Rapid and Repeatable Elimination of a Parental Genome-Specific DNA Repeat (pGc1R-1a) in Newly Synthesized Wheat Allopolyploids

Fangpu Han,*1 George Fedak,1 Wanli Guo* and Bao Liu*,2

*Laboratory of Molecular Epigenetics, Institute of Genetics and Cytology, Northeast Normal University, Changchun 130024, China and 1Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-Food Canada, Ottawa, Ontario K1A 0C6, Canada

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ABSTRACT

Recent work in the Triticum-Aegilops complex demonstrates that allopolyploidization is associated with an array of changes in low-copy coding and noncoding sequences. Nevertheless, the behavior and fate of repetitive DNA elements that constitute the bulk of nuclear DNA of these plant species is less clear following allopolyploidy. To gain further insight into the genomic events that accompany allopolyploid formation, we investigated fluorescence in situ hybridization (FISH) patterns of a parental-specific, tandem DNA repeat (pGc1R-1) on three sets of newly synthesized amphiploids with different parental species. It was found that drastic physical elimination of pGc1R-1 copies occurred in all three amphiploids in early generations. DNA gel-blot analysis confirmed the FISH data and estimates indicated that ~70-90% of the copies of the pGc1R-1 repeat family were eliminated from the amphiploids by the second to third selfed generations. Thus, allopolyploidy in Triticum-Aegilops can be accompanied by rapid and extensive elimination of parental-specific repetitive DNA sequences, which presumably play a role in the initial stabilization of the nascent amphiploid plants.

ALLOPOLYPLOIDS, derived from interspecific or intergeneric hybridizations, contain two or more divergent homeologous genomes. Following initial hybridization and genome doubling, the newly formed amphiploid may undergo a one-step specification process that can be a traumatic experience to the combined allopolyploid genomes (reviewed in Leitch and Bennett 1997; Matzke et al. 1999; Comai 2000; Wendel 2000; Rieseberg 2001; Adams and Wendel 2004; Feldman and Levy 2005). Indeed, a number of recent reports have documented rapid genetic and epigenetic instability that often accompany nascent allopolyploidy (reviewed in Pikaard 2001; Levy and Feldman 2002, 2004; Liu and Wendel 2002; Comai et al. 2003; Lawton-Rauh 2003; Osborn et al. 2003b; Chen et al. 2004; Madlung and Comai 2004; Soltis et al. 2004; Ma and Gustafson 2005).

A series of studies on newly synthesized allopolyploids of Triticeae, and particularly of the Triticum-Aegilops complex, has been particularly revealing in detecting rapid genomic and epigenomic changes (Ozkan et al. 2001; Shaked et al. 2001; Han et al. 2003, 2004; Ma et al. 2004). Among the changes it was found that the most tantalizing but still mysterious phenomenon was rapid, reproducible, and often nonrandom elimination of low-copy, coding and noncoding DNA sequences (Feldman et al. 1997; Liu et al. 1998; Ozkan et al. 2001; Shaked et al. 2001; Kashkusht et al. 2002; Ma et al. 2004). Surprisingly, probably due to intrinsic difficulties in monitoring changes in only some members of a given repetitive DNA family, little attention has been paid to the behavior and fate of this type of sequence, which constitutes the bulk of these plant genomes. Nonetheless, for the few relevant studies available, a generic finding is that reduction in copy number of some DNA repeats appeared to be associated with interspecific hybridization and allopolyploidy in Triticeae. For example, it was found that, on the basis of DNA gel-blot analysis, although the DNA repeat pAesKB52 hybridized to Aegilops speltoides, Ae. sharonensis, and Ae. longissima—three probable diploid progenitors to the B genome of various polyploid wheats—it did not hybridize to any of the polyploid wheat species tested, thus suggesting elimination and/or extensive sequence divergence of the DNA repeat since allopolyploid formation (Anamthawat-Jonsson and Heslop-Harrison 1993).

Moreover, significant reduction in copy numbers of Spelt1, a repetitive subtelomeric DNA family that represents 2% of the Ae. speltoides genome, was found in natural tetra- and hexaploid wheat, Triticum turgidum and T. aestivum, as well as in the first generations of amphiploids that have Ae. speltoides as a parent (Pestsova et al. 1998; Salina et al. 2004). Similarly, a dispersed repetitive DNA family (pSp89.XI) that is Ae. Speltoides specific was also found to have a much reduced abundance in tetra- and hexaploid wheat (Daud and

1Present address: Division of Biological Sciences, University of Missouri, Columbia, MO 65211.
2Corresponding author: Laboratory of Molecular Epigenetics, Northeast Normal University, Renmin St. 5268, Changchun 130024, China. E-mail: baoliu6677@yahoo.com.cn

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Gustafson 1996). Finally, a global comparison of the C-values (genome sizes) of newly synthesized wheat amphiploids and their parents indicates nonadditivity and significant downsizing of the amphiploid genomes, although specific sequences underlying the reduction were not identified (Ozkan et al. 2003). More significantly, this less-than-proportional increase in genome size in a polyploid species expected from the addition of its diploid progenitors appeared to be a widespread phenomenon in flowering plants (Leitch and Bennett 2004). Thus, it is clear that, similar to the situation for some of the unstable low-copy sequences that have been extensively studied (reviewed in Feldman and Levy 2005), some repetitive DNA families may be extremely labile following allopolyploidization in plants and may undergo gradual or drastic elimination. Nonetheless, because none of the above studies has used independently synthesized multiple sets of new amphiploids with known exact parental plants, it remains inconclusive with regard to elimination or divergence as a cause for the observed phenomenon or the timing and repeatability of its occurrence.

Clone pGc1R-1 is a tandem DNA repeat, isolated from Ae. speltoides, which hybridizes at the fluorescence in situ hybridization (FISH) level to three species of the diploid Aegilops Sitopsis section, Ae. speltoides, Ae. longissima, and Ae. sharonensis, but not to the other two species, Ae. bicornis and Ae. searsii, nor to tetra- and hexaploid wheat (Friebe et al. 2000; Zhang et al. 2002). It has been suggested that the most parsimonious explanation for the differential occurrence of pGc1R-1 and its related sequences among the Aegilops species, as well as between the diploid Aegilops species (the proposed genome donors to polyploid wheat) and polyploid wheat, is elimination rather than multiple, independent amplification in different species (Zhang et al. 2002). However, because only natural plants were studied, direct evidence for allopolyploidy-associated elimination of this sequence is lacking.

In this study, we investigated behavior of pGc1R-1 in three sets of newly synthesized wheat allopolyploids (amphiploids) (Ozkan et al. 2001), each having as a parental one of the three Sitopsis species, Ae. speltoides, Ae. longissima, and Ae. sharonensis, that contain the DNA repeat. We report that rapid elimination of pGc1R-1 copies occurred in all three sets of synthetic amphiploids irrespective of the difference in species combination or ploidy levels. We discuss potential causes for this elimination of parental-specific DNA repeats and its possible role in the stabilization of newly formed allopolyploid plants.

MATERIALS AND METHODS

Plant materials: Plant materials used for this study consisted of three sets of synthetic amphiploids and their exact parental plants, namely Aegilops longissima (accession TL05) × Triticum urartu (accession TMU06), Ae. sharonensis (accession TH02) × T. monococcum (accession TMB02), and T. aestivum (accession 252) × Ae. speltoides (accession 15-1). All three sets of amphiploids were produced in the laboratory of M. Feldman at the Weizmann Institute of Science, Rehovot, Israel. Since production, all plant materials (amphiploids and parents) were maintained by strict selfing under normal greenhouse conditions.

FISH: Clone pGc1R-1 is a 258-bp fragment of a tandem repetitive DNA element cloned from Ae. speltoides and kindly supplied by B. Friebe of the Wheat Genetics Resource Center, Kansas State University (Manhattan, KS). Actively growing roots were removed and placed in ice water for 24–28 hr, fixed in Carnoy’s (3:1) fixative for 24 hr, and stored in 70% ethanol. Root tips were stained with 1% acetic-carmine for 0.5–2 hr and squashed in 45% acetic acid. The slides were frozen in liquid nitrogen and the coverslips were removed with a razor blade. The slides were dehydrated in 95% ethanol for 5 min and stored at −20° until use. The probes were labeled with biotin-16-dUTP by the random primer method. Slide pretreatment, hybridization, signal amplification, and detection of fluorescent signals were as described by Han et al. (2004). At least 20 well-spread metaphase cells were examined for each plant line.

DNA gel-blot analysis: Young leaves of individual plants were collected and stored in liquid nitrogen until DNA extraction. Genomic DNA was isolated by a modified CTAB method (Kidwell and Osborn 1992). DNA (~10 μg each sample) from each individual was digested to completion with one of four restriction enzymes, BamHI, DraI, EcoRV, or TaqI (New England Biolabs, Beverly, MA). Digested DNA was fractionated by electrophoresis in 0.8% agarose gel and transferred onto Hybond N+ filter by the alkaline method. The probes, clone pGc1R-1 (see results), and three mapped low-copy RFLP markers, PSR301, PSR593, and PSR743 (Gale et al. 1993), were radioactively labeled with [32P]dCTP by the random primer method. Prehybridization, hybridization, and blot washing conditions were as described earlier (Liu et al. 1997). To have a general quantitative estimation on the extent of reduction in copy number of clone pGc1R-1 in the three amphiploids relative to their parents, each lane in the blots was scanned and densitometrically measured by using the UTHSCSA ImageTool software (http://ddsdx.uthscsa.edu/). The values (in arbitrary units) were normalized against those of the corresponding low-copy control probes. Mean values were calculated on the basis of all four enzyme digests and used for comparison of an amphiploid and its parents.

RESULTS AND DISCUSSION

Rapid elimination of pGc1R-1a-containing DNA sequences in three sets of synthetic wheat allopolyploids as revealed by FISH analysis: Clone pGc1R-1a is a 258-bp fragment of a tandem repetitive element cloned from Ae. speltoides, which hybridizes, at the FISH level, to the telomeric and subtelomeric regions of most Ae. speltoides chromosomes (Friebe et al. 2000). This element also hybridizes, albeit to a lesser extent, to both the number of hybridization sites and the strength of the FISH signal, to two other species of the diploid Aegilops Sitopsis section, Ae. longissima and Ae. sharonensis, but does not hybridize to Ae. searsii and Ae. bicornis (Zhang et al. 2002). Interestingly, although multiple lines of evidence implicate Ae. speltoides as the most probable progenitor to the B genome of tetraploid wheat,
T. turgidum (genomes AABB), and hexaploid wheat, T. aestivum (genomes AABBDD) (Gill and Appels 1987; Kerby et al. 1988; Dvorak and Zhang 1990; Jiang and Gill 1994; Badaeva et al. 1996; Daud and Gustafson 1996; Sasanuma et al. 1998; Wang et al. 2000), pGc1R-1a hybridizes to neither of the polyploid species (Friebe et al. 2000; Zhang et al. 2002; also Figure 1i). On the basis of this finding, it was suggested that this element was likely eliminated during and/or following the allopolyploidization event leading to speciation of the tetraploid wheat, T. turgidum (Zhang et al. 2002). Nevertheless, because T. turgidum is hundreds of thousands of years old (Feldman 2001), an equally plausible explanation is gradual sequence divergence after tetraploid formation. To distinguish these two possibilities, we investigated the FISH patterns of pGc1R-1 in three sets of newly synthesized amphiploids, each involving one of the three diploid species, Ae. longissima, Ae. sharonensis, and Ae. speltoides, as a parent. It was found that drastic loss of FISH signals (hybridization sites) occurred in all three sets of synthetic amphiploids (Figure 1), which indicates rapid elimination and strongly argues against gradual sequence divergence as a cause. Specifically, there were no chromosomes bearing a FISH site in T. urartu (accession TMU06, Figure 1a) and six (presumably three pairs) chromosomes bearing the FISH sites (hybridization signals) of pGc1R-1 in Ae. longissima (accession TL05, Figure 1b), but only four (presumably two pairs) chromosomes had FISH sites in the second selfed generation (S2) of an amphiploid plant between the two species (Figure 1c). This suggests elimination of two pairs of FISH sites by the second selfed generation (S2). In the third and fourth selfed generations (S3 and S4) of this amphiploid, further elimination of pGc1R-1 was apparent: two chromosomes were found to have the FISH sites in S3 (Figure 1d) and only one chromosome still had the FISH site in S4 (Figure 1e). Moreover, sizes and intensities of the hybridization signal in the amphiploid plants were also notably reduced compared with those in the parent (Ae. longissima). Similarly, elimination of the pGc1R-1 FISH sites also occurred in the S1 generation amphiploid between Ae. sharonensis (accession TH02) and T. monococcum (accession TMB02) (compare Figure 1, f and g, with Figure 1h), as well as in the S1 generation amphiploid between common wheat (T. aestivum) and Ae. speltoides (compare Figure 1, i and j, with Figure 1k). In all three sets of amphiploids, the changed FISH patterns, as compared with the respective parental line, are largely uniform among the >20 metaphase cells examined for each plant, indicating the lack of chimerical cells. This is in contrast with the findings of Salina et al. (2004) on a different DNA repeat Spelt1, where cells within a given synthetic amphiploid plant were found largely heterogeneous with regard to the number of FISH sites. This discrepancy suggests that differential mechanisms may underlie the elimination of different DNA repeats under allopolyploidy condi-
an independent approach, we performed DNA gel-blot analysis with pGc1R-1a as a probe on multiple enzyme digestions (see MATERIALS AND METHODS). It was found that, in all enzyme digests, the strength of the gel-blot hybridization signal of pGc1R-1a was drastically reduced in all three sets of amphiploids compared with that of the corresponding pGc1R-1a-containing diploid parent (Figure 2, a, c, and e; data not shown). Equal loading and quality of the DNA samples were confirmed by probing the same blots (after stripping off the pGc1R-1a signals) with three low-copy RFLP probes, PSR301, PSR593, and PSR743 (Gale et al. 1993), that are known to present in the plant lines (Figure 2, b, d, and f; data not shown). To have a rough estimation of the elimination in a quantitative manner, we took into consideration the different exposure time (2 hr for pGc1R-1a vs. 6 days for the two low-copy RFLP probes, respectively) during autoradiography, and the genome size difference between the amphiploids and their parents (assuming the basic null hypothesis for genomic additivity; Wendel 2000). Thus, taking these two factors into consideration and using the low-copy probes as a normalizing control, we estimated, by densitometric scanning of the gel blots, that ~70–80% of the pGc1R-1a family was eliminated from the two tetraploid amphiploids, Ae. longissima × T. urartu and Ae. sharonensis × T. monococcum, with >90% of the pGc1R-1a family being

![Figure 2](https://academic.oup.com/genetics/article/170/3/1239/6060413)
eliminated from the octoploid amphiploid of *T. aestivum* × *Ae. speltoides*. Thus, the gel-blot results appeared in full agreement with the FISH data (Figure 1), and the combined evidence is more than compelling to allow the conclusion that rapid and extensive elimination of pGc1R-1 copies occurred in all three sets of newly synthesized amphiploids, each with an element-containing Aegilops diploid species as a parent.

Previous studies on another DNA repeat called pAesKB52 whose 5′-region shares 98% sequence homology to pGc1R-1 (Anamthawat-Jonsson and Heslop-Harrison 1993) showed that it hybridizes, at the gel-blot level, to *Ae. speltoides*, *Ae. sharonensis*, and *Ae. longissima* but not to the natural tetra- and hexaploid wheats, *T. turgidum* and *T. aestivum*, hence implicating elimination of the DNA repeat after allopolyploid formation (Anamthawat-Jonsson and Heslop-Harrison 1993). Our data on the three sets of synthetic wheat amphiploids have not only confirmed the earlier speculation by providing solid experimental evidence, but also showed that the elimination may occur rapidly, i.e., at the very initial stages following allopolyploidization.

**Comparison between elimination of low-copy and repetitive DNA sequences with regard to possible causes and roles following allopolyploidy in Triticeae:** A series of previous studies have reported rapid elimination of low-copy, coding or noncoding sequences upon allopolyploidization in Triticeae (Feldman et al. 1997; Liu et al. 1998; Ozkan et al. 2001; Shaked et al. 2001; Kashkush et al. 2002; Ma et al. 2004). Although similar in phenomenology, we note that there are at least two lines of apparent difference between the elimination of low-copy and repetitive sequences. The first difference lies in possible causes for the elimination of the two types of DNA sequences. Probably due to technical reasons for detection, the results of both this study and previously reported works (Daud and Gustafson 1996; Pestsova et al. 1998; Salina et al. 2004) on the elimination of repetitive DNA elements following allopolyploidization are confined to genome-specific sequences, i.e., sequences present in only one of the parental species. In contrast, all eliminated low-copy sequences described so far are present in both parental species, being rendered chromosome or genome specific only after allopolyploid formation (the so-called group II sequences in Feldman et al. 1997). Thus, the elimination or reduction of the DNA repeat hitherto described is obviously not caused by incompatibility among divergent members of the specific repeat family originally residing in the two parental species and being brought together by allopolyploidy, while incongruence of homology-dependent interaction between the parental copies has been thought to be a major cause for the elimination of the group II low-copy sequences (Liu and Wendel 2002; Feldman and Levy 2005).

The second line of difference lies in a possible biological role, if any, that the elimination of the two types of sequences may have played. It has been proposed that a possible function for the nonrandom and rapid elimination of the low-copy sequences and rendering them as chromosome or genome specific in the resultant allopolyploid is to accentuate the physical and/or genetic divergence between the homeologous chromosomes, such that strict homologous meiotic paring (cytological diploidization) and reduced genetic redundancy (genetic diploidization) will be facilitated and hence may contribute to allopolyploid speciation (Levy and Feldman 2002; Feldman and Levy 2005; Ma and Gustafson 2005). Although direct evidence for this proposition is lacking, correlative evidence that showed a positive correlation between the amount and rapidity of sequence elimination and the fertility of the various newly synthesized wheat allopolyploids investigated appeared to corroborate this possibility (Ozkan et al. 2001). On the other hand, the elimination of a parental-specific DNA repeat in newly formed allopolyploids would by no means have such a role; on the contrary, its elimination will reduce the divergence of the parental genomes. Thus, we speculate that a possible role, if any, for the elimination of parental-specific DNA repeats upon allopolyploidy is to eliminate or mitigate the genomic incompatibility of parental genomes that would otherwise be too divergent for harmonious coexistence and coordination. Moreover, it has been suggested that the purging of genetic incompatibility is essential for high fertility in a hybrid or allopolyploid with divergent parental genomes (Rieseberg 2001). Nevertheless, because of the proposed scarcity, if not absence, of homeologous recombinations under allopolyploid conditions in the Aegilops-Triticum complex (Feldman et al. 1997; Ozkan et al. 2001; Salina et al. 2004), the purging of unfavorable genic interactions cannot be accomplished by Mendelian segregation (Rieseberg 2001). Therefore, it is conceivable that the drastic elimination of the parental-specific, yet dispensable, DNA repeats would lead to a more harmonious cellular environment and hence might improve fertility in newly formed wheat allopolyploids. It should be noted, however, that compelling recent evidence has showed that homeologous recombinations do occur in other (mainly dicotyledonous) plant allopolyploids (synthetic or natural), such as the Brassica complex (Osborn et al. 2003a; Osborn 2004; Pires et al. 2004; Udall et al. 2005), Arabidopsis (Madlung et al. 2005), and Nicotiana (Lim et al. 2004).

It is currently not clear whether the rapid elimination of DNA repeats that we observed represents a general, directed event associated with allopolyploidy or merely a stochastic anomalous incident triggered by specific parental combinations. Nonetheless, the fact that the strikingly similar elimination events have repeatedly occurred in all three sets of independently synthesized amphiploids supports the former possibility. In addition, a recent study showed that elimination of parental-
specific satellite DNA also repeatedly occurred in newly formed Nicotiana allopolyploids (Skalicka et al. 2005).

It has been well established in Drosophila and in some mammalian animals that hybridization between some divergent species (the dysgenic cross) will induce an array of genomic instabilities, including activation of transposable elements, genomic rearrangements, and alterations in DNA methylation patterns, presumably due to breakdown of normal repressive controls in the hybrids (Petrov et al. 1995; O'Neill et al. 1998; Vranova et al. 2000; Brown et al. 2002). Remarkably, all these phenomena also appeared widespread in plant hybrids and allopolyploids (reviewed in Comai 2000; Levy and Feldman 2002, 2004; Comai et al. 2003; Madlung and Comai 2004; Melayah et al. 2004; Jones and Pasakinskii 2005). Apparently, both the dysgenesis phenomenon in animals and the allopolyploidy-induced genomic instability in plants accord well with the "genomic shock" theory proposed by McClintock (1984) nearly 2 decades ago. Thus, it seems possible that a similarly preevolved response to genomic stress caused by the merging of two divergent genomes following interspecific hybridization exists in diverse organisms. Conceivably, the direct consequence of this response and/or some by-products thereof has facilitated genome evolution and speciation either at the homoploid level or via allopolyploidy in both animals and plants.

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