

RESEARCH ARTICLE

Meiotic behaviour of tetraploid wheats (*Triticum turgidum* L.) and their synthetic hexaploid wheat derivatives influenced by meiotic restitution and heat stress

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Abstract

Meiotic restitution is considered to be a common mechanism of polyploidization in plants and hence is one of the most important processes in plant speciation. Meiotic behaviour of plant chromosomes is influenced by both genetic and environmental factors. In this study, the meiotic behaviour of cereal crops was investigated, which includes tetraploid wheat genotypes (with and without the meiotic restitution trait) and their derivatives (synthetic hexaploid wheats and a doubled haploid (DH) line), grown at two planting dates in the field. In addition, two local landraces of emmer wheat (*Triticum turgidum* ssp. *dicoccum*), one wheat cultivar (Chinese spring), one DH triticale cultivar (Eleanor) and one rye accession were included. Immature spikes of mid-autumn and end-winter sowing plants were collected in April and May 2008, respectively, fixed in Carnoy's solution and stained with hematoxylin. Pollen mother cells (PMCs) from anthers at different stages of meiotic process were analysed for their chromosomal behaviour and irregularities. Meiotic aberrations such as laggards, chromosome bridges, micronuclei, abnormal cytokines, chromatin pulling and meiotic restitution were observed and the studied genotypes were accordingly ranked as follows: triticale > synthetic hexaploid wheats > tetraploid wheats possessing meiotic restitution > tetraploid wheats lacking meiotic restitution > rye. The results indicated that the samples that had been planted in the autumn, thus experiencing an optimum temperature level at the flowering stage, exhibited less meiotic irregularities than winter planting samples that encountered heat stress at the flowering period.

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Introduction

Polyploidy plays an important role in the plant evolution, and it is now known that genomes of flowering plants, including many crop plants of worldwide importance, are often polyploid (Rieseberg and Willis 2007; Doyle *et al.* 2008; Leitch and Leitch 2008). Unreduced gametes ($2n$) are recognized as a common mechanism of origin of most polyploids in plants (Sang *et al.* 2004; Otto 2007). Generally, $2n$ gametes originate from deviating meiosis in plants (Ramanna and Jacobsen 2003).

Meiosis is a highly dynamic cellular process controlled by a complex genetic network (Golubovskaya 1979). In plants, it has long been recognized that mutant genes can affect meiosis in various ways and that some of these may

lead to the formation of $2n$ gametes (Golubovskaya 1979; Kaul and Murthy 1985). During meiosis, different types of cytological irregularities can lead to $2n$ gametes with variable genetic composition (Matsuoka and Nasuda 2004).

Meiotic restitution (functioning of unreduced female and male gametes) plays a predominant role in producing allopolyploids in nature. This phenomenon, including first division restitution (FDR) and second division restitution (SDR), has been documented in cereal crops (Jauhar 2003, 2007; Matsuoka and Nasuda 2004; Zhang *et al.* 2007). It has been suggested that the functioning of unreduced gametes produced through meiotic restitution may have been a major mechanism for the widespread occurrence of polyploidy in nature (Jauhar 2003, 2007; Ramanna and Jacobsen 2003).

Studies in some crop plants have revealed that the reproductive developmental stage is much more sensitive to abiotic stresses than the vegetative developmental stage (Baker

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et al. 1992; Sato et al. 2002, 2006; Fuzinatto et al. 2008). Several authors have stated that meiosis is the most sensitive stage in the life cycle of crop plants, and is influenced by both genetic and environmental factors (Ahmad et al. 1984; Namuco and O'Toole 1986; Saini 1997; Porch and Jahn 2001; Erickson and Markhart 2002).

Among the environmental factors that influence the meiotic behaviour of chromosomes, the effects of high temperature (Ahmad et al. 1984; Bajpai and Singh 2006), water deficit (Saini 1997), nutrient levels, fluence rate, soil salinity (Sun et al. 2004), irradiation (Vicini and Carvalho 2002) and chemicals like herbicides (Bajpai and Singh 2006) and fungicides (Fairbanks et al. 2002) have been reported. The better studied abiotic factors affecting reproductive processes are water deficit and temperature. The sensitivity of flower development, particularly microsporogenesis, to high temperatures has been demonstrated in many crops, with high temperature reducing microspore development, pollen viability, and pollen shed (Fuzinatto et al. 2008).

The objectives of this study were (i) to compare the meiotic behaviour of tetraploid wheat (*T. turgidum*) with and without the meiotic restitution potential and their synthetic hexaploid and DH derivatives with those of other cereals; and (ii) to determine the effect of planting date and, consequently, temperature at flowering stage on the meiotic behaviour of tetraploid wheat (*T. turgidum*) with and without the meiotic restitution potential and their synthetic hexaploid and DH wheat derivatives.

Materials and methods

Plant materials

The materials used in this study included two lines of *T. turgidum*, one accession of *T. turgidum* ssp. *carthlicum*, one accession of *T. turgidum* ssp. *durum*, three synthetic hexaploid wheat, one doubled-haploid (DH) wheat line, two local land races of emmer wheat (*T. turgidum* ssp. *dicoccum*), one wheat cultivar (Chinese spring), one DH triticale cultivar (Eleanor) and one rye accession. Among the plant materials were also included tetraploid wheat genotypes with and without the meiotic restitution trait and their derivatives (synthetic hexaploid wheat and DH line). The meiotic restitution of the tetraploid wheat genotypes (E1, E3 and DO1) was previously described by Balatero and Darvey (1993) and Sayed-Tabatabaei (1996). Details of the genetic materials including their origins are given in table 1.

Meiotic observations

Genotypes were grown at two planting dates: mid-autumn (15 November 2007) and end-winter (5 March 2007) growing seasons, in the research field at Isfahan University of Technology, Iran. The immature spikes at the appropriate developmental stage of pollen mother cells (PMCs) possessing meiotic division were collected from the autumn sowing

plants on 21–25 April 2008 when average min/max temperatures were 9°C/22.4°C. Immature spikes were collected from the winter sowing plants on 11–15 May 2008 when average max/min temperatures were 16.7°C/31.4°C. They were fixed in Carnoy's solution (3:1 ethanol and glacial acetic acid) for 24 h and refrigerated in 70% ethanol. Then they were stained with hematoxylin and smeared preparations were observed under light microscope. PMCs from anthers in different stages of meiotic process were analysed. Ten plants per genotype (five plants at each planting date) and about 100 PMCs per plant were counted and the frequency of cells showing at least one symptom of irregularity was used for statistical analysis. Meiotic restitution was not counted as meiotic irregularities. Chromosome images were taken under a Nikon Eclipse E600 (Tokyo, Japan) light microscope using Photo grab 300Z software Fujix TM 300 z sh-3z version 2.1 (Fuji, Japan).

Statistical analysis

The mean percentage irregularity was tested for normal distribution using the Kolmogorov–Smirnov test using SPSS for windows version 13.0 statistical package (SPSS, Chicago, USA). Normal distribution was considered if *P* values were above 0.05. Data were then subjected to analysis of variance (ANOVA) as a factorial experiment with an unbalanced randomized design using PROC GLM of the SAS statistical package (SAS 2003). Multiple comparisons were performed using Fisher's least significant difference test (LSD).

Results

Results of ANOVA indicated that the meiotic irregularities of the studied cereal genotypes were highly influenced by genotype, environment (planting date) and genotype × environment interaction (table 2). Mean comparisons of the cereal genotypes tested for meiotic irregularities are presented in table 3. In general, meiotic irregularities were clearly much higher for all genotypes in the winter sown plants than in the autumn sown plants, most likely due to heat stress at the flowering stage.

Meiotic aberrations such as laggards, chromosome bridges, micronuclei, abnormal cytokinesis and chromatin pulling were observed in the studied genotypes with a higher frequency in the triticale, which was followed by synthetic hexaploid and tetraploid wheat genotypes possessed the meiotic restitution trait. Rye had the least meiotic irregularities (0.5%) while triticale displayed the greatest irregularities (23%) in its winter planting samples. In the autumn sown plants, meiotic irregularities in rye and triticale were 0.2% and 15%, respectively. The meiotic behaviour of the genotypes was differentially affected by heat (from autumn planting to winter planting), with rye as the least affected (about 0.3%) and synthetic hexaploid wheat DH as the most affected (about 17.3%).

Table 1. Genetic materials and their origin used in this study.

Line/accession no.	Species (genome)	Origin
E1	<i>Triticum turgidum</i> (AABB)	<i>T. turgidum</i> ssp. <i>carthlicum</i> Nevski × <i>T. turgidum</i> ssp. <i>dicoccoides</i> Korn. var. <i>spontaneonigrum</i> ¹
E3	<i>T. turgidum</i> (AABB)	<i>T. turgidum</i> ssp. <i>carthlicum</i> Nevski × <i>T. turgidum</i> ssp. <i>dicoccoides</i> Korn. var. <i>spontaneonigrum</i> ¹
DO1	<i>T. turgidum</i> (AABB)	<i>T. turgidum</i> ssp. <i>carthlicum</i> Nevski × <i>T. turgidum</i> ssp. <i>dicoccoides</i> Korn. var. <i>spontaneonigrum</i> ¹
C1	<i>T. turgidum</i> (AABB)	Acc. 4B925, Univ. Manitoba collection, Canada
E1NB (synthetic hexaploid wheat)	E1 × <i>Aegilops tauschii</i> NB (AABBDD)	<i>Triticum turgidum</i> × <i>Ae. tauschii</i> (nonbrittle)
E3NB (synthetic hexaploid wheat)	E1 × <i>Ae. tauschii</i> -NB (AABBDD)	<i>Triticum turgidum</i> × <i>Ae. tauschii</i> (nonbrittle)
DO1NB (synthetic hexaploid wheat)	DO1 × <i>Aegilops tauschii</i> -NB (AABBDD)	<i>Triticum carthlicum</i> × <i>Ae. tauschii</i> (nonbrittle)
DH (doubled haploid line)	DO1NB × 'Grebe' (AABBDD)	Synthetic wheat × 'Grebe' (Australian wheat cultivar)
Emmer wheat-1	<i>T. turgidum</i> ssp. <i>dicoccum</i> (AABB)	Local cultivated land race collected from Jonegan, Charmahal Bakhtiari province, Iran
Emmer wheat-2	<i>T. turgidum</i> ssp. <i>dicoccum</i> (AABB)	Local cultivated landrace collected from Singard, Charmahal Bakhtiari province, Iran
Eleanor (DH)	<i>X. Tritico-secale</i> Wittmack (AABBRR)	Australian doubled haploid cultivar
Chinese spring	<i>T. aestivum</i> L. (AABBDD)	Wheat cultivar, CIMMYT
R57	King II sel. × Univeta (K102) <i>Secale cereale</i> L. (RR)	University of Sydney, Australia

¹Developed by Dr B. Lapinski, Institute of Plant Genetics, Poznan, Poland, and provided by N. L. Darvey, University of Sydney, Australia.

Table 2. Analysis of variance of meiotic irregularities influenced by genotypes and environmental conditions.

Source of variation	df	Mean square
Planting date	1	800.36 **
Genotype	12	308.98 **
Planting date × genotype	12	53.75 **
Residual	98	0.586

** $P \leq 0.01$, CV = 11.79; $R^2 = 99\%$.

Tetraploid wheat genotypes were classified into two groups. The first group included E1, E3 and DO1 that possessed meiotic restitution and contained higher meiotic aberrations than the 'Chinese spring' bread wheat cultivar (control). It is interesting to note that tetraploid wheat C1 (lacking meiotic restitution), emmer-1 and emmer-2 contained fewer meiotic aberrations than the control.

Irregular chromosome segregation was the most common meiotic abnormality observed in all samples, which was

characterized by precocious chromosome ascension and lag-gards in both meiotic divisions (figure 1, a&b). The highest frequency of univalents was observed in triticale samples harvested from both planting dates. Chromosome bridge was the second anomaly encountered in triticale, synthetic hexaploid and tetraploid wheat genotypes possessing the meiotic restitution trait. This abnormality includes linking chromosomes together in the metaphase and causing them to form bridge(s) in the anaphase, a process which could continue up to the telophase (figure 1c). The thickness of bridges observed and the number of chromosomes involved in their formation varied among different meiocytes and the genotypes studied. Although most of them were easily broken by spindle pulling, some were hardly broken by forming cell plates in the cytokines stage (figure 1d).

The incidence of micronuclei in telophase I (dyads) and telophase II (tetrad) stages of meiosis was another irregularity most commonly observed in the studied genotypes. Some

Table 3. Mean comparisons of cereal genotypes tested for meiotic irregularities grown in planting dates under field conditions.

Genotype	Description	Number of PMCs	Mean (%)	
			Autumn/winter	Autumn
Eleanor	Triticale	480/410	15.2a	23.0a
E3NB	Syn. hexaploid wheat	340/330	9.5b	21.0ab
E1NB	Syn. hexaploid wheat	385/370	8.7b	19.8ab
DO1NB	Syn. hexaploid wheat	430/290	7.6b	19.6b
DH	Syn. hexaploid wheat	350/360	3.7c	21.0ab
E3	Tetraploid wheat	300/350	2.1d	4.4d
E1	Tetraploid wheat	400/330	0.5e	8.9e
DO1	Tetraploid wheat	410/320	0.5e	4.5d
Chinese spring	Hexaploid wheat	360/325	0.3e	2.6de
Emmer wheat-1	Tetraploid wheat	410/330	0.2e	1.1e
Emmer wheat-2	Tetraploid wheat	430/295	0.2e	0.8e
C1	Tetraploid wheat	390/310	0.2e	0.9e
R57	Rye	490/380	0.2e	0.5e

*Means with same letter not significantly different at $P < 0.05$, using Fisher's LSD.

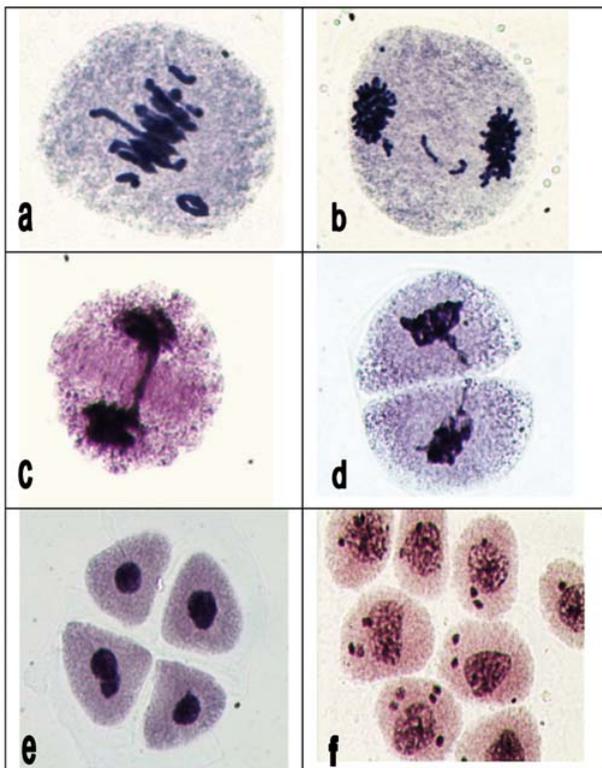


Figure 1. Irregular chromosome segregations, chromosome bridges and micronuclei in the studied genotypes. Metaphase I with precocious chromosome migration to the poles (a) and anaphase I with lagging (b) in tetraploid wheat DO1; thick bridge continued to telophase I (c) and broken due to cytokinesis (d) in synthetic hexaploid wheat E1NB; tetrad with one big micronuclei (e) and microspores with different number of small micronuclei (f) in triticale.

dyads and tetrads contained one or more micronuclei (figure 1, e&f). Chromatin pulling occurred only at meiosis in the

synthetic hexaploid wheat genotypes, especially in the winter planting samples (figure 2a).

Abnormal cytokinesis was observed in both autumn and winter planting samples of triticale and winter planting synthetic hexaploid wheat genotypes which caused triad or different sizes of microspores to form at the end of meiosis II (figure 2b).

The most likely cause for production of unreduced gametes, that were mainly observed in E1, E3 and Do1 tetraploid wheat genotypes only in the winter planting samples, is heat stress at the flowering stage (figure 2, c&d).

Discussion

The finding of significant genetic and environmental effects and interactions in the present study are in agreement with those of other researchers who reported the effects of either genetic (Golubovskaya 1979; Xu and Joppa 2000; Zhang *et al.* 2009) or environmental factors (Ahmad *et al.* 1984; Namuco and O'Toole 1986; Fuzinato *et al.* 2008) on meiotic chromosome segregation. However, to date, no report has been found in the literature on the effect of genotype \times environment interaction (G \times E) on meiotic irregularities.

Several studies have demonstrated that the peak reproductive sensitivity to abiotic stresses of cereal crops is in the period from meiosis to tetrad break-up in anthers. The best studied abiotic factors affecting reproductive processes are water deficit and temperature. Sensitivity of flower development, particularly microsporogenesis, to high temperatures has been reported in many crops (Namuco and O'Toole 1986; Porch and Jahn 2001; Erickson and Markhart 2002; Sato *et al.* 2002, 2006; Fuzinato *et al.* 2008), where microspore development, pollen viability and pollen shed reduced under high temperatures. Ahmad *et al.* (1984) reported that high temperatures increased

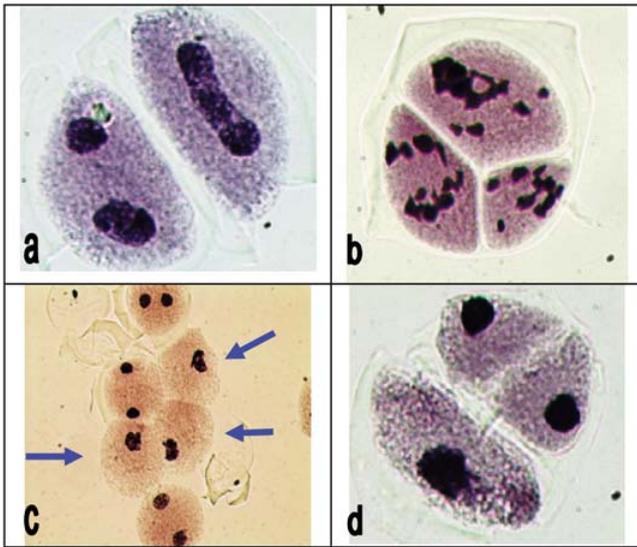


Figure 2. Chromatin pulling, irregular cytokinesis and first and second meiotic restitutions (FDR and SDR) observed in studied genotypes. a) Decondensed chromatin pulled to the poles in anaphase II in synthetic hexaploid wheats E3NB; b) triad formation in triticales; c) cells marked with arrows stayed at prophase I (the delay causes FDR), while the others moved to telophase I in tetraploid wheat DO1 and d) triad induces SDR in tetraploid wheat E3.

meiotic aberrations in interspecific hybrids in soybean. Heat stress could affect the meiotic pathway by altering the functioning of certain genes governing meiosis.

Two hypotheses could be put forward as to why triticales and synthetic hexaploid wheat genotypes exhibited the greatest meiotic irregularities among the studied cereal genotypes in this study. First, synthetic hexaploid wheats used in this study inherited their meiotic restitution trait from their female tetraploid parents (E1, E3 and DO1); a similar situation could be assumed for triticales. Second, both triticales and synthetic hexaploid wheat include man-made compound genomes. The synthetic hexaploid wheat genotype has a combination of wheat \times *Aegilopes tauschii* genomes and triticales has a combination of wheat \times rye genomes. The duration of the meiotic cycle varied in different components of the compound genome, which could be the first cause for the meiotic instability (Oettler 2005). Meiotic instability in triticales seems to have another molecular cause. Rye chromosomes generally have large telomeric blocks of heterochromatin, in contrast to the smaller and intercalary heterochromatin bands in wheat chromosomes. Our results of greater meiotic irregularities observed in triticales than in synthetic hexaploid wheat are consistent with the suggestion by Zhang *et al.* (2009) that *T. turgidum* genotypes play a more important role than *Ae. tauschii* genotypes in producing $2n$ gametes. The greater meiotic aberrations of triticales could also be explained by the greater genetic distance of the rye genome from the *Ae. tauschii* genome. Further, meiotic pairing is generally expected to start at the telomeric ends

of chromosomes and DNA replication in the telomeric heterochromatin of rye chromosomes is delayed. It has, therefore, been hypothesized that meiotic pairing fails in such hybrids, leading to a univalent formation (Lukaszewski and Gustafson 1987).

The behaviour of plant chromosomes during meiosis has been studied for many years and their irregularities have received considerable attention in cytogenetic investigations. The results of present study was in agreement with those of Pagliarini (2000) who observed the irregular chromosome segregation (laggards) as the most common meiotic irregularity in about 50 plant species. The existence of laggard chromosomes has been found to be highly genotype-dependent (Pagliarini 2000; Fuzinato *et al.* 2008). A number of workers have examined the causes of univalent formation in triticales. Asynapsis, desynapsis, failure of chiasma formation and premature disjunction of bivalents have been proposed as possible causes (Gupta and Priyadarshan 1982). Synaptic mutants drastically change the normal behaviour of chromosomes during prophase-I. They cause meiotic irregularities which, in turn, generate chromosomally unbalanced male and female microspores and megaspores, resulting in reduced pollen and ovule viability (Cai and Xu 2007).

Chromosome bridges characterized by chromosome clustering during different stages of the cell cycle have been reported in some species like maize, *Centella asiatica*, *Brassica napus* and *B. campestris*, *Glycine max* (Pagliarini 2000), and *Bromus* L. (Sheidai and Fadaei 2005). Genotypic and environmental variations of chromosome bridges reported for Brazilian oat cultivars are consistent with our results on wheat (Baptista-Giacomelli *et al.* 2000).

The observation of micronuclei in telophase I and II stages of meiosis was another irregularity in the studied genotypes. Micronuclei could originate from precocious ascension at the metaphase, or from laggards at the anaphase. The chromosome segments of broken bridges also form micronuclei. Zhang *et al.* (2007) reported one or two micronuclei in some dyads in their study of the meiotic behaviour of *T. turgidum*—*Ae. tauschii* F₁ hybrids using emmer wheat as the female parent with the meiotic restitution trait.

The higher frequency of abnormal cytokinesis in triticales and synthetic hexaploid wheat genotypes observed in the present study could be attributed to their interspecific hybrid nature, and due to noncoordination of the composed genomes. Similarly, Tai (1970) reported, in a hybrid, the spindle organizers of both parents may be present, and multipolar divisions may separate different genomes into different groups. However this phenomenon occurred in the winter planting plants of the synthetic hexaploid wheat genotypes, thus it can be assumed that heat stress induced abnormal cytokinesis in this group of samples.

In the present study, chromatin pulling was another abnormality observed in only synthetic hexaploid wheat genotypes. In this case, the chromosomes lost their condensation before the end of anaphase II and decondensed chromatin

pulled to the poles. Silkova *et al.* (2007) also reported this phenomenon in some wheat-rye polyploids.

Unreduced gametes were observed in E1, E3 and Do1 tetraploid wheat genotypes possessed meiotic restitution. This result support previous reports which suggested that some *T. turgidum* genotypes are more capable of inducing unreduced gamete production than others and demonstrate that the modified meiosis leading to $2n$ pollen formation is under genetic control (Xu and Joppa 2000). These results are consistent with those of a previous study (Zhang *et al.* 2009) which reported the genotypic variation in *T. turgidum* unreduced gamete production.

In this study, the occurrence of unreduced gamete formation was promoted in winter planting samples, most likely due to high temperature at the flowering stage. High temperature has also been reported to enhance $2n$ gamete production in *Lotus tenuis* (Negri and Lemmi 1998). Formation of $2n$ gametes has also been reported to depend not only on genotype, but also on environment and the interaction of genotype and environment (Veilleux and Lauer 1981).

It is understood that some mutant genes may affect meiosis and lead to the formation of unreduced $2n$ gametes (Golubovskaya 1979; Kaul and Murthy 1985). The genes that control the meiotic nuclear restitution are greatly influenced by environmental conditions (Ramanna and Jacobsen 2003), and it can, therefore, be hypothesized that both major and minor genes govern this trait. Several workers reported that the trait of $2n$ gamete formation is controlled by a single gene (Mok and Peloquin 1975; Xu and Joppa 2000), but the results are not unequivocal. This is because the genes that induce meiotic nuclear restitution are greatly influenced by environmental conditions as previously described by Ramanna and Jacobsen (2003) and further confirmed in this study.

Meiotic nuclear restitution, as the most important phenomenon of $2n$ gamete formation, has been reported in several crop species and their potential for the induction of polyploids has been perceived (Jauhar 2003, 2007; Ramanna and Jacobsen 2003; Matsuoka and Nasuda 2004; Zhang *et al.* 2007). In spite of much attention paid to $2n$ gamete formation as a complex meiotic process, its cytological mechanisms and their genetic control are still largely obscure (Camadro 1994; Cai and Xu 2007). Although previous studies have indicated that the meiotic restitution gene (or genes) of *T. turgidum* are functional in the derived interspecific or intergeneric F_1 hybrids (Jauhar *et al.* 2000; Zhang *et al.* 2007) and in its hexaploid triticale derivations (Oettler 2005), there are still limited data on the functions of the genes in derived synthetic hexaploid wheat.

The adverse effects of high temperature on plant reproduction have severe implications for worldwide crop production. Heat stress may cause various structural and functional irregularities in the reproductive organs leading to failure of gamete formation, fertilization, or premature abortion of seed or fruit. Thus, the damage to productivity from stress at this stage is particularly severe for crops in which the

economic yield is the product of sexual reproduction (Saini 1997). Global warming is now considered as a threat to both natural and managed ecosystems since temperature is one of the major environmental factors that affect plant productivity. Therefore, not only a good understanding of changes in the ecosystems will be required, but also an appropriate germplasm needs to be developed to cope with the changes.

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