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Full Length Research Paper

Genetic instability in neoallopolyploids: Exploring DNA introgression in synthetic hexaploid wheat × *Aegilops peregrine*

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SHW-L1 is a newly synthetic hexaploid wheat, which has a genomic combination analogous to that of natural common wheat. In the present study, intergeneric F_1 hybrids of SHW-L1 - *Aegilops peregrina* AS24 were produced without embryo rescue. Among the 31 F_1 hybrid plants observed, 20 had the expected chromosome number 2n = 35 and were euploids (genome ABDUS^l). The remainder 11 plants were aneuploids with 33, 34, 36 and 37 chromosomes, indicating that the neoallohexaploid SHW-L1 was cytologically instable and produced aneuhaploid gametes with 19, 20, 22 and 23 chromosomes, respectively. The hybrid plant lacking chromosome 5B carrying *Ph1* showed a very high level of homoeologous chromosome pairing. The absence of *Ph* gene provides a potent cytological mechanism for DNA introgression among homoeologous chromosomes between newly synthetic wheat and wild species.

Key words: Aneuploids, common wheat, gene flow, neopolyploid, *Ph1.*

INTRODUCTION

Allopolyploids are produced by the merger of two or more distinct but related genomes by inter-specific or inter-generic hybridization and then genome doubling. Allopolyploids are very common in plants, including many important crops. One of the most remarkable allopolyploid crops is bread wheat or common wheat (*Triticum aestivum* L., genome AABBDD, 2n = 6x = 42), which was formed by the polyploidization after the intercrossing between cultivated *T. turgidum* L. (AABB, 2n = 4x = 28) and *Aegilops tauschii* Coss. (DD, 2n = 2x = 14) followed by spontaneous chromosome doubling (Kihara, 1944; McFadden and Sears, 1944). Corresponding chromosomes among genomes A, B and D have partially homologous (homoeologous) relationship with each other. However, common wheat behaves effectively as diploids during meiosis, only true homologous chromosomes pair, which is controlled by *Ph* gene system, including the major paring gene *Ph1* on chromosome 5B (Okamoto, 1957; Riley and Chapman, 1958), and intermediate-pairing gene *Ph2* on 3D (Mello-Sampayo, 1971), and a number of minor loci (Sears, 1976). The *Ph1* gene also prevents nonhomologous yet homoeologous chromosome pairing in wheat-alien hybrids (Sears, 1976).

Introgression, the incorporation of DNA from one species into the gene pool of another species, has played a crucial role in the evolution of many plant species (Arnold, 1997). Introgression of genes from wild species into crops by cytological technology has been widely used in plant breeding and improvement. However, introgression of genes from crops into the wild species

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may increase the capability of the wild species to adapt to agricultural environments and compete with the cultivated forms, which is viewed as a possible threat to the environment and the agriculture (Ellstrand, 2003). With the development of the genetic modification technique, an increasing number of studies are now addressing gene flow from wheats to their wild relatives (David et al., 2004; Hegde and Waines, 2004; Weissmann et al., 2005; Zaharieva and Monneveux, 2006; Schoenenberger et al., 2006). There were some reports on the potential risk for gene transfer via homologous recombination. For example, homologous DNA fragments of wheat can be introgressed into *A. cylindrica* (genome CCDD), a tetraploid species having one genome homologous to the D genome of common wheat (Caldwell et al., 2004; Schoenenberger et al., 2006). Gene flow among homoeologous chromosomes is prevented by *Ph1* gene (Sears, 1976; Weissmann et al., 2008). However, Weissmann et al. (2005) provided the emipirical evidence on spontaneous DNA introgression from wheat into *A. peregrina* and introgressed DNA fragments were stabilized in naturally wild populations of *A. peregrina*. However, data on cytological mechanism for spontaneous DNA introgression among homoeologous chromosomes are lacking.

In the present study, we observed the cytological instability of newly synthetic wheat and the spontaneous production of aneuhaploid gametes absent for 5B chromosome carrying *Ph1* gene. The *Ph1* absence is a potent cytological mechanism for DNA introgression among homoeologous chromosomes between newly synthetic wheat and wild species.

MATERIALS AND METHODS

Plant materials

Plant materials used in this study included *A. peregrina* (Hack.) Maire and Weiller (syn. *Aegilops variabilis*, 2n = 4x = 28, S^lS^lUU) accession AS24 and newly synthetic hexaploid wheat SHW-L1 (2n = 6x = 42, AABBDD), which is an amphidiploid between *T. turgidum* ssp. *turgidum* line Yuanzhuimai (AS2255) and *Ae. tauschii* accession AS60 (Zhang et al., 2004). SHW-L1 was obtained in 2002.

Production of hybrids

In 2003, SHW-L1 plants with 2n = 42 were crossed to *A. peregrina* AS24. The emasculation and pollination techniques described by Zhang et al. (2007) were followed. No embryo rescue technique or hormone treatment was applied when producing the hybrids. Hybrid seeds were germinated in Petri dishes and then transplanted into the field of Triticeae Research Institute of Sichuan Agricultural University, located at Dujiangyan city of Sichuan province. The plants were grown at 10 cm apart with 60 cm row spacing.

Cytological observations

The procedures for cytological observations were the same as described previously (Zhang et al., 2007). Cytological observation was documented with an Olympus BX-51 microscope coupled with a Photometric SenSys CCD camera. Chiasmata frequency was estimated from the number of chromosome arm paired per cell at meiotic metaphase I (MI). The student's t-test was applied for statistical evaluation of the differences between the means of the MI parameters in the hybrid genotypes.

Microsatellite (SSR) analysis

According to genetic map for common wheat developed by Röder et al. (1998) and previous SSR analysis on synthetic wheat SHW-L1 (Zhang et al., 2004, 2007), SSR markers *gwm*183 and *gwm*544 were used for the identification of chromosomes 3D and 5B, respectively. PCR reactions were performed as described by Röder et al. (1998). The amplified fragments were separated by electrophoresis on 6% denatured polyacrylamide gel and visualized following the silver-staining method (Zhang et al., 2004).

RESULTS

Hybrid F_1 seeds were obtained from SHW-L1 - *A. peregrina* AS24 without embryo rescue. The F_1 seeds germinated giving vigorously growing F_1 plants and they inherited tough and tenacious glumes from AS24 (Zhang et al., 2007). Among the 31 F_1 hybrid plants observed (Table 1), 20 (64.52%) had the expected chromosome number 2n = 35 and were euploids (genome $ABDUS^l$). The remainder 11 plants (35.48%) were aneuploids with 33 (1 plants, 3.23%), 34 (6 plants, 19.35%), 36 (2 plants, 6.45%), and 37 (2 plants, 6.45%) chromosomes, respectively. Almost all pollen-mother-cells (PMCs) of *A. peregrina* AS24 showed 14 ring bivalents during meiotic metaphase I (MI) and should produce normal male gametes with n = 14 chromosomes. During MI of PMCs, however, the 42 chromosomes of newly synthetic wheat SHW-L1 showed a pairing configuration of 0.5 univalents + 3.57 rod bivalents + 17.09 ring bivalents + 0.05 quadrivalents. The high proportion of rod-shaped bivalents and the occurrence of univalents and quadrivalents indicated that the chromosome pairing of SHW-L1 was irregular to a certain extent. Aneuhaploid gametes could be produced in irregular PMCs. According to chromosome number of SHW-L1 - *A. peregrina* hybrids, it was estimated that besides 64.52% euhaploid gametes, SHW-L1 produced 3.23, 19.35, 6.45 and 6.45% functional aneuhaploid gametes (female) with 19, 20, 22 and 23 chromosomes, respectively.

The chromosome pairing during meiotic MI was observed (Table 1). Based on the pairing configurations, SHW-L1 - *A. peregrina* hyhrids were classified into three groups: (1) hybrids exhibiting low pairing with 0-2 chiasmata per cell (Figure 1A). All the plants with 2n=34 and 2n=35 chromosomes were included in this group; (2) hybrids exhibiting intermediate pairing with 2-5 chiasmata per cell. All the plants with 36 and 37 chromosomes were included in this group; (3) hybrid exhibiting high pairing more than 5 chiasmata per cell. Only plant 2 having 33

Table 1. Mean values of pairing configurations at metaphase I (MI) of meiosis in F_1 hybrids between SHW-L1 and *A. peregrina.*

Hybrid individual	Cells observed	Chromosome number	Pairing configurations						Chiasmata ± SEM
			I	II			III	IV	
				Rod	Ring	Total			
2	31	33	13.20**	5.72**	0.72**	6.44**	1.84**	0.04**	11.04 ± 1.05**
3	49	34	29.86	1.59	0.10	1.69	0.02	-	1.84 ± 0.20
6	34	34	32.18	0.38	0.06	0.44	-	-	0.50 ± 0.14
7	49	34	31.61	0.82	0.10	0.92	-	-	1.02 ± 0.17
14	60	34	31.60	0.78	0.07	0.85	0.03	-	1.02 ± 0.16
21	42	34	32.29	0.43	0.02	0.45	-	-	0.02 ± 0.02
23	47	34	32.60	0.23	0.11	0.34	-	-	0.45 ± 0.13
		Group means	31.69*	0.71	0.08	0.78	0.03	-	0.81 ± 0.14
1	45	36	30.20	1.42	0.87	2.29	0.11	-	3.38 ± 0.23
10	32	36	31.63	0.72	0.88	1.60	-	-	2.56 ± 0.18
		Group means	30.92*	1.07	0.88**	1.95**	0.06	-	2.97 ± 0.21**
8	29	37	28.62	2.07	1.38	3.45	0.03	-	4.97 ± 0.36
12	44	37	32.66	-	1.75	1.75	-	-	3.59 ± 0.15
		Group means	30.64*	1.04	1.57**	2.6**	0.02	-	4.28 ± 0.26**
4	54	35	31.39	1.39	0.11	1.50	0.11	-	1.61 ± 0.17
5	43	35	31.98	0.98	0.09	1.07	0.02	-	1.21 ± 0.24
9	42	35	31.79	0.98	0.07	1.05	0.10	-	1.31 ± 0.20
11	43	35	32.84	-	0.67	0.67	-	-	1.35 ± 0.15
13	59	35	32.58	0.92	0.02	0.94	-	-	0.95 ± 0.15
15	53	35	33.09	0.36	0.26	0.62	-	-	0.89 ± 0.14
16	52	35	33.71	0.17	0.14	0.31	-	-	0.44 ± 0.11
17	51	35	33.76	0.18	0.10	0.28	-	-	0.37 ± 0.11
18	45	35	32.71	0.60	0.16	0.76	-	-	0.91 ± 0.17
19	43	35	32.88	0.54	0.16	0.70	-	-	0.86 ± 0.15
20	50	35	32.94	0.70	0.08	0.78	-	-	0.86 ± 0.18
22	54	35	32.98	0.65	0.04	0.69	-	-	0.72 ± 0.12
24	77	35	32.74	0.77	0.09	0.86	0.03	-	1.00 ± 0.14
26	59	35	32.92	0.68	0.07	0.75	-	-	0.81 ± 0.14
27	45	35	33.38	0.42	-	0.42	-	-	0.42 ± 0.14
30	33	35	30.70	1.46	0.09	1.55	0.03	-	1.76 ± 0.29
32	61	35	32.78	0.74	0.10	0.84	0.02	-	0.97 ± 0.14
1[a]	58	35	34.26	0.05	0.02	0.07	-	-	0.09 ± 0.05
2[a]	30	35	32.57	0.03	0.60	0.63	-	-	1.23 ± 0.22
4[a]	70	35	33.39	0.33	0.23	0.56	0.03	-	0.81 ± 0.13
		Group means	32.77	0.63	0.16	0.75	0.02	-	0.93 ± 0.16

*, ** Significantly different from the hybrids group with 2n = 35 chromosomes at *P* = 0.05 and 0.01, respectively (t-test). [a] indicates the reciprocal *A.*

chromosomes with 11.04 chiasmata with an average pairing configuration of 13.20 univalents + 5.72 rod bivalents + 0.72 ring bivalents + 1.84 trivalents + 0.05 quadrivalents was included in this group (one of PMCs was shown in Figure 1B).

SSR analysis indicated that the band for marker *gwm*544-5B specific for chromosomes 5B was absent in plant 2 (Figure 2A, lane 4), which suggested the loss of chromosome 5B in this plant. Meanwhile, the presence of marker *gwm*183 specific for 3D indicated the presence of chromosome 3D with *Ph2* gene in plant 2 (Figure 2B).

DISCUSSION

Variations on chromosome pairing

Generally, there is a low pairing level among the 35 chromosomes of A, B, D, U and S^l genomes for the hexaploid wheat - *A. peregrina* hybrids in the presence

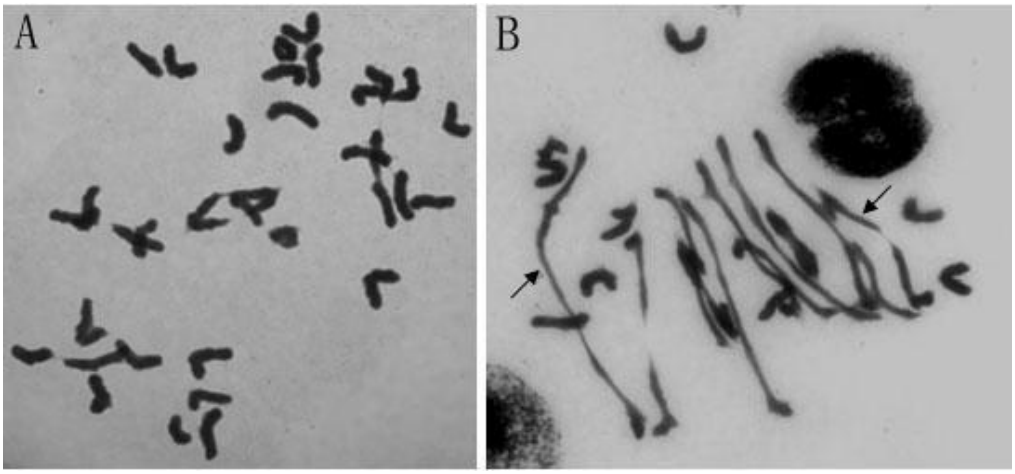

Figure 1. Meiotic chromosome pairing at MI in SHW-L1-*A. peregrina* AS24 hybrids. (A) 33 univalents + 1 ring bivalent for a PMC in the hybrid plant 5 (2n = 35); (B) 9 univalents + 2 ring bivalents + 7 rod bivalents + 2 trivalents (arrowed) for a PMC in the hybrid plant 2 (2n = 33).

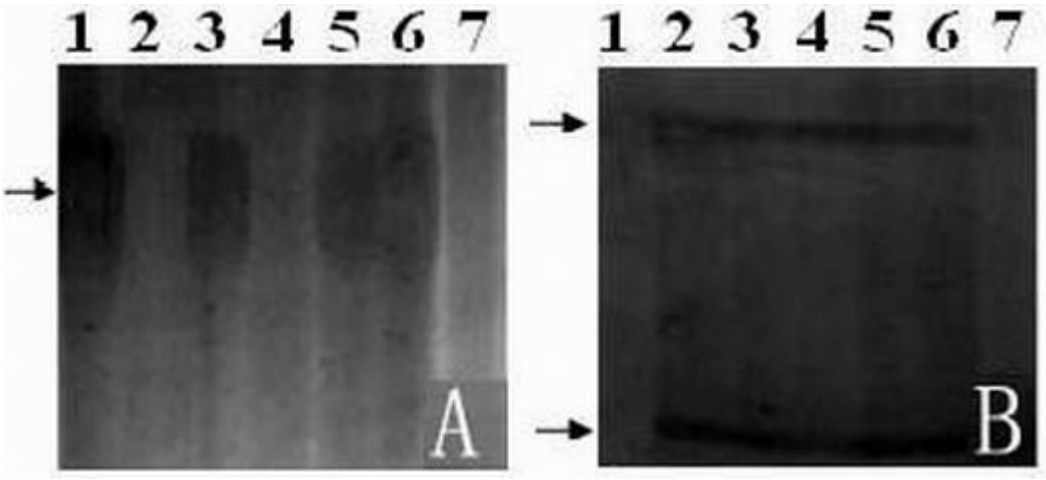

Figure 2. SSR amplification of SHW-L1-*A. peregrina* AS24 hybrids (lane 4: plant 2 with 2n = 33; lane 5: plant 4 with 2n = 35; lane 6: plant 5 with 2n=35) and their parents (lane 1: *T. turgidum* AS2255, the female parent of SHW-L1; lane 2: *A. tauschii* AS60, the male parent of SHW-L1; lane 3: synthetic hexaploid wheat SHW-L1; lane 7: *A. peregrina* AS24). (A) SSR products by marker *gwm*544-5B. The arrow indicated the specific SSR band from *T. turgidum* AS2255 (lane 1) disappeared in hybrid plant 2 (lane 4); (B) SSR products by marker *gwm*183 specific for 3D, which appeared in *A. tauschii* AS60 and all of its progenies (arrowed).

of *Ph1* and *Ph2*, which distinguishes between the differentiated sets of chromosomes and precludes pairing between homoeologues (Sears, 1976). The pairing data from the hybrid plants with 35 chromosomes in SHW-L1 - *A. peregrina* was agreed with this (Table 1). The intermediate pairing level for plants with 36 and 37 chromosomes in group 2 could be ascribed to the homologous pairing. The plants with 36 and 37 chromosomes had one and two pairs of homologous chromosomes due to the additional chromosomes of aneuhaploid gametes of SHW-L1, respectively. The high pairing level in plant 2 with 33 chromosomes was caused by the loss of chromosome 5B, the carrier of *Ph1* gene (Okamoto, 1957; Riley and Chapman, 1958). The loss of chromosome 5B result in high pairing level by promoting the pairing of homoeologous chromosomes among A, B, D, U and S^{l} genomes.

Cytological instability in newly synthetic hexaploid wheat

Cytological instability was frequently observed in newly synthetic polyploids (neopolyploids), which leads to the

production of aneuhaploid gametes or aneuploids (Ramsey and Schemske, 2002). In tribe Triticeae (Poaceae), cytological instability was clearly demonstrated in the first man-made crop, *Triticale* (x *Triticosecale*) including hexaploid (2n = 6x =42, AABBRR) and octaploid (2n = 8x = 56, AABBDDRR) (Gupta and Priyadarshan, 1982). The high frequency of aneuploids was a shortcoming for commercial use of the new crop. Present study demonstrated that newly synthetic hexaploid wheat SHW-L1 was cytologically instable and produced a high frequency of aneuhaploid gametes. Different from those neopolyploids with genomic combinations that do not exist in natural allopolyploids (nonnatural), SHW-L1 has genomic combination analogous to that of natural common wheat (natural). As common wheat does, SHW-L1 has *Ph* genes from its donor parent *T. turgidum*, which show strictly diploid-like meiotic behaviors. However, chromosome pairing of SHW-L1 was irregular to a certain extent. This result was agreed with the suggestion that besides *Ph* genes other factors were also involved in meiotic pairing (Feldman et al., 1997). A lot of studies on neopolyploids have presented extensive molecular evidences on rapid genomic changes from parental genomes accompanying wide hybridization and polyploidization, which may provide additional genetic base for enforcing exclusive homologous chromosome pairing and stabilizing newly formed hybrid genomes (Liu and Wendel, 2002; Adams and Wendel, 2005; Feldman and Levy, 2005; Ma and Gustafson, 2005).

The implications of gametes lacking *Ph1* gene for DNA introgression

The genetic system controlling diploid-like meiotic behavior is important for allopolyploids since it ensures allopolyploids full fertility, disomic inheritance and karyotypic stability (Okamoto, 1957; Riley and Chapman, 1958; Mello-Sampayo, 1971; Sears, 1976; Sánchez-Morán et al., 2001). In *T. turgidum* and common wheat, *Ph1* is by far the most effective gene responsible for the diploid-like meiotic behavior by the suppression of homoeologous pairing. *Ph1* also prevents pairing between wheat and alien chromosomes in wheat-alien hybrids. As shown in the present study, however, when *Ph1* gene is deficient, a large number of homoeologous chromosomes are paired in wheat - *A. peregrina* hybrid. The high level of pairing largely increases the chance for DNA introgression between wheat and alien species. As a consequence of introgression, genetic diversity and plasticity may be increased, which contributes to the adaptive potential of species. These results suggest that cytological instability of neopolyploids has a potential biological significance on DNA introgression.

In *Triticum-Aegilops* complex, the spontaneous production of neopolyploids is possible in the fields. Wheat sympatrically grows with wild wheat relatives of *Triticum-Aegilops* complex over large areas. The spontaneous interspecific hybridization is known to occur frequently (Zaharieva and Monneveux, 2006; Weissmann et al., 2008). Amphidiploids (neopolyploids) can be spontaneously produced from the hybrids of wheat with alien species by a union of unreduced gametes as a result of failure of either the first or the second meiotic division, which is controlled by the genes from wheat (Maan and Sasakuma, 1977; Xu and Dong, 1992; Pignone, 1993; Jauhar et al., 2000; Xu and Joppa, 2000; David et al., 2004; Jauhar, 2007; Zhang et al., 2007). When *Ph* gene is absent, neopolyploid provides a 'bridge' for transgenic walk from wheat to their wild relatives via recombination of homoeologous chromosomes.

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