation following the manufacturer's instructions (Roche Diagnostics, Indianapolis, IN). Sheared genomic DNA of Chinese Spring wheat (CS, genomes ABD, 2n = 42) was used as blocking DNA. The hybridization mixture was prepared as described by Mukai et al. (1993). The GISH signal was detected with fluorescein-conjugated antidigoxigenin antibody (Roche Diagnostics, Indianapolis, IN), and the slide was mounted in propidium iodide dissolved in Vectrashield® antifade solution (Vector Laboratories, Burlingame, CA). Microphotographs of C-banded and GISH chromosomes were taken with an Olympus BX-51 microscope using a DP-70 CCD camera.

Disease resistance screening

Wheat line X484-3 and its parents were evaluated for adult-plant resistance to *P. striiformis* f. sp. *tritici* strains CRY30, CRY-31 and CRY-32, which were provided by the Plant Protection Institute, Sichuan Academy of Agricultural Sciences. During the 2008 and 2009 cropping seasons, adult plants were inoculated with these strains in the field at Xindu city, Sichuan. Infection types (IT) were evaluated 2–3 weeks after inoculation when uredinia were fully developed. Stripe rust responses were recorded following Ma et al. (1995).

Molecular marker analysis

DNA was extracted from fresh leaves of accession *Th. intermedium, Ps. spicata,* lines X484-3 and CS (Yang et al. 2006). PCR-based Landmark Unique Gene (PLUG) primers were made according to Ishikawa et al. (2009). Polymerase chain reaction (PCR) was performed in an Icycler thermalcycler (Bio-RAD Laboratories, Emeryville, CA) in reaction volumes of 25 µl, containing 10 mmol Tris-HCl (pH 8.3), 2.5 mmol $MgCl_2$, 200 µmol of each dNTP, 100 ng template DNA, 0.2 U Taq polymerase (Takara, Japan) and 400 nmol primer. The cycling parameters were 94ºC for 3 min for predenaturing; followed by 35 cycles at 94ºC for 1 min, 55ºC for 1 min, 72ºC for 2 min; and then a final extension at 72ºC for 10 min. The amplified products were cloned and sequenced as described by Hu et al. (2011).

Results

Morphology and chromosome number of X484-3

Wheat-*Th. intermedium* ssp. *trichophorum* partial amphiploid TE-1508 contained wheat background of Chinese Spring, which was similar pedigree to TE-3 by Yang et al. (2006). Wheat parent MY11 was a semi-winter type wheat cultivar in Sichuan at 33 degrees north latitude agriculture region of China. TE1508 was crossed to wheat line MY11, then backcrossed and self-fertilized. Line X484-3 was selected from the BC_1F_5 progenies. The adult plant of X484-3 displayed the similar heading time as the Sichuan wheat cultivars. The X484-3 plant was 90–105 cm in height, produced 7–10 spikes per plant, and displayed higher tillering ability than that of MY11 (3–5 spikes). Plants of X484-3 had 20–23 spike-

lets per spike, closely resembling MY11, but with longer spikes (Fig. 1A). The heavy glume pubescence on the spikes of TE-1508 possibly inherited from *Th. intermedium* ssp. *trichophorum* was not observed in X484-3. Observation of root-tip chromosome number and meiotic PMCs of 20 X484-3 progenies, the results showed that all plants of X484-3 progenies were 2n = 44 at somatic chromosomes and 22 bivalents at meiotic MI, which indicating that line X484-3 was a cytologically stable addition line.

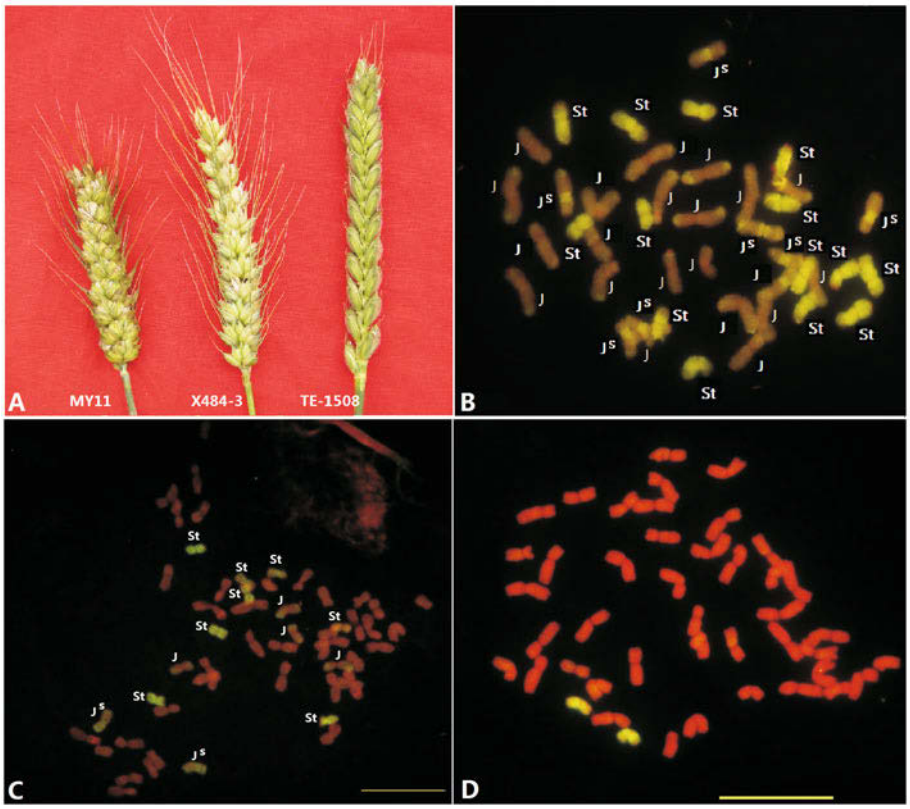

Figure 1. The spikes morphology (A) and GISH (B–D) of disomic addition lines X484-3 and their parents. GISH of *Th. intermedium* ssp. *trichophorum* accession PI440125 (B), TE-1508 (C) and X484-3 (D) using *Ps. spicata* genomic DNA as probe. Bar showed the 20 μm

In situ *hybridization*

GISH using total genomic DNA from *Ps. spicata* (St-genome) as a probe was performed on mitotic metaphase chromosomes of X484-3 and its parents TE-1508 as well as *Th. intermedium* ssp. *trichophorum* (Fig. 1). Based on the chromosomes assignment of GISH by St genomic DNA outlined by Chen et al. (1998), the genomic constitution of *Th. intermedium* ssp. *trichophorum* PI440125 was 14St+18J+6J^{s} (Fig. 1B), and the alien chromosomes of partial amphiploid TE1508 was designed as 8St+4J+2J^{s}(Fig. 1C). The

X484-3 contained the alien chromosomes with probe hybridized uniformly along the entire chromosome lengths (Fig. 1D), indicating that the two chromosomes were St-genome chromosomes from *Th. intermedium*. The St-chromosomes were clearly shorter than those of the wheat chromosomes.

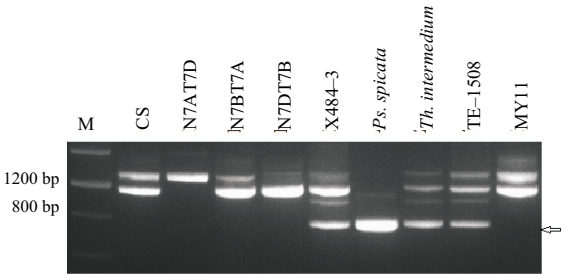

Figure 2. PCR using PLUG primers TNAC1812. The arrow indicates the St specific band identical with that of *Th. intermedium* and *Ps. spicata* derived band

Molecular markers

The PLUG primers were designed based on rice syntenic region, and presumably amplify fragments corresponding to the similar linkage group(s) of wheat genomes (Ishikawa et al. 2009). Our previous studies showed that the PLUG markers were useful for producing alien chromosome-specific markers (Jia et al. 2010; Hu et al. 2012). Total 145 PLUG markers were tested X484-3 and its parents MY11 and TE-1508. We found that 4 PLUG markers, named TNAC1805, TNAC1806, TNAC1812 and TNAC1815 (Ishikawa et al. 2009), gave rise to the specific amplification of between X484-3 and TE-1508 DNA. As shown in Figure 2, the PLUG marker TNAC1812 amplified diagnostic fragments in wheat long arms of chromosomes 7A, 7B and 7D, respectively, which revealed by amplification of wheat CS nulli-tetrasomic lines. A strong specific band was clearly observed in both *Th. intermedium, Ps. spicata* and X484-3 (Fig. 2). The sequences of the specific band from *Th. intermedium, Ps. spicata* and X484-3 were 733 bp, 735 bp and 727 bp, respectively. The sequence alignment indicated that the St-derived band had 99% homology to the St-band in X484-3 (Fig. 3). Similarly, another PLUG primer, TNAC1805, specific to short arms of wheat homoeologous group 7 also generated the St band from X484-3 identical to that of *Th. intermedium* and *Ps. spicata* (data not shown). These results suggested that the St-chromosome in X484-3 belonged to homoeologous group 7.

Disease responses

Line X484-3 and the parental lines TE-1508 and MY11 were inoculated with *Blumeria graminis* f. sp. *tritici* isolates (seedling) and *P. striiformis* f. sp. *tritici* races CYR30, CYR31 and CYR32 (adult plant). TE-1508 was immune to these isolates, whereas wheat parent MY11 was highly susceptible. X484-3 was highly resistant to stripe rust but sus-

ceptible to powdery mildew. These results indicated that the stripe rust resistance in X484-3 was from the TE-1508 parent, and can be traced to *Th. intermedium* ssp. *trichophorum*.

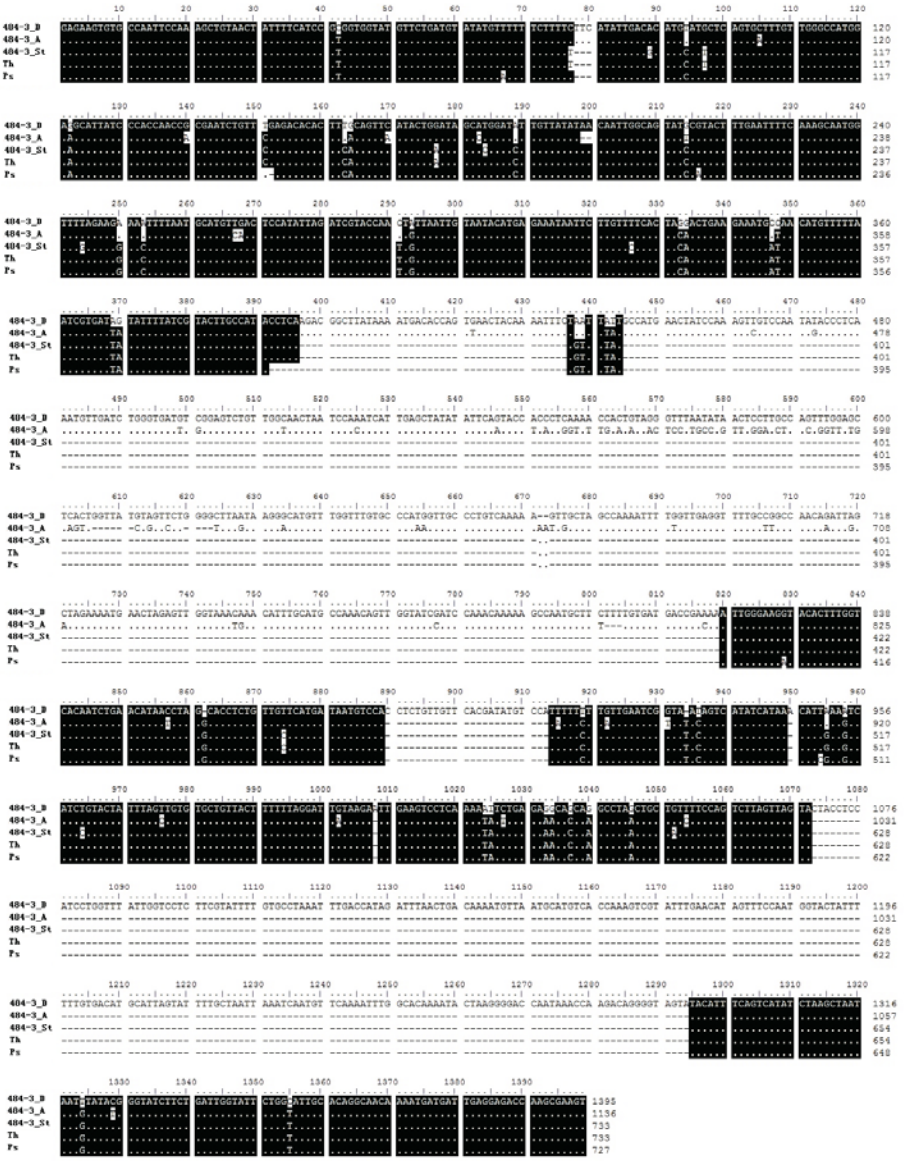

Figure 3. Alignment of the nucleotide sequences from X484-3 bands (A, D, St) with sequences of *Ps. spicata* (St) and *Th. intermedium* (Th). Base similarities are indicated with dots, and gaps were introduced to optimize alignment are indicated with dashes

Discussion

Thinopyrum intermedium has been described as a segmental autoallohexaploid, consisting of two closely related, partially homologous, genomes and one distinctly diverse genome (Li and Wang 2009). The studies indicated that three distinguishable chromosome sets of *Th. intermedium* were designated J, J^S and St-genomes. The J genome was related to both *Th. elongatum* and Th. *bessarabicum,* however, the J^S genome referred to a modified *Th. elongatum*/*Th. bessarabicum* genome (Chen et al. 1998), but further evidences illustrated the *Dasypyrum* species may possibly be the progenitor for the J^s genome (Kishii et al. 2005; Liu et al. 2009; Mahelka et al. 2011), and thus the genomic structure of *Th. intermedium* is likely with some potential progenitors still unidentified. There is only St-genome originated from *Ps. strigosa* were confirmed to be a basic genome of *Th. intermedium*. The GISH and C-banding techniques revealed remarkably that a large amount of genetic polymorphism and genomic structure modifications occurred among inter-population and intra-populations. Chen et al. (1998) showed that the identified *Th. intermedium* accessions included with 17–21 J, 6–11 J^S and 13–14 St-chromosomes, respectively. Tang et al. (2000) described the genomic composition of *Th. intermedium* as 21J + 7J^S +14St. It indicated that the genomic variation among different *Th. intermedium* accessions needs to be further investigated (Li and Wang 2009). The *Th. intermedium* ssp. *trichophroum* exhibited strong heterochromatin bands in their terminal regions of the chromosomes, and were quite different from those of the *Th. intermedium* ssp. *intermedium* (Xu and Conner 1994; Yang et al. 2006). In the present study, we investigated the GISH pattern of *Th. intermedium* ssp. *trichophorum* PI440125, and found that its genomic composition was 14St+18J+6J^s (Fig. 1B), which indicating that the number of St-chromosomes was stable in different *Th. intermedium* subspecies. Moreover, the partial amphiploid TE-1508 were similar pedigree of TE-3 (Yang et al. 2006), but it contained different alien composition from previous reported wheat-*Th. intermedium* partial amphiploids (Chen 2005; Georgieva et al. 2011). Therefore, the polymorphism of *Th. intermedium* subspecies and accessions and wheat-*Thinopyrum* partial amphiploids allowed continuously transferring the novel genes from *Th. intermedium* to cultivated wheat.

Th. intermedium has been regarded as novel resistance resource for wheat breeding, in particular for resistance to barely yellow dwarf virus (BYDV) and rust (Li and Wang 2009). A disomic addition line L1 originating from TAF 46 (Cauderon et al. 1973) was first identified to have BYDV resistance gene Bdv2 in chromosome 7Ai#1 (Friebe et al. 1992; Hohmann et al. 1996). The St-genome based GISH revealed that L1 contained the J chromosomes from *Th. intermedium* (Chen et al. (1998). Friebe et al. (1993) identified 7Ai#2(7D) and 7Ai#2(7A) chromosome substitution lines contained a leaf rust resistance gene *Lr38* which located in the distal half of the long arm of chromosome 7Ai#2. Tang et al. (2000) identified that a pair of chromosome 7Ai#2 in a disomic addition line Z4 was belong to J^S chromosomes by St-genome based GISH. Moreover, the 7E (J or J^s genome)-(7D) substitution line P29 and 7E addition line P107 carried gene Bdv3 for resistance to BYDV genes on 7AiL (Ohm et al. 2005; Kong et al. 2009; Ayala-Navarrete et al. 2010). Both Bdv2 and Bdv3 are derived from chromosome 7 and from different genomes

of *Th. intermedium*. Recently, Liu et al. (2011) identified a novel gene wsm3 for resistance to wheat streak mosaic virus (WSMV) presented on the *Th. intermedium* chromosome arm 7S#3L present in the T7BS·7S#3L translocation line KS12WGGRC59. Consequently, we considered to further transfer new orthologous rust resistance gene(s) from different sources of the *Th. intermedium* accessions. In the present study, we investigated the addition line X484-3 by GISH, and found a pair of typical St-chromosomes in wheat background. Further using group-7 PLUG markers confirmed that the introduced *Th. intermedium* derived St-chromosomes in X484-3 belong to group 7, and thus the chromosomes in line X484-3 can be described as 7St#4 from *Th. intermedium* ssp. *trichophorum*. Line X484-3 appeared high resistance to stripe rust races. It is thus to note that the *Th. intermedium* derived 7St chromosomes displayed novel resistance which worthwhile to study further. In addition, other wheat-*Th. intermedium* addition or substitution lines including the L series derived from TAF46 (Cauderon et al. 1973) and Z series from Zhong 5 (Larkin et al. 1995) displayed hard winter type and they are difficult for flowering in semi-winter or spring type regions for breeding practices. The present addition line X484-3 was clearly semi-winter type, and can be easily used as parent to transfer the chromosome 7St#4 carried novel genes for wheat breeding.

Fluorescence *in situ* hybridization has been commonly used to determine the distribution of the repetitive sequences on chromosomes, and also used to identify the specific organization of the chromatin. Apart from for the above-mentioned St-genome based GISH for *Th. intermedium* (Chen 2005), the repetitive DNA sequences have been useful for identifying the chromosomes and genomes in allopolyploid (Heslop-Harrison 2000), and we also developed J and J^s specific probes for *Th. intermedium* identification (Liu et al. 2009; Tang et al. 2011). However, the GISH or FISH probes are hard to distinguish the homologous group of the individual chromosomes. The traditional RFLP markers were effective for identifying the alien chromatin and assign the linkage group (Friebe et al. 1996). However, it is time-consuming and cost methods. The PCR-based markers were simple and fast to target the alien species in a wheat background, and can be used to detect materials that contain *Thinopyrum* chromatin. In particularly, the comparative genome analysis revealed that there was a high collinearity level of the coding regions existing between genomes from rice, Brachypodium and wheat (Dubcovsky et al. 2001; Quraishi et al. 2009). The markers based on the conserved gene regions can be used to produce alien chromosome-specific markers. We previously developed a group of *Th. ponticum* chromosome-specific markers including PLUG markers (Jia et al. 2010; Hu et al. 2012), and also use the markers to confirmed the 1St (1D) substitution lines (Hu et al. 2011). It is thus to note that this type of markers can be useful for alien chromatin identification and assignment of their corresponding linkage group. In the present study, the group-7 PLUG markers detected polymorphic fragments specific to the *Th. intermedium* chromosome in X484-3, which were also observed in the homeologous group-7 wheat chromosomes (Fig. 3). The PCR amplification of *Th. interemdium* specific bands in X484-3 was identical to the amplification of *Ps. spicata* (St-genome). It is thus to assign the introduced St chromosomes pairs in line X484-3 belong to group 7. The line X484-3 can also be used to further localized other molecular markers of 7St, and compared the previously mapped 7J (L1)

and Z4 ($7J^s$) to investigate the genomic recombination among chromosomes in *Th. intermedium* allopolyploidy.

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References

Ayala-Navarrete, L., Thompson, N., Ohm, H., Anderson, J. 2010. Molecular markers show a complex mosaic pattern of wheat-*Thinopyrum intermedium* translocations carrying resistance to YDV. Theor. Appl. Genet. **121**:961–970.

Cauderon, Y., Saigne, B., Dauge, M. 1973. The resistance to wheat rusts of *Agropyron intermedium* and its use in wheat improvement. In: Sears, E.R., Sears, L.M.S. (eds), Proc. 4th Int. Wheat Genet. Symp., University of Missouri, Columbia, MI, USA, pp. 401–407.

Chen, Q. 2005. Detection of alien chromatin introgression from *Thinopyrum* into wheat using S genomic DNA as a probe – A landmark approach for *Thinopyrum* genome research. Cytogenet. Genome Res. **109**:350–359.

Chen, Q., Friebe, B., Conner, R.L., Laroche, A., Thomas, J.B., Gill, B.S. 1998. Molecular cytogenetic characterization of *Thinopyrum intermedium*-derived wheat germplasm specifying resistance to wheat streak mosaic virus. Theor. Appl. Genet. **96**:1–7.

Dubcovsky, J., Ramakrishna, W., SanMiguel, P.J., Busso, C.S., Yan, L., Shiloff, B.A., Bennetzen, J.L. 2001. Comparative sequence analysis of colinear barley and rice bacterial artificial chromosomes. Plant Physiol. **125**:1342–1353.

Friebe, B., Zeller, F.J., Mukai, Y., Forster, B.P., Bartos, P., McIntosh, R.A. 1992. Characterization of rust-resistant wheat-*Agropyron intermedium* derivatives by C-banding, in situ hybridization and isozyme analysis. Theor. Appl. Genet. **83**:775–782.

Friebe, B., Jiang, J.M., Gill, B.S., Dyck, P.L. 1993. Radiation-induced nonhomoeologous wheat-*Agropyron intermedium* chromosomal translocations conferring resistance to leaf rust. Theor. Appl. Genet. **86**:141–149.

Friebe, B., Jiang, J., Raupp, W.J., McIntosh, R.A., Gill, B.S. 1996. Characterization of wheat-alien translocations conferring resistance to diseases and pests: Current status. Euphytica **91**:59–87.

Georgieva, M., Sepsi, A., Tyankova, N., Molnár-Láng, M. 2011. Molecular cytogenetic characterization of two high protein wheat-*Thinopyrum intermedium* partial amphiploids. J. Appl. Genetics **52**:269–277.

Heslop-Harrison, J.S. 2000. Comparative genome organization in plants: From sequence and markers to chromatin and chromosomes. Plant Cell **12**:617–636.

Hohmann, U., Badaeva, E.D., Busch, W., Friebe, B., Gill, B.S. 1996. Molecular cytogenetic analysis of *Agropyron* chromatin specifying resistance to barley yellow dwarf virus in wheat. Genome **39**:336–347.

Hu, L.J., Li, G.R., Zeng, Z.X., Chang, Z.J., Liu, C., Zhou, J.P., Yang, Z.J. 2011. Molecular cytogenetic identification of a new wheat-*Thinopyrum* substitution line with stripe rust resistance. Euphytica **177**:169–177.

Hu, L.J., Liu, C., Zeng, Z.X.,·Li, G.R., Song, X.J., Yang, Z.J. 2012. Genomic rearrangement between wheat and *Thinopyrum elongatum* revealed by mapped functional molecular markers. Genes and Genomics **34**:67–75.

Ishikawa, G., Nakamura, T., Ashida, T., Saito, M., Nasuda, S., Endo, T., Wu, J., Matsumoto, T. 2009. Localization of anchor loci representing five hundred annotated rice genes to wheat chromosomes using PLUG markers. Theor. Appl. Genet. **118**:499–514.

Jia, J., Li, G., Liu, C., Zhou, J., Yang, Z. 2010. Sequence variations of PDHA1 gene in *Triticeae* species allow for identifying wheat-alien introgression lines. Frontiers of Agriculture in China **4**:137–144.

Jiang, J., Friebe, B., Gill, B.S. 1994. Recent advances in alien gene transfer in wheat. Euphytica **73**:199–212.

Kang, Z., Zhao, J., Han, D., Zhang, H., Wang, X., Wang, C., Han, Q., Guo, J., Huang, L. 2010. Status of wheat rust research and control in China. BGRI 2010 Technical Workshop, St Petersburg, Russia, pp. 1–21.

Kishii, M., Wang, R.R.C., Tsujimoto, H. 2005. GISH analysis revealed new aspect of genomic constitution of *Thinopyrum intermedium*. Czech J. Genet Plant Breed. **41**(Special issue):91–95.

Kong, L., Anderson, J.M., Ohm, H.W. 2009. Segregation distortion in common wheat of a segment of *Thinopyrum intermedium* chromosome 7E carrying Bdv3 and development of a Bdv3 marker. Plant Breed. **128**:591–597.

Larkin, P.J., Banks, P.M., Lagudah, E.S., Apple, R., Chen, X., Xin, Z.Y., Ohm, H.W., McIntosh, R.A. 1995. Disomic *Thinopyrum intermedium* addition lines in wheat with barley yellow dwarf virus resistance and with rust resistances. Genome **38**:385–394.

Li, H., Wang, X. 2009. *Thinopyrum ponticum* and the promising source of resistance to fungal and viral diseases of wheat. J Genet. Genomics **36**:557–565.

Liu, C., Yang, Z.J., Jia, J.Q., Li, G.R., Zhou, J.P., Ren, Z.L. 2009. Genomic distribution of a Long Terminal Repeat (LTR) *Sabrina*-like retrotransposon in *Triticeae* species. Cereal Res. Commun **37**:363–372.

Liu, W., Seifers, D.L., Qi, L.L., Friebe, B., Gill, B.S. 2011. A compensating wheat–*Thinopyrum intermedium* Robertsonian translocation conferring resistance to wheat streak mosaic virus and *Triticum* mosaic virus. Crop Sci. **51**:2382–2390.

Ma, H., Singh, R.P., Mujeeb-Kazi, A. 1995. Suppression/expression of resistance to stripe rust in synthetic hexaploid wheat (*Triticum turgidum* × *T. tauschii*). Euphytica **83**:87–93.

Mahelka, V., Kopecký, D., Paštová, L. 2011. On the genome constitution and evolution of intermediate wheatgrass (*Thinopyrum intermedium:* Poaceae, Triticeae). BMC Evol. Biol. **11**:127.

McIntosh, R.A., Dubcovsky, J., Rogers, J., Morris, C., Appels, R., Xia, X. 2010. Catalogue of gene symbols for wheat: 2010 supplement. http://www.shigen.nig.ac.jp/wheat/komugi/genes/

Mukai, Y., Friebe, B., Hatchett, J.H., Yamamoto, M., Gill, B.S. 1993. Molecular cytogenetic analysis of radiation-induced wheat rye terminal and intercalary chromosomal translocations and the detection of rye chromatin specifying resistance to Hessian fly. Chromosoma **102**:88–95.

Ohm, H.W., Anderson, J.M., Sharma, H.C., Ayala, N.L., Thompson, N., Uphaus, J.J. 2005. Registration of yellow dwarf virus resistant wheat germplasm line P961341. Crop Sci. **45**:805–806.

Quraishi, U.M., Abrouk, M., Bolot, S., Pont, C., Throude, M., Guilhot, N., Confolent, C., Bortolini, F., Praud, S., Murigneux, A., Charmet, G., Salse, J. 2009. Genomics in cereals: From genome-wide conserved orthologous set (COS) sequences to candidate genes for trait dissection. Funct. Integr. Genomics **9**:473–484.

Roelfs, A.P., Singh, R.P., Saari, E.E. 1992. Rust Diseases of Wheat: Concepts and Methods of Disease Management. CIMMYT, Mexico.

Tang, S., Li, Z., Jia, X., Larkin, P.J. 2000. Genomic in situ hybridization (GISH) analyses of *Thinopyrum intermedium,* its partial amphiploid Zhong 5, and disease-resistant derivatives in wheat. Theor. Appl. Genet. **100**:344–352.

Tang, Z.X., Yang, Z.J., Fu, S.L., Yang, M.Y., Li, G.R., Zhang, H.Q., Tan, F.Q., Ren, Z.L. 2011. A new long terminal repeat (LTR) sequence allows to identify J genome from J^S and St genomes of Thinopyrum intermedium. J. Appl. Genet. **52**:31–33.

Wellings, C.R. 2011. Global status of stripe rust: A review of historical and current threats. Euphytica **179**:129–141.

Xu, J., Conner, R.L. 1994. Intravarietal variation in satellites and C-banded chromosomes of *Agropyron intermedium* ssp. *trichophorum* cv. Greenleaf. Genome **37**:305–310.

Yang, Z.J., Li, G.R., Chang, Z.J., Zhou, J.P., Ren, Z.L. 2006. Characterization of a partial amphiploid between *Triticum aestivum* cv. Chinese Spring and *Thinopyrum intermedium* ssp. *trichophorum*. Euphytica **149**:11–17.