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Nonadditive Changes in Genome Size During Allopolyploidization in the Wheat (*Aegilops-Triticum*) Group

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Interspecific or intergeneric hybridization, followed by chromosome doubling, can lead to the formation of new allopolyploid species. Recent studies indicate that allopolyploid formation is associated with genetic and epigenetic changes. Despite these studies, it is not yet clear whether the C value of an allopolyploid is the sum of its diploid parents. To address this question, six newly synthesized wheat allopolyploids and their parental plants were investigated. It was found that allopolyploids have a genome size significantly smaller than the expected value. The reduction of the nuclear genome size in the synthetic allotetraploids and allohexaploids was 2 pg DNA at 2C. It was also found that changes in the genome size already existed in the first generation amphiploids, indicating that the change was a rapid event. There was no difference in the reduction of nuclear genome size between the allotetraploid and the allohexaploid. These data clearly show that genome differentiation in allopolyploids was not related to the ploidy level. The data obtained clearly suggested that the nonadditive change in genome size that occurred during allopolyploidization may represent a preprogrammed adaptive response to genomic stress caused by hybridization and allopolyploidy, which serves to stabilize polyploid genomes.

Wide variation in eukaryotic genome size is a pervasive feature of evolution. Large differences in haploid DNA content (C value) are found within protozoa (5,800-fold range), arthropods (250-fold), fish (350-fold), algae (5,000-fold), and angiosperms (1,000-fold; Cavalier-Smith 1985). Many factors can affect the genome size, including polyploidy, fixation of accessory chromosomes, large duplications and expansions of satellite DNA, or transposable elements (SanMiguel et al. 1998). Polyploidy has played an important role in the evolution of higher plants. Between 50% and 70% of all angiosperm species are of polyploid origin (Wendel 2000). During the last two decades molecular data have provided new insights into the effects that changes in ploidy have on evolution, leading to significant progress in understanding the mechanisms and evolutionary aspects of polyploidy.

Among the cereals, the *Aegilops* and *Triticum* genera comprise many polyploids, including their diploid progenitors. The genome relationship between the naturally occuring *Aegilops-Triticum* allopolyploids and their diploid progenitors has been well established (Feldman et al. 1995). Newly formed allopolyploids of *Aegilops* and *Triticum*, therefore, are an excellent system for studying genome evolution. For instance, bread wheat (*Triticum aestivum*) is hexaploid ($2n = 6\times = 42$) with three (A, B, and D) genomes, each containing seven pairs of homoeologous chromosomes. It is a classical example of allopolyploidization, originating from the hybridization of three different diploid progenitors from *Aegilops* and *Triticum* (Kihara 1944; McFadden and Sears 1944). Studies of synthetic allopolyploids such as *Brassica* and wheat have shown that polyploidization can lead to rapid and extensive genome changes (Feldman et al. 1997; Liu et al. 1998a,b; Song et al. 1995). In particular, studies of newly synthesized allopolyploid wheats have shown that allopolyploid formation is accompanied by extensive genome changes at the molecular level, including rapid and nonrandom elimination of specific low-copy DNA sequences, as well as other types of genomic modifications (Ozkan et al. 2001; Shaked et al. 2001).

Despite these studies, it is not yet clear whether the C value of an allopolyploid is the sum of that of its diploid parents. In the wheat (*Aegilops-Triticum*) group, previous studies (Furuta et al. 1974; Furuta et al. 1986; Pegington and Rees 1970) have shown that the genome size of tetraploid and hexaploid wheat were additive when they were

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Table 1. Newly synthesized allopolyploids of *Aegilops* and *Triticum* used in this study

Cross combination	Genome constitution	Studied generation		
		S_1	S_2	S_3
Diploid × diploid				
Ae. longissima (TL02)–*Ae. umbellulata* (TU02)	S^lS^lUU		+	
Ae. sharonensis (TH01)–*Ae. umbellulata* (TU02)	S^hS^hUU	+		+
T. urartu (TMB38)–*Ae. tauschii* (TQ27)	AADD	+	+	
Tetraploid × diploid				
T. turgidum ssp. *dicoccoides* (TTD20)–*Ae. tauschii* (TQ27)	BBAADD			+
T. turgidum ssp. *carthlicum* (TTH01)–*Ae. tauschii* (TQ27)	BBAADD	+	+	+
T. turgidum ssp. *durum* (TTR19)–*Ae. sharonensis* (TH01)	$BBAAS^hS^h$		+	

Designation of parental lines in parentheses.

compared to parental species. However, Boyko et al. (1984) reported that DNA content decreased during the course of triticale (X *Tritisecale Wittmack*) formation, as compared to the expected value for the combined wheat and rye (*Secale cereale*) genomes. They found a 9% decrease in genome size for octoploid triticale and as much as a 28%–30% decrease for hexaploid triticale. In the above studies, except for the work on triticale, synthetic amphiploids were compared with parental accessions rather than the exact parental plant. Therefore, it was impossible to determine the exact genome size deviation from additivity, because of intra-accession genome size polymorphism (Bennett and Leitch 1991; Furuta 1975; Nishikawa and Sawai 1969). To address this question, in this study we used six newly synthesized allopolyploids of wheat. These allopolyploids have a genome size significantly smaller than predicted with an additive model.

Materials and Methods

Six newly synthesized amphiploids and their parental plants were used in this study (Table 1). The crosses were performed between species of the same ploidy level, as well as between species of different ploidy level. At the three to four tiller stages, hybrids were treated with 0.2% (w/v) colchicine (Sigma) for 5 hr at room temperature and then washed in tap water for 1 hr. After treatment plants were grown in the greenhouse until maturity, and all spikes were bagged. The designation of the different allopolyploid generations is S (selfed). Accordingly, polyploidy tissues on F_1 plants are S_0, the seed produced on S_0 tissues (i.e., after meiosis) and plants developed from them are S_1, and so on. Single plants used as parents were bagged and selfed so that the synthetic allopolyploids could be traced to specific parental lines. The parental plants and the synthetic allopolyploids are maintained in our collection (University of Çukurova, Adana, Turkey). The amphiploid *T. turgidum* ssp. *carthlicum–Ae. tauschii* is hexaploid, with a genomic constitution similar to hexaploid bread wheat (*T. aestivum*), whereas the amphiploid *T. urartu–Ae. tauschii* is tetraploid, with a genomic constitution that does not exist in nature.

For the study, five seeds of each parental line and each amphidiploid were planted into individual containers in a greenhouse. The chromosome numbers of the newly synthesized amphiploids were counted, and aneuploid plants were discarded before analysis. Genome size was determined by measuring nuclear DNA content with flow cytometry at the University of Nebraska Flow Cytometry Core Reseach Facilities [FACScan flow cytometer (Becton Dickinson Immunocytometry system, San Jose, CA)]. Both barley ($2n = 2\times = 14$) and wheat ($2n = 6\times = 42$) were used as standards because of the large variation in DNA content of plants analyzed. The methods are described in Tuna et al. (2001). Briefly, the procedure consists of preparing suspensions of intact nuclei by chopping plant tissues and lysing protoplasts in a $MgSO_4$ buffer mixed with DNA standards and then staining the nuclei with propidium iodide (PI) in a solution containing DNAase-free RNAase. Fluorescence intensities of the stained nuclei were measured by flow cytometry. Values for nuclear DNA contents were estimated by comparing fluorescence intensities of the nuclei of the test population with those of an appropriate internal DNA standard that was included with the tissue being tested. For each measurement, propidium iodide fluorescence area signals (FL2-A) from 1,000 nuclei were collected with use of CellQuest software (Becton Dickinson Immunocytometry system, San Jose, CA). A live gate was set using the FL2-2 and FSC parameters, allowing the fluorescence measurements from the nuclei to generate a histogram of FL2-A. The mean positions of the G0/G1 (nuclei) peaks for the samples and the internal standards were determined with use of CellQuest software to analyze the data. The mean DNA content per plant was based on the 1,000 scanned nuclei. The formula used for converting florescence values to DNA content was Nuclear DNA content = (mean position of unknown peak)/(mean position of known) × DNA content of known standard.

Results

The chromosome number, the 2C nuclear DNA amounts expressed in picogram (pg), and the ploidy levels of both the newly synthesized amphiploids and their parents are given in Table 2. Table 2 also contains the expected DNA values for these newly synthesized amphiploids, estimated as a sum of the 2C DNA values of their parents. The data show that there has been a loss of DNA from the newly synthesized

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Table 2. Nuclear 2C DNA amounts (pg) of newly synthesized amphiploids and of their parents

Parents and amphiploids	Generation	2*n*	Genome	Observed DNA value	Expected DNA value	Reduction (pg)
T. turgidum ssp. *carthlicum*		28	BBAA	23.64 ± 0.23		
Ae. tauschii		14	DD	10.16 ± 0.02		
T. turgidum ssp. *carthlicum–Ae. tauschii*	S_1	42	BBAADD	32.13 ± 0.13	33.80	1.67
	S_2	42	BBAADD	31.23 ± 0.06	33.80	2.57
	S_3	42	BBAADD	31.44 ± 0.06	33.80	2.36
T. turgidum ssp. *dicoccoides*		28	BBAA	23.97 ± 0.04		
Ae. tauschii		14	DD	10.16 ± 0.06		
T. turgidum ssp. *dicoccoides–Ae. tauschii*	S_2	42	BBAADD	31.80 ± 0.11	34.13	2.33
Ae. longissima		14	S^lS^l	14.35 ± 0.09		
Ae. umbellulat		14	UU	10.87 ± 0.11		
Ae. longissima–Ae. umbellulata	S_2	28	S^lS^lUU	23.21 ± 0.04	25.22	2.01
Ae. sharonensis		14	S^hS^h	14.65 ± 0.07		
Ae. umbellulata		14	UU	10.80 ± 0.09		
Ae. sharonensis–Ae. umbellulata	S_1	28	S^hS^hUU	23.15 ± 0.06	25.45	2.30
	S_3	28	S^hS^hUU	23.17 ± 0.10	25.45	2.28
T. turgidum ssp. *durum*		28	BBAA	23.91 ± 0.12		
Ae. sharonensis		14	S^hS^h	14.66 ± 0.07		
T. turgidum ssp. *durum–Ae. sharonensis*	S_3	42	BBAASS	36.52 ± 0.10	38.57	2.05
T. urartu		14	AA	11.76 ± 0.07		
Ae. tauschii		14	DD	10.16 ± 0.13		
T. urartu–Ae. tauschii	S_1	28	AADD	19.67 ± 0.26	21.92	2.25
	S_2	28	AADD	19.80 ± 0.07	21.92	2.12

S, selfing generation.

allopolyploids by the first generation of the amphiploid (S_1), and this loss was fixed in the second amphiploid generation (S_2). Genome size in the synthetic allohexaploids and allotetraploids that exist in nature were less than the expected value (Table 2). In order to determine whether DNA loss was specific for the newly synthesized allopolyploids that had a genomic constitution analogous to that of natural allopolyploids or not, we also analyzed an artificial allotetraploid and allohexaploid containing the A and D genomes (*T. urartu–Ae. tauschii*), and BBAA and S genomes (*T. turgidum* ssp. *durum–Ae. sharonensis*), genomic constitutions that do not exist in nature. In these allopolyploids DNA loss was also observed (Table 2). In addition, it was found that whole allopolyploids, whether they had a genomic constitution analogous to that of natural allopolyploids or not, had the same amount of DNA reduction (Table 2).

Discussion

Although many higher plants, including many important crops (wheat, cotton, *Brassica*, etc.) underwent speciation through allopolyploidy, little is known about the nature of genome size changes during this event. The relationship between polyploidy and genome size has been discussed by several authors. For instance, Furuka et al. (1974) reported that two natural and six synthesized hexaploid wheats had similar DNA contents that were approximately equal to the sum of those of their parents. This was in agreement with the results of Rees (1963), Rees and Walters (1965), Nishikawa and Furuta (1969), and Pegington and Rees (1970) in the wheat (*Aegilops-Triticum*) group. The DNA content of the amphiploids in *Brassica* (Verma and Rees 1974), *Arachis* (Sing et al. 1996), *Glycine* (Hammatt et al. 1991), and *Allium* (Ohri et al. 1998) corresponded to the sum value estimated for parental species. However, this is not always the case with other plant species. For instance, Narayan (1998) found DNA content less than the sum of the putative parents in *Brassica* allopolyploids. He reported that the genome sizes of present-day allopolyploids of *Brassica* were, on average, 6.81% less than the expected value. He also compared *Nicotiana* allopolyploids to their putative progenitors and observed an average of 13% or 1.84 pg reduction of genome size in *N. arentsii*. In addition, increases in genome size have been observed (on average 2%) in *N. rustica* and *N. tabacum* (Narayan 1998). Grant (1969) postulated that a reduction in DNA content was associated with the adaptation necessary for establishment of the highest ploidy levels (12×) in *Betula*. Boyko et al. (1984) reported that DNA content decreased in the course of triticale breeding as compared to the expected value for the combined wheat and rye genomes. They found that this decrease was about 9% for octoploid triticale and reached 28%–30% for hexaploid triticale. Raina et al. (1994) studied the changes in DNA content in C_0 (first generation) and subsequent generations of induced autopolyploids of *Tephrosia* and *Phlox*. Although DNA content increased in C_0 of *Tephrosia oxygona* L. and *T. purpure* L., it decreased by 16.7 % of the expected doubled value in the C_0 generation of *Phlox drummondii*, and in C_2 an overall reduction of 25% was noticed. They reported that this loss of DNA was achieved by equal reduction in all of the chromosomes in the complement. Vogel et al. (1999) used flow cytometry to determine the base DNA content of the genomes of the perennial *Triticeae* and concluded that gain or loss of nuclear DNA content occurred during the evolution of perennial *Triticeae* and was probably a part of the speciation process.

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Tuna et al. (2001) used nuclear DNA content information determined by flow cytometery in the ploidy determination of bromegrass germplasm accessions. Their results indicated a slight tendency toward diminution of DNA content with increased ploidy.

A shortcoming of many of these studies reported was the absence of data for the parental plants that directly gave rise to the amphiploid. We therefore used newly synthesized amphiploids with exact parental lines. The chromosome number of newly synthesized amphiploids was counted and aneuploid plants were discarded before analysis. Moreover, parental plants were checked for homozygosity as described by Ozkan et al. (2001). Three to four individual plants randomly chosen from the S_1, S_2, and S_3 generations of the synthetic amphiploids (Table 1), and their parental plants were analyzed. We found that the DNA content was less than the sum of the parental plants in the wheat (*Aegilops-Triticum*) group allopolyploids. It was also found that changes in the genome size already existed in first generation amphiploids, indicating that the change in the genome size occurs rapidly. It was found that during allopolyploidization two pg DNA at 2C was approximately eliminated in the synthetic allotetraploids and allohexaploids (Table 2). We were unable to determine whether this elimination was due to hybridity or allopolyploidization. Therefore, further work is required in order to clarify this point. There was no difference in the reduction of nuclear genome size between the allotetraploid and the allohexaploid. These data clearly show that genome differentiation in allopolyploids was not related to the ploidy level. However, using flow cytometry, we were not able to determine if all of the parental genomes were affected equally. In previous works Ozkan et al. (2001) and Shaked et al. (2001) have shown that a limited set of loci could undergo rapid elimination in newly synthesized allopolyploids from the wheat (*Aegilops-Triticum*) group. Ozkan et al. (2001) focused the rate and time of elimination of two kinds of low-copy DNA sequences (namely, chromosome-specific sequence and genome-specific sequences) in F_1 hybrids and newly formed allopolyploids of *Aegilops* and *Triticum*. They reported that allopolyploidy-induced sequence elimination occurred in a sizable fraction of the genome and in sequences that were apparently noncoding. In addition, Shaked et al. (2001) used a different strategy to study genomic changes. Rather than monitoring a small number of known sequences in many hybrids and allopolyploids combinations, they studied F_1 hybrids between diploid species from the wheat (*Aegilops-Triticum*) group and their derived allotetraploids. They did this by screening a large number of loci, using Amplified Fragment Length Polymorphism (AFLP) technology. Specifically, they analyzed two newly synthesized amphiploids, *Ae. sharonensis–Ae. umbellulata* (used in this study) and *T. urartu–Ae. longissima*. They found that sequence elimination was one of the major and immediate responses of the wheat genome to wide hybridization or allopolyploidy and that it affects a large fraction of both of the genomes. Interestingly, they reported that the parental genomes were not affected equally. Indeed, they provided a quantitative assessment that the process of allopolyploidization could affect up to 14% of a genome sequences in allopolyploids. They also determined that the timing of elimination was dependent on the genomic combination; most elimination occurred in the F_1 hybrids of *Ae. sharonensis–Ae. umbellulata*, whereas in *T. urartu–Ae. longissima*, most elimination occurred after chromosome doubling.

The finding that 2 pg DNA could be eliminated in a single generation shows that allopolyploidy leads not only to the establishment of new species in one step, but also to rapid evolution of the individual genomes in the allopolyploid background. Such rapid evolution could explain the elusive nature of the B genome of wheat (Talbet et al. 1995). Interestingly, Kerber (1964) mentioned that the extracted tetraploid (A and B genomes) from hexaploid bread wheat (A, B, and D genomes) did not closely resemble the present-day varieties of emmer wheat, as it was dwarfish, was partially sterile, and lacked vigor. He therefore considered that genetic changes took place within the A and B genomes of tetraploid wheat after polyploidization. Kerber's conclusion can be supported by our results. These results also suggest that genomes do not have a one-way ticket to obesity (Bennetzen and Kellogg 1997).

Flow cytometry provides a fast and accurate way to look at changes in genome size during evolution and differentiation. Our work extends previous studies on wide hybrids in cereals (Ozkan et al. 2001; Shaked et al. 2001), studies which looked at single loci: here we quantified this response on a genome-wide basis, using flow cytometry. Our data concur with previous work that showed rapid sequence elimination (Ozkan et al. 2001; Shaked et al. 2001). Although allopolyploidy leads to an increase in genome size, this increase is less than expected through additivity (Table 1). Although the mechanism underlying the widespread excision of genomic sequences is unknown, several molecular mechanisms were mentioned by Shaked et al. (2001).

According to the example offered by the wheat model, genome size reduction may be a mechanism promoting successful polyploid speciation events. This kind of genetic modification with associated quantitative changes in the amount of DNA would be one of the ways by which polyploids acquire stability at both a cytological and genetic level. The present results suggest that the 2-pg DNA reduction during the allopolyploidization is partly neutralized by the remarkably inherent capacity in the wheat (*Aegilops-Triticum*) genomes to bring about rapid adaptative change in nuclear DNA. This change leads to other beneficial changes, such as the regulation of meiosis to ensure good seed set. According to Stebbins (1980), the quantitative change in chromosome number and nuclear DNA is only one of a series of complex processes that must take place for polyploidy to be successful in nature. For instance, significant reduction in genome size in triticale, one of the most promising human-made amphiploids (Stebbins 1956) resulted in improved agronomic performance (Bennett, 1985).

In conclusion, allopolyploidization in the wheat group induced a 2-pg DNA loss. This loss, which augments the differentiation of two genomes in the allopolyploid background, may provide the physical basis for the diploid-like

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meiotic behavior of the raw allopolyploids. The resultant strict bivalent pairing may prevent intergenomic recombination, and therefore may allow higher fertility and permanent heterosis between homoeoalleles. This effect fosters the successful establishment of the newly formed allopolyploid species in nature (Ozkan et al. 2001). The data obtained clearly suggest that the nonadditive change in genome size during allopolyploidization may be a one-step process with no further reduction of genome size during subsequent generations, and that this process may be one way of establishing a stable polyploid species in nature.

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References

Bennett MD, 1985. Intraspecific variation in DNA amount and the nucleotypic dimension in plant genetics. In: Plant genetics (UCLA symposia on molecular and cellular biology) (Freeling M, ed). New York: Liss; 283–302.

Bennett MD and Leitch IJ, 1991. Nuclear DNA amounts in angiosperm. Ann Bot. 76:113–176.

Bennetzen JL and Kellogg EA, 1997. Do plants have a one-way ticket to genomic obesity? Plant Cell 9:1509–1514.

Boyko EV, Badaev NS, Maximov NG, and Zelenin AV, 1984. Does DNA content change in the course of Triticale breeding? Cereal Res Com 12(1–2):99–100.

Cavalier-Smith T, 1985. The evolution of genome size. New York: Wiley.

Feldman M, Liu B, Segal G, Abbo S, Levy AA, and Vega JM, 1997. Rapid elimination of low-copy DNA sequences in polyploid wheat: A possible mechanism for differentiation of homoeologous chromosomes. Genetics 147:1381–1387.

Feldman M, Lupton FGH, and Miller TE, 1995. Wheats. In: Evolution of crop plants, 2nd ed. (Smartt J and Simmonds NW, eds). London: Longman Scientific; 184–192.

Furuka Y, Nishikawa K, and Tanino T, 1974. Stability in DNA content of AB genome component of common wheat during the past seven thousand years. J Genet 49:(4):179–187.

Furuta Y, 1975. Quantitative variation of nuclear DNA in genus *Aegilops*. Jpn J Genet. 50:383–392.

Furuta Y, Nishikawa K, and Yamaguchi S, 1986. Nuclear DNA content in diploid wheat and its relatives in relation to the phylogeny of tetraploid wheat. Jpn J Genet 61:97–105.

Grant WF, 1969. Decreased DNA content of birch (Betula) chromosomes at high ploidy as determined by cytophotometry. Chromosoma 26:326–336.

Hammatt N, Blackall NW, and Davey MR, 1991. Variation in the DNA content of *Glycine* species. J Exp Bot 42:659–665.

Kerber ER, 1964. Wheat: Reconstitution of the tetraploid component (AABB) of hexaploid. Science 143:253–255.

Kihara H, 1944. Discovery of the DD-analyzer, one of the ancestors of *Triticum vulgare* (in Japanese). Agr Hort Jpn 19:889–890.

Liu B, Vega JM, and Feldman M, 1998a. Rapid genomic changes in newly synthesized amphiploids of *Triticum* and *Aegilops*: II. Changes in low-copy DNA sequences. Genome 41:535–542.

Liu B, Vega JM, Segal G, Abbo S, Rodova M, and Feldman M, 1998b. Rapid genomic changes in newly synthesized amphiploids of *Triticum* and *Aegilops*: I. Changes in low-copy non-coding DNA sequences. Genome 41:272–277.

McFadden ES and Sears ER, 1944. The artificial synthesis of *Triticum spelta*. Rec Genet Soc Am. 13:26–27.

Narayan RKJ, 1998. The role of genomic constraints upon evolutionary changes in genome size and chromosome organization. Ann Bot 82:57–66.

Nishikawa K and Furuta Y, 1969. DNA content per nucleus in relation to phylogeny of wheat and its relatives. Jpn J Genet 44:23–29.

Nishikawa K and Sawai Y, 1969. Relative amount of nuclear DNA in tetraploid wheat. Wheat Inf Serv 29:2–3.

Ohri D, Fritsch RM, and Hanelt P, 1998. Evolution of genome size in *Allium* (Alliaceae). Plant Syst Evol 210:57–86.

Ozkan H, Levy AA, and Feldman M, 2001. Allopolyploidy-induced rapid genome evolution in the wheat (*Aegilops-Triticum*) group. Plant Cell 13:1735–1747.

Pegington C and Rees H, 1970. Chromosome weights and measures in the Triticinae. Heredity 25:195–205.

Raina SN, Parida A, Koul KK, Salimath SS, Bisht MS, Raja V, and Khostoo TN, 1994. Associated chromosomal DNA changes in polyploids. Genome 37:560–564.

Rees H, 1963. Deoxyribonucleic acid and the ancester of wheat. Nature 198:108–109.

Rees H and Walters MR, 1965. Nuclear DNA and the evolution of wheat. Heredity 20:73–82.

SanMiguel P, Gaut BS, Tikhonov A, Nakajima Y, and Bennetzen JL, 1998. The paleontology of intergene retrotransposons of maize: Dating the strata. Nat Genet. 20:43–45.

Shaked H, Kashkush K, Ozkan H, Feldman M, and Levy AA, 2001. Sequence elimination and cytosine methylation are rapid and reproducible responses of the genome to wide hybridization and allopolyploidy in wheat. Plant Cell 13:1749–1759.

Sing KP, Raina SN, and Singh AK, 1996. Variation in chromosomal DNA associated with the evolution of *Arachis* species. Genome 39:890–897.

Song K, Lu P, Tang K, and Osborn TC, 1995. Rapid genome change in synthetic polyploids of *Brassica* and its amplications for polyploid evolution. Proc Natl Acad Sci USA 92:7719–7723.

Stebbins GL, 1956. Artificial polyploidy as a tool in plant breeding. Brookhaven Symp Biol 9:37–52.

Stebbins GL, 1980. Polyploidy in plants: unsolved problems and prospects In: Polyploidy: biological relevance (Lewis WH, ed). New York: Plenum; 495–520.

Talbert LE, Blake NK, Starlie EW, and Lavin M, 1995. Variability in wheat based on low-copy DNA-sequence comparisons. Genome 38:951–957.

Tuna M, Vogel KP, Arumuganathan K, and Gill BS, 2001. DNA content and ploidy determination of bromegrass germplasm accessions by flow cytometry. Crop Sci 41:1629–1634.

Verma SC and Rees H, 1974. Nuclear DNA and evolution of allotetraploid *Brassicae*. Heredity 33:61–68.

Vogel KP, Arumuganathan K, and Jensen KB, 1999. Nuclear DNA content of perennial grasses of the Triticeae. Crop Sci 39:661–667.

Wendel JF, 2000. Genome evolution in polyploids. Plant Mol Biol 42: 225–249.

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