MEIOTIC BEHAVIOR OF INTERSPECIFIC HYBRIDS BETWEEN HEXAPLOID AND TETRAPLOID WHEAT SPECIES

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Wheat is the most important crop in the world, occupying 17% of crop acreage world over, feeding about 40% of the world population, and providing 20% of total food calories and proteins in human nutrition (Gupta *et al*., 2005& 2008). In the past, extensive cytogenetic studies were undertaken on this crop, not only for the elucidation of its genomic constitution, but also for manipulation of its chromosomes to achieve improved yield potential. Currently, about 95% of the wheat grown worldwide is hexaploid bread wheat and most of the remaining 5% being tetraploid durum wheat.

In wheat *(Triticum* spp.), five genomes originally are found in diploid species, have been identified. A^m: present in wild einkorn (*T. boeoticum*), A^u: present in *T. urartu* (closely related to *T. boeoticum* but not interfertile), B: present in most tetraploid wheats; its source not identified, but similar to *Aegilops speltoides* (Sandhu and Gill, 2002; Paux *et al*., 2006; Salse *et al*., 2008), G: present in *timopheevi* group of wheat; source also not identified, but similar to *Ae. speltoides*, and D: present in *Ae. Tauschii* Coss., and all hexaploid wheat (Akhunov *et al*., 2003; Sˇafa´r *et al*., 2004 and Takumi *et al*., 2009).

Common wheat or bread wheat (*T. aestivum*) is a hexaploid species (AABBDD, 2*n*=6x=42) containing three related ancestral genomes, each having seven chromosomes, giving 42 chromosomes in diploid cells. Durum wheat (*T. durum*); the only widely used cultivated tetraploid form, is a tetraploid (AABB, 2*n*=4x=28) containing two related ancestral genomes, each having seven chromosomes, giving 28 chromosomes in diploid cells (Martínez-Pérez *et al*., 1999; Maestra *et al*., 2002).

Wheat species has huge genome sizes and a complex organization that consists unique or low copy sequence surrounded by highly repetitive DNA, which represents more than 75% of the genome (Vedel and Delseny, 1987). The A, B, and D genomes in cultivated wheat are homoeologues; In all polyploids, the homoeologues (related chromosomes) have a similar linear sequence of genes but a different repetitive content, while homologues have the same linear sequence of genes and repetitive content

(Martinez-Perez *et al*., 2003; Su *et al*., 2016). Wheat has emerged as a classic polyploidy model. For more than 60 years, polyploidy has been considered to be largely important because of concepts of genome buffering, increased allelic diversity, increased or fixed heterozygosity, and the opportunity for novel phenotypic variation that arises from duplicated genes acquiring new function (Qi *et al*., 2004).

Specific level utilization depends on the production of successful interspecific hybrids with adequate fertility. Attempts of intraspecific and interspecific hybridization in cultivated and wild wheat species of different ploidy levels have been reported as early as the 1890s. The interspecific hybrids have been mainly used for understanding the cytological behavior of wild and domesticated species. This has further aid in the utilization of exotic gene pools for wheat improvement. Interspecific crosses remain a major challenge to wheat breeders. The complex fertilization behavior of different wheat species needs to be understood in detail to transfer desirable genes from the wild to the cultivated species (Bhagyalakshmi *et al.*, 2008). So interspecific hybrids merge parental species genomes which thus can pair and originate recombinant chromosomes that stably incorporate genetic material from one species into the other species genome either in the meiosis of the F_1 hybrid itself and/or in derived selfing or backcrossing progenies (Ellstrand *et al.*, 1999; Zamir, 2001). Furthermore, a specific chromosome or part of a chromosome in a basic genome is genetically related to a specific chromosome or a part of it in all other genomes of the *Triticeae* species. This is because gene synteny has been conserved throughout genome evolution and speciation of the genera in the *Triticeae* tribe and *Poaceae* family (Paterson *et al*., 2000; Eckardt, 2009).

The present study was undertaken to study the cytological behavior of interspecific hybrids between two wheat species; *Triticum aestivum* L. em Thell (bread wheat) and *Triticum turgidum durum* (desf.) Husn (durum wheat), for understanding a cytological basis of affinity between parents and their F_1 hybrids, also, to evaluate maternal effects and interspecific sterility of F_1 crosses. Such information could help in wheat improvement.

MATERIALS AND METHODS

The present study was carried out at the Faculty of Agriculture Experimental Farm during 2014/2015 and 2015/2016 growing seasons and Laboratory of Genetics Department, Faculty of Agriculture, Kafrelsheikh University, Egypt.

Experimental materials

Two wheat species were used in this study; a hexaploid species; *Triticum aestivum* L. em Thell and a tetraploid species; *Triticum turgidum durum* (Desf.) Husn. Five Egyptian wheat cultivars consist of three bread cultivars (Shandweel 1, Misr 2 and Gemmiza 11) and two durum

cultivars (Benisouef 5 and Benisouef 6) were used in this study. All cultivars were highly self-pollinated. Details of pedigree and origin of the five used genotypes are presented in Table (1).

Breeding behavior

All possible crosses between bread and durum wheat cultivars were made in 2014/2015 season including the top and reciprocal crosses in a full diallel mating design. The crosses and their reciprocals are presented in Table (2).

Hand-emasculated crosses were performed by removing the three anthers from the fertile spikelets of the selected spike, then emasculated spikes were covered by paper bags. After 3-4 days, emasculated spikes were pollinated by the male parent pollens (Lukjanenko, 1934; Pissareva, 1935). The mature spike of the female parent; either generated from selfing or crossing, were separately harvested and threshed, then treated with insecticides and kept for the next season. In the second season; 2015/2016, the five parents and their 20 F_1 hybrids were planted in a Randomized Complete Block Design (RCBD) with three replicates.

Meiotic preparation and analysis

Spikes of hybrids and their parents were randomly collected from the three replicates at booting stage; around 10:30 to 11:30 AM, and immediately fixed in Carnoy's solution. Whole spikes were fixed for two days, then washed with absolute ethanol for 5 sec. and stored in 70% ethanol in the refrigerator.

For smear preparation of meiotic phases, anthers were placed on a clean slide in a drop of 2% acetocarmine stain and the contents of anthers were squeezed out with an unplated iron needle. The best preparation of diakinesis and metaphase I were used to determine chromosomal associations (univalents, bivalents, trivalents .. etc.,). Lagging chromosomes were counted at the phases of anaphase I, anaphase II and telophase II. The frequencies of micronuclei were also determined at telophase I and quartet stages. A hundred cells have been examined at different stages of meiosis and the good preparations were photographed.

Pollen viability

Percentage of fertile pollen grains was estimated by testing the stainability of pollen grains with 2% acetocarmine (Morira and Gurgel, 1941). About 500 pollen grains were taken from each parent and hybrid.

RESULTS AND DISCUSSION

Chromosomal associations

The chromosomal associations helped to investigate the frequencies of various configurations, i.e., univalent, bivalent and multivalents at both diakinesis and metaphase I stages for parents and their hybrids (Table 3 and Fig. 1).

Data in Table (3) showed normal chromosomal associations at both diakinesis and metaphase I in all parental genotypes. For bread wheat cultivars at diakinesis stage, the highest average number of associations was observed for bivalents which were 18.61, 20.09 and 20.23 for Shandweel 1, Misr 2 and Gemmiza 11, respectively, while at metaphase I, the average number of bivalents were 20.36, 19.51 and 20.36, respectively. For the two genotypes of durum wheat, the highest average number at diakinesis for bivalents were 13.83 and 13.88 for Benisouef 5 and Benisouef 6, respectively, while at metaphase I, the average number of bivalents was 13.83 and 13.80, respectively.

Meiotic analysis of the interspecific hexaploid × hexaploid hybrids (2n= 42); C_1, RC_1, C_2, RC_2 and RC_5 (C_5 failed to produce hybrid seeds), showed normal diploid pairing at diakinesis with average number of bivalents ranged from 18.16 (C_2) to 20.49 (RC_2). At metaphase I stage, the average number of bivalents ranged from 16.77 (C_2) to 20.22 (C_1). Various associations were also observed; such as univalents, trivalents and quadrivalents, which observed at both diakinesis and metaphase I, in addition to hexavalents that observed at metaphase I for only C_1 and C_2. Despite the three bread wheat being hexaploids and carrying the same set of genomes A, B, and D, variation in pairing failure was observed, such as univalents, trivalents, quadrivalents and pentavalents. This implied that genome stabilization that occurred independently during the course of evolution could induce incompatibility. These genomes; though homoeological, are incorporated with specific homoeologous pairing suppressors similar to *Ph1* allele on the long arm of chromosome 5B (Salseb *et al*., 2005). The presence of precocious chromosomes of about 1-2 pairs possibly points to this evidence. Another factor responsible for the observed variation in pairing failure could be the dosage with which the telomeric heterochromatin is present in the chromosome arms. Since pairing starts mainly from the telomeres, homozygotes should have more affinity than heterozygotes, and association should be higher (Naranjo and Lacadena, 1980). This suggests that some plants having 42 with all the wheat A, B, D chromosomes will appear in the F_1 population which provides a chance to obtain stable bread wheat lines from the self-pollinated progenies. These results were in agreement with those reported by Khalaf (2000).

Six forms of interspecific hexaploid × tetraploid hybrids (2n=35); C_3, C_4, C_6, C_7, C_8 and C_9, could be described as abnormal behavior of the interspecific hybridization chromosomes. At diakinesis stage, the average number of univalents ranged from 3.70 (C_9) to 7.38 (C_4), bivalents ranged from 9.89 (C_3) to 13.70 (C_9) and trivalents ranged from 0.66 (C_8) to 1.36 (C_6). Also, the average number of quadrivalents ranged from 0.15 (C_8) to 0.79 (C_3), but it did not appear in C_9 hybrid. On the other hand, pentavalents appeared only in C_4 (0.09) and C_6 (0.05), while hexavalents were only in C_6 (0.05).

At metaphase I, the three configurations of univalents, bivalents and trivalents were observed for all hexaploid × tetraploid hybrids with average numbers ranged from 4.35 (C_9) to 7.30 (C_4), 10.53 (C_3) to 14.05 (C_9) and 0.63 (C_7) to 1.33 (C_3), respectively. Quadrivalents were observed in all hybrids; ranged from 0.40 (C_6) to 0.97 (C_3), except C_8 and C_9. Pentavalents appeared only in C_4 and C_6 hybrids and hexavalents in C_3 and C_6. The results showed that interspecific hexaploid × tetraploid hybrids presented higher average numbers of univalents; at diakinesis and metaphase I, than expected.

For the interspecific tetraploid × hexaploid hybrids (2n=35), six forms of RC_3, RC_4, RC_6, RC_7, RC_8 and RC_9 could be described as normal behavior of the interspecific hybridization chromosomes. The three configurations of univalents, bivalents and trivalents were observed for all the six hybrids at both diakinesis and metaphase I stages. At diakinesis, the average number of univalents, bivalents and trivalents ranged from 0.85 (RC_8) to 1.96 (RC_9), 14.52 (RC_3) to 16.55 (RC_8), and 0.15 (RC_6) to 0.76 (RC_9), respectively. While at metaphase I, the average number of univalents ranged from 0.85 (RC_6) to 1.76 (RC_4), bivalents from 14.50 (RC_3) to 16.73 (RC_7) and trivalents from 0.08 (RC_7) to 0.76 (RC_4). The other three multivalents; quadrivalents, pentavalents and hexavalents, appeared in some tetraploid × hexaploid hybrids with a low average number. quadrivalents ranged from 0.15 (RC_6) to 0.23 (RC_3) at diakinesis and from 0.05 (RC_7) to 0.25 (RC_3) at metaphase I. Pentavalents and hexavalents were appeared only in RC_3 and RC_6 at diakinesis and metaphase I, in addition to RC_7 at metaphase I. This unexpected normality in interspecific tetraploid × hexaploid hybrids may be due to gametocidal genes (cytoplasmic genes) that cause chromosomal breakage. The broken chromosomes were stabilized by telomere capture, in addition to telomere to telomere recombination allowing the broken univalent to associate forming bivalents (Tsujimoto *et al*., 1997). Also, tetraploid × tetraploid hybrids (2n=28); C_{10} and RC_{10} showed normal diploid pairing at diakinesis with the average number of 13.94 bivalents for each, while at metaphase I, the average of bivalents were 13.95 and 13.98 for C_{10} and RC_{10} hybrids, respectively. Also, two configurations; univalents and trivalents were observed at diakinesis and metaphase I stages, except trivalents which did not appear at diakinesis for C_{10} hybrid.

These results were in agreement with Colas *et al*., (2008) who reported that recombination does not occur between the bread and durum wheat chromosomes. Even possessing two homologous chromosomes, it is not sufficient to induce chromatin remodelling of both homologues in the presence of *Ph1* locus. Both homologues need to be identical or near-identical for remodelling to occur. Thus, *Ph1* in wheat affects the ability to coordinate and control chromatin remodelling at meiosis. The chromatin remodelling ena-

bles chromosomes to become competent to pair and recombine. Although clustering of telomeres into a bouquet early in meiosis has been suggested to facilitate homologue pairing, the *Ph1* locus acts both meiotically and somatically by reducing non-homologous centromere associations (Martinez-Perez *et al*., 2001).

In the majority of cells, the presence of trivalents indicated that the alleged translocation involves one of the extra seven *T. aestivum* chromosomes (the D-genome) which are usually seen unpaired in the hybrids, with one of the chromosomes from the A or B genomes (Badaeva *et al.*, 2007).

Strange phenomenons were detected in chromosome pairing during the investigation of diakinesis and metaphase I (Fig. 2). Asynaptic behavior (Fig. 2a) was observed in durum wheat cultivars (Benisouef 5 and Benisouef 6) as well as C_3 hybrid. This aberration may be due to that the telomeres or their proximal regions are the major initiation points of pairing and it does not start till DNA replication is finished, the overlapping of these two processes might produce a delay in the time of wheat pairing initiation, thus causing asynaptic behavior (Martinez-Perez *et al*., 2003). Also, the tripartite structures (Fig. 2b) were observed in the C_2 hybrid at metaphase I stage. Schwarzacher (1997) reported that this phenomenon is a consequent of these centromeres paired either correctly or incorrectly before meiosis during anther development. At meiosis, just before the telomere bouquet was fully formed, the paired centromeres clustered in seven diffuse groupings. These clusters then formed tripartite structures, indicating three-way pairing. Finally, the 'parts' of the tri-partite structures resolved to leave the 21 elongated centromeres sites, which then condense.

Secondary arm-to-arm chromosome associations (Fig. 2c) were induced in C_3 hybrid, this may be a result of the high frequency of univalents at diakinesis and metaphase I (Lima-Brito *et al*., 2006).

The fourth phenomenon that appeared was a telomere to telomere recombination (Fig. 2d), which was observed in metaphase I for interspecific tetraploid × hexaploid hybrids to stabilized the broken chromosomes as mentioned above previously.

Lagging chromosomes and micronuclei

The number of lagging chromosomes was detected at anaphase I, anaphase II and telophase II stages in the five parents and their hybrids (Table 4 and Fig.3). For parental genotypes at anaphase I stage, *T. aestivum* cultivars (Shandweel 1, Misr 2 and Gemmiza 11) contained lagging chromosomes with an average of 0.28, 0.63 and 0.18 laggards/cell, respectively. Also, *T. durum* cultivars (Benisouef 5 and Benisouef 6) showed laggards at anaphase I with an average of 0.10 and 0.21 laggards/cell, respectively. At anaphase II, the three *T. aestivum* cultivars showed laggards number with an

average of 0.10, 0.31 and 0.27 laggards/cell for Shandweel 1, Misr 2 and Gemmiza 11, respectively, while the two *T. durum* cultivars showed laggards number with an average of 0.22 and 0.27 laggards/cell for Benisouef 5 and Benisouef 6, respectively. At telophase II, Shandweel 1, Misr 2 and Gemmiza 11 cultivars showed laggards number with an average of 0.16, 0.23 and 0.20 laggards/cell, respectively, while Benisouef 5 and Benisouef 6 cultivars showed an average of 0.07 and 0.09 laggards/cell, respectively.

Irregular separations in parents were seen because of *T. aestivum* and *T. durum* are an allohexaploid and alloteraploid species with 42 and 28 chromosomes which normally forms 21 and 14 bivalents at meiosis, respectively. The 21 and 14 pairs of chromosomes representing the genomes obtained from different diploid parents. The complement can also be classified into seven homoeologous groups each of three and two pairs. Homoeologous chromosomes have similar genetic activities and their relationships probably depend upon their origin from the same chromosome of the diploid progenitor of the wheat group. There is one representative of every genome in every homoeologous and of every homoeologous group in every genome (Riley, 1974). Precocity of certain chromosomes in laggard formation was evident, pointing towards evolutionary self-balance of the genomes which prevented homeologous pairing. This abnormality was observed as an unequal association between these chromosomes.

For hexaploid × hexaploid hybrids genotypes; C_1, RC_1, C_2, RC_2 and RC_5, results in Table (4) revealed a normal behavior for decreasing in laggards frequency at anaphase I, anaphase II and telophase II. Results revealed that; at anaphase I, anaphase II and telophase II, the highest laggards number was detected in RC_1 hybrid with an average of 0.82, 0.32 and 0.22 laggards/cell, respectively. On the other hand, the lowest average of laggards was found in hybrids C_2 (0.15 laggards/cell) at anaphase I, C_1 (0.13 laggards/cell) at anaphase II and RC_2 (0.02 laggards/cell) at telophase II.

As shown in Table (4); for six forms of interspecific hexaploid × tetraploid hybrids (C_3 , C_4, C_6, C_7, C_8 and C_9) and the other six forms of tetraploid × hexaploid hybrids (RC_3, RC_4, RC_6, RC_7, RC_8 and RC_9), results revealed that C_4 hybrid had the highest average of laggards (6.95 laggards/cell) while RC_4 hybrid had the lowest (0.09 laggards/cell); at anaphase I stage. At anaphase II, the highest average of laggards was recorded in C_3 hybrid (6.49 laggards/cell) and the lowest one was found in RC_4 hybrid (0.05 laggards/cell). At telophase II, the highest average of laggards was also found in C_4 hybrid (5.46 laggards/cell), while the lowest one was found in RC_9 hybrid which showed one lagging chromosome at one cell with the average number of 0.01 laggards/cell. Generally, these results demonstrated that all the interspecific hexaploid

× tetraploid hybrids showed a high average of laggards compared to their reciprocals; the interspecific tetraploid × hexaploid hybrids. Thus, it was clear that hexaploid × tetraploid hybrids behaved as an abnormal in increasing laggards number, while the tetraploid × hexaploid hybrids were highly unexpected normality in decreasing number of laggards.

For interspecific tetraploid × tetraploid hybrids (C_{10} and RC_{10}), results revealed that the average of laggards was 0.18 and 0.21, respectively, at anaphase I stage, while it was (0.38 and 0.19) and (0.22 and 0.12) at anaphase II and telophase II, respectively.

The number of micronuclei was also detected at telophase I and quartet stages (Table 4 and Fig. 3). Micronuclei were observed in all parental genotypes as well as their hybrids, as consequences for some laggards at anaphase I, anaphase II and telophase II**.** These delayed chromosomes that result in F_1 crosses are a usual consequence of the existence of univalents of the single genomes which often appeared unpaired or probably resulted from the early disjunction of chiasmata at metaphase I stages. Such laggards usually travel to the poles but sometimes arrive too late to be included with the daughter nuclei. These results agreed with those reported by Naseer (1976), El- Baghdady (2002) and Gameil (2010). Such irregularity would appear to arise from the asynchronous disjunction of chromosomes between metaphase I stage and anaphase I, resulting in meiotic disturbances and a high frequency of abnormal microspores. In extreme cases with many chromosome rearrangements, the cell cycle is completely arrested and further development of pollen is stopped at the two nuclei stages.

Pollen grains viability

Data in Table (4) for pollen fertility demonstrated that all parental genotypes showed high percentages of viable grains; the highest percentage of pollen fertility was observed for Benisouef 5 (0.83%) and the lowest one was detected for Shandweel 1 (0.67%). Concerning hybrids, the highest percentages of pollen fertility were 90% (RC_6 hybrid) followed by 0.85% (RC_1, RC_4 and RC_9 hybrids). On the other hand, the lowest values were observed for C_7 hybrid (0.50%) followed by C_6 hybrid (0.53%). The decreasing in fertility percentages is a consequence of an occurrence of univalent, trivalent and quadrivalent associations in addition to laggards and micronuclei in the meiotic behavior which may be attributed to the failure of pairing and/or failure of chiasmata formation in one or two bivalents in addition to a rare frequency of trivalents and quadrivalents. This was in agreement with Nasser (1976) and Khalaf (2000). Disharmonious interactions between cytoplasm and nucleus might also have resulted in hybrid sterility (Suemoto, 1973).

SUMMARY

Cytogenetic behavior of five wheat genotypes of *Triticum aestivum* (Shandweel 1, Misr 2 and Gemmiza 11)

and *T. durum* (Benisouef 5 and Benisouef 6) in addition to their interspecific hybrids was studied. All five parental genotypes showed normal behavior in meiosis. Also, the interspecific hexaploid × hexaploid showed normal diploid pairing at diakinesis and metaphase I with average number ranged from 18.16 (C_2) to 20.49 (RC_2) and from 16.77 (C_2) to 20.22 (C_1) bivalents, respectively. And tetraploid × tetraploid showed normal diploid pairing at diakinesis and the average of bivalents were 13.95 and 13.98 for C_{10} and RC_{10} hybrids at metaphase I, respectively. So the normal decrease of laggards and micronuclei averages was recorded. Higher incidences of aberrant chromosomal structure such as the formation of univalent, laggards and micronuclei were observed in all the six interspecific pentaploid (hexaploid × tetraploid) which could be described as an abnormal compared to the six reciprocals hybrids (tetraploid × hexaploid) which were highly unexpected normality to form normal bivalents and a low frequency of laggards and micronuclei. Pollen grains of hexaploid × tetraploid hybrids were found to have markedly lower values of viability; ranged from 0.50 to 0.72, compared to parents and the other interspecific hybrids. Thus, the present study succeeded in proving that interspecific hybridization produced fertile pentaploid hybrids.

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Table (1): Pedigree of the five used wheat parents.

Species	Parents	Pedigree
Triticum aestivum L.(hexaploid species)	Shandweel 1	SITE/MO/4/NAC/TH.AC//3*PVN/3/MIRLO/BUC. CMss93B00567S-72Y-010M-010Y-010M-3Y-0M-0THY-0SH.
	Misr 2	SKAUZ/BAV92. CMss96M03611S-1M-0105Y-010M-010SY-8M-0Y-0S.
	Gemmiza 11	BOW"S"/KVZ"S"//7C/SER182/3/GIZA168/SAKHA 61 GM78922-GM-1GM-2GM-1GM-0GM.
Triticum durum (tetraploid species)	Benisouef 5	Dippers 3/ BUSHEN 3 CD SS 92 b(book) 128/ 1M/OY/OM/OY/3B/OY/ OSD
	Benisouef 6	BOOMER-21/BUSEC 3 CD SS 95 YOO 1185-8Y- OM-OY-OB-IY-OB-OSD

Table (2): All possible crosses and their reciprocals between the five used parents.

Cross (C)	Reciprocal cross (RC)
Shandweel 1× Misr 2 (C_1)	Misr 2 × Shandweel 1 (RC_1)
Shandweel 1 × Gemmiza 11 (C_2)	Gemmiza 11× Shandweel 1 (RC_2)
Shandweel 1 × Benisouef 5 (C_3)	Benisouef 5 × Shandweel 1 (RC_3)
Shandweel 1 × Benisouef 6 (C_4)	Benisouef 6 × Shandweel 1 (RC_4)
Misr 2 × Gemmiza 11 (C_5)	Gemmiza 11 × Misr 2 (RC_5)
Misr 2 × Benisouef 5 (C_6)	Benisouef 5 × Misr 2 (RC_6)
Misr 2 × Benisouef 6 (C_7)	Benisouef 6 × Misr 2 (RC_7)
Gemmiza 11 × Benisouef 5 (C_8)	Benisouef 5 × Gemmiza 11 (RC_8)
Gemmiza 11 × Benisouef 6 (C_9)	Benisouef 6 × Gemmiza 11 (RC_9)
Benisouef 5 × Benisouef 6 (C_{10})	Benisouef 6 × Benisouef 5 (RC_{10})

Table (3): The average number of chromosomal associations at diakinesis and metaphase I stages for parental and hybrid genotypes including reciprocals.

Genotype		Diakinesis						Metaphase I					
		I	II	III	IV	V	VI	I	II	III	IV	V	VI
Parents	Shandweel 1	0.20	18.61	0.12	0.01	0.08	-	0.27	20.36	0.26	0.02	0.03	-
	Misr 2	0.30	20.09	0.44	0.05	-	-	0.3	19.51	0.75	0.14	0.11	-
	Gemmiza 11	0.57	20.23	0.34	-	-	-	0.5	20.36	0.26	-	-	-
	Benisouef 5	0.09	13.83	0.07	0.01	-	-	0.08	13.83	0.06	0.02	-	-
	Benisouef 6	0.06	13.88	0.06	-	-	-	-	13.80	0.1	-	-	-
Hexaploid × hexaploid hybrids	Shandweel 1 × Misr 2 (C_1)	0.15	19.19	0.49	0.10	-	-	0.13	20.22	0.37	0.14	-	0.02
	Misr 2 × Shandweel 1(RC_1)	0.9	19.94	0.34	0.05	-	-	0.92	19.94	0.28	0.09	-	-
	Shandweel 1 × Gemmiza 11(C_2)	1.35	18.16	0.55	0.47	-	-	1.33	16.77	1.23	0.52	-	0.2
	Gemmiza 11 × Shandweel 1 (RC_2)	13.5	20.49	0.18	0.12	-	-	0.23	20.18	0.19	0.21	-	-
	Gemmiza 11 × Misr 2 (RC_5)	0.15	19.96	0.2	0.22	-	-	0.39	19.35	0.27	0.57	-	-
Hexaploid × tetraploidhybrids	Shandweel 1 × Benisouef 5 (C_3)	6.55	9.89	1.03	0.79	-	-	6.34	10.53	1.33	0.97	-	0.09
	Shandweel 1 × Benisouef 6 (C_4)	7.38	11.29	0.9	0.45	0.09	-	7.30	10.70	1.20	0.45	0.15	-
	Misr 2 × Benisouef 5 (C_6)	4.67	11.79	1.36	0.59	0.05	0.05	4.65	12.09	1.26	0.40	0.05	0.12
	Misr 2 × Benisouef 6 (C_7)	7.01	12.90	0.72	0.46	-	-	7.05	12.67	0.63	0.46	-	-
	Gemmiza 11 × Benisouef 5 (C_8)	5.61	13.30	0.66	0.15	-	-	5.35	13.44	0.82	-	-	-
	Gemmiza 11 × Benisouef 6 (C_9)	3.70	13.70	1.30	-	-	-	4.35	14.05	0.85	-	-	-
Tetraploid × hexaploid hybrids	Benisouef 5 × Shandweel 1 (RC_3)	1.62	14.52	0.67	0.23	0.15	0.15	1.49	14.50	0.81	0.25	0.09	0.09
	Benisouef 6 × Shandweel 1(RC_4)	1.65	15.70	0.65	-	-	-	1.76	15.48	0.76	-	-	-

	Table (3): Cont''												
	Benisouef 5 × Misr 2 (RC_6)	0.95	16.42	0.15	0.15	0.02	0.01	0.85	14.72	0.15	0.15	0.02	0.01
	Benisouef 6 × Misr 2 (RC_7)	1.02	16.31	0.2	0.19	-	-	1.05	16.73	0.08	0.05	0.01	-
	Benisouef 5 × Gemmiza 11 (RC_8)	0.85	16.55	0.35	-	-	-	1.10	15.90	0.3	0.30	-	-
	Benisouef 6 × Gemmiza 11(RC_9)	1.96	15.38	0.76	-	-	-	1.71	15.52	0.75	-	-	-
Tetraploid × tetraploidhybrids	Benisouef 5 × Benisouef 6 (C_{10})	0.12	13.94		-	-	-	0.1	13.95	0.75	-	-	-
	Benisouef 6 ×Benisouef 5 (RC_{10})	0.03	13.94	0.03	-	-	-	0.01	13.98	0.01	-	-	-

I= univalent, **II**= bivalents, **III**= trivalents, **IV**= quadrivalents, **V= pentavalents and VI= hexavalents**

Table (4): Minimum and maximum number as well as average of laggards and micronuclei per cells (between practice), in addition to pollen fertility (%) of parental and hybrid genotypes including reciprocals.

Genotypes		Laggards									Micronuclei						Pollen fertility (%)
		Anaphase I			Anaphase II			Telophase II			Telophase I			Quartet stage			
		Laggards No. (cells)		Average	Laggards No. (cells)		Average	Laggards No. (cells)		Average	Micronuclei No. (cells)		Average	Micronuclei No. (tetrads)		Average	
		Min.	Max.		Min.	Max.		Min.	Max.		Min	Max.		Min.	Max.		
Parents	Shandweel 1	1 (10)	5 (2)	0.28	1 (1)	5 (1)	0.10	1 (9)	3 (1)	0.16	1(9)	5(1)	0.22	1(7)	3(1)	0.12	0.67
	Misr 2	1 (10)	6 (2)	0.63	1 (15)	3 (2)	0.31	1 (10)	3 (1)	0.23	1(9)	6 (2)	0.36	1(7)	3(1)	0.18	0.77
	Gemmiza 11	1 (7)	4 (2)	0.18	1 (4)	4 (3)	0.27	1 (4)	4 (2)	0.20	1(7)	-	0.07	1(3)	4 (1)	0.12	0.75
	Benisouef 5	1 (2)	3 (2)	0.10	1 (4)	5 (1)	0.22	1 (3)	2 (2)	0.07	1(1)	2(1)	0.03	1(2)	-	0.02	0.83
	Benisouef 6	1 (3)	6 (1)	0.21	1 (3)	5 (2)	0.27	1 (3)	2 (3)	0.09	1(3)	2(2)	0.07	1(1)	3(1)	0.04	0.77
Hexaploid × hexaploid hybrids	Shandweel 1 × Misr 2 (C_1)	1(4)	6(1)	0.55	1(1)	6(1)	0.13	1(4)	1(4)	0.04	1(4)	6(1)	0.15	1(1)	1(1)	0.01	0.84
	Misr 2 × Shandweel 1(RC_1)	1(2)	12(1)	0.82	1(5)	4(2)	0.32	1(4)	4 (2)	0.22	1(4)	4(1)	0.25	1(3)	3(5)	0.24	0.85
	Shandweel 1 × Gemmiza 11(C_2)	1(1)	8 (1)	0.15	1(3)	3(2)	0.15	1(2)	2(3)	0.08	1(1)	3(2)	0.11	1(2)	3(1)	0.07	0.78
	Gemmiza 11 × Shandweel 1 RC_2)	1(4)	5(1)	0.20	1(1)	5(1)	0.15	2(1)	2(1)	0.02	1(1)	2(1)	0.03	1(1)	3(1)	0.06	0.80
	Table (4): Cont''																
	Gemmiza 11 × Misr 2 (RC_5)	5(1)	17(1)	0.30	1(2)	3(5)	0.23	1(1)	3(1)	0.04	1(2)	3(2)	0.1	1(1)	1(1)	0.01	0.84
Hexaploid × tetraploid hybrids	Shandweel 1 × Benisouef 5 (C_3)	1(8)	13(10	6.63	1(9)	13(15)	6.49	1(22)	22(3)	3.15	1(24)	5(10)	2.03	1(18)	4(8)	2.3	0.59
	Shandweel 1 × Benisouef	1(8)	18(3)	6.95	1(9)	14(5)	5.69	1(10)	14(3)	5.46	1(14)	13(6)	4.68	1(28)	5(9)	1.91	0.64

	6 (C_4)																
	Misr 2 × Benisouef 5(C_6)	1(8)	16(2)	5.06	1(14)	14(3)	4.09	1(14)	9(10)	4.13	1(6)	13(7)	5.07	1(24)	7(6)	2.7	0.53
	Misr 2 × Benisouef 6(C_7)	1(8)	1(13)	5.1	1(15)	14(1)	3.52	1(15)	9(1)	2.87	1(10)	13(1)	4.45	1(14)	7(1)	2.57	0.50
	Table (4): Cont''																
	Gemmiza 11 × Benisouef 5(C_8)	1(2)	10(20)	6.82	1(1)	8(20)	5.12	1(4)	8(21)	5.43	4(5)	11(10)	6.58	1(4)	6(30)	3.92	0.70
	Gemmiza 11 × Benisouef 6 (C_9)	1 (9)	9 (12)	4.73	1(21)	7(4)	2.93	1(25)	7(5)	2.93	1(21)	6(5)	2.19	1(32)	6(6)	2.21	0.72
Tetraploid × tetraploidhybrids	Benisouef 5 × Shandweel 1 (RC_3)	1(1)	4 (1)	0.10	2(2)	5(2)	0.17	2(1)	-	0.02	0	0	0.00	1(2)	2(2)	0.06	0.80
	Benisouef 6 × Shandweel 1(RC_4)	3(1)	6(1)	0.09	1(1)	2(2)	0.05	1(1)	2(1)	0.07	1(1)	-	0.01	1(1)	4 (1)	0.05	0.85
	Benisouef 5 × Misr 2 (RC_6)	1(2)	9(1)	0.18	1(2)	9(1)	0.37	1(8)	4(2)	0.19	1(4)	-	0.04	1(5)	3(1)	0.12	0.90
	Benisouef 6 × Misr 2 (RC_7)	1(6)	8(1)	0.40	1(5)	7(1)	0.27	1(2)	3(2)	0.12	1(4)	5(1)	0.2	1(1)	2(1)	0.03	0.74
	Benisouef 5 × Gemmiza 11 (RC_8)	3(1)	5(2)	0.13	2(1)	4(1)	0.09	1(3)	-	0.03	1(1)	2(2)	0.05	1(1)	2(1)	0.03	0.79
	Benisouef 6 × Gemmiza 11(RC_9)	3 (1)	6(1)	0.09	1(1)	4(1)	0.07	1(1)	-	0.01	1(1)	2(2)	0.05	1(1)	4(1)	0.05	0.85
	Benisouef 5 × Benisouef 6 (C_{10})	1(4)	3(2)	0.18	1(6)	6(1)	0.38	1(8)	5(1)	0.22	1(4)	3(1)	0.15	1(8)	2(2)	0.12	0.81
	Benisouef 6 ×Benisouef 5 (RC_{10})	1(2)	5(1)	0.21	1(5)	4(1)	0.19	1(2)	3(2)	0.12	1(2)	2(2)	0.06	1(6)	2(1	0.08	0.84

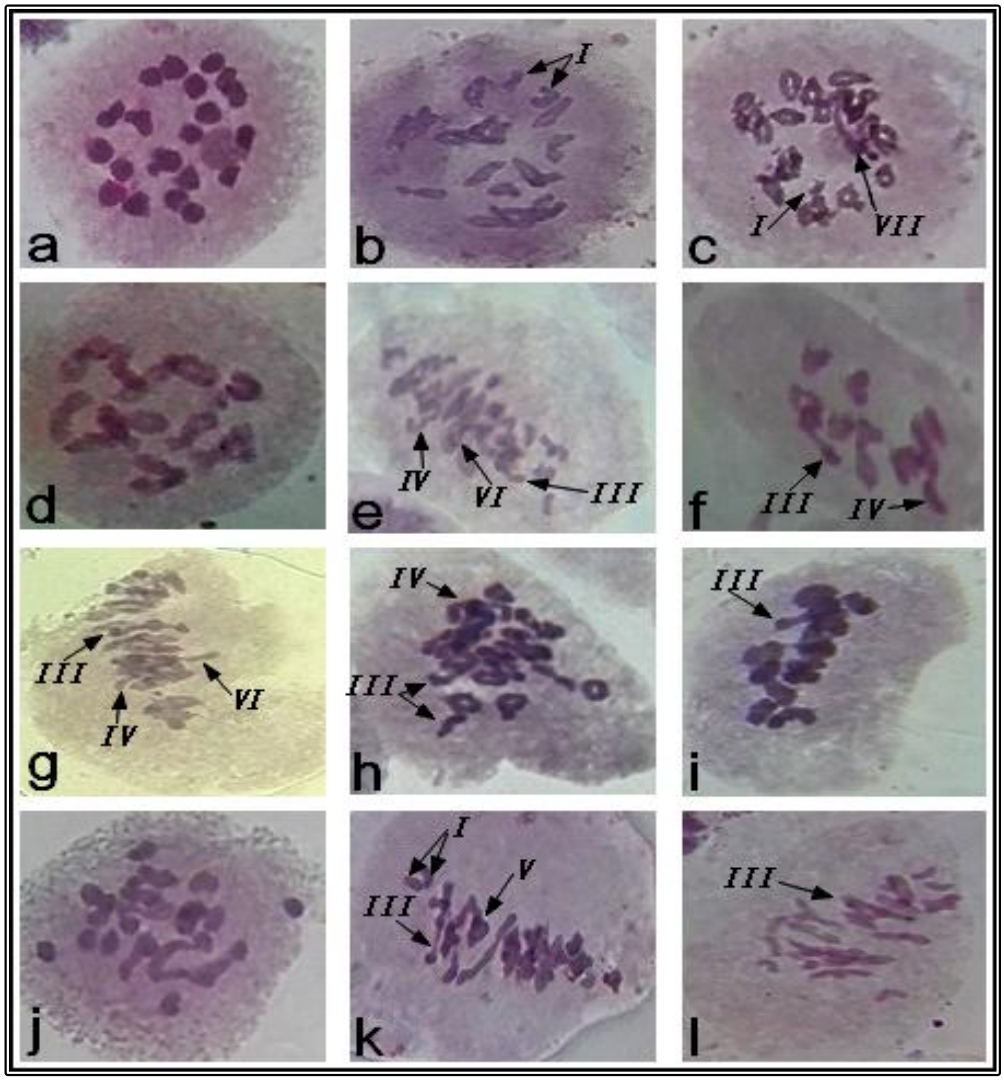

Fig. (1): Chromosomal associations of interspecific hybrids of the used bread and durum wheat cultivars at diakinesis and metaphase I stages. Arrows indicate locations of abnormalities. Figures (a, b, c and d) show meiotic behavior of microsporocytes at diakinesis; a) 21II in Shandweel 1, b) 5 I + 15 II in Benisouef 6 × Shandweel 1 hybrid, c) 1 I + 1 VII + 13 II in Shandweel 1 × Benisouef 6 hybrid, and d) 14 II in Benisouef 6 × Benisouef 5 hybrid. Figures (e, f, g, h, i, j, k and l) show meiotic behavior of microsporocytes at metaphase I; e) 1 III + 1 IV + 1 VI + 15 II in Misr 2, f) 14 II + 1 III + 1 IV in Benisouef 5 × Misr 2 hybrid, g) 1 III + 1 IV + 1 VI + 15 II in Shandweel 1 × Misr 2, h) 2 III + 1 IV + 16 II in Shandweel 1, i) 1 III + 16 II in Benisouef 5 × Misr 2, j) the end of metaphase I and beginning of formation of dyads ;k) 5 I + 11 II + 1 III + 1 V in Shandweel 1 × Benisouef 5 and l) metaphase 1 at Shandweel 1 × Benisouef 6 showing 7 I + 11 II + 2 III. (1600 X)

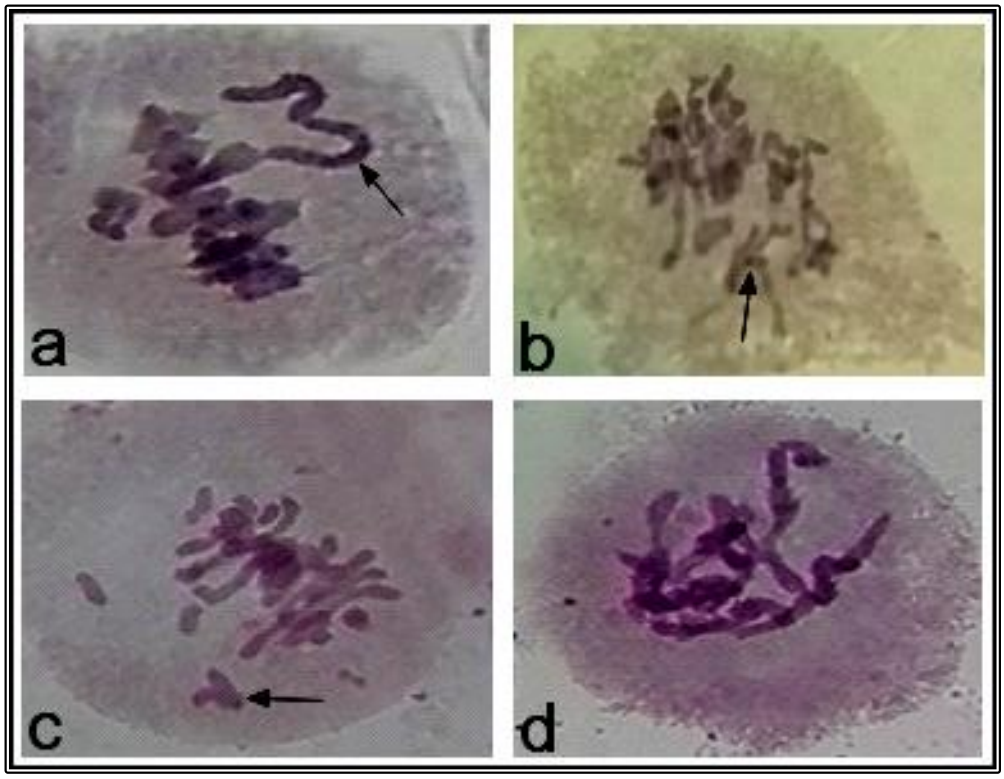

Fig. (2): Arrows show strange phenomenons in chromosomal associations; a) asynaptic behavior at metaphase I stage, b) a tri-partite structures at metaphase I with 5 III + 10 II + 1 IV, c) secondary arm-to-arm chromosome associations and d) the broken chromosomes were stabilized by telomere to telomere recombination.

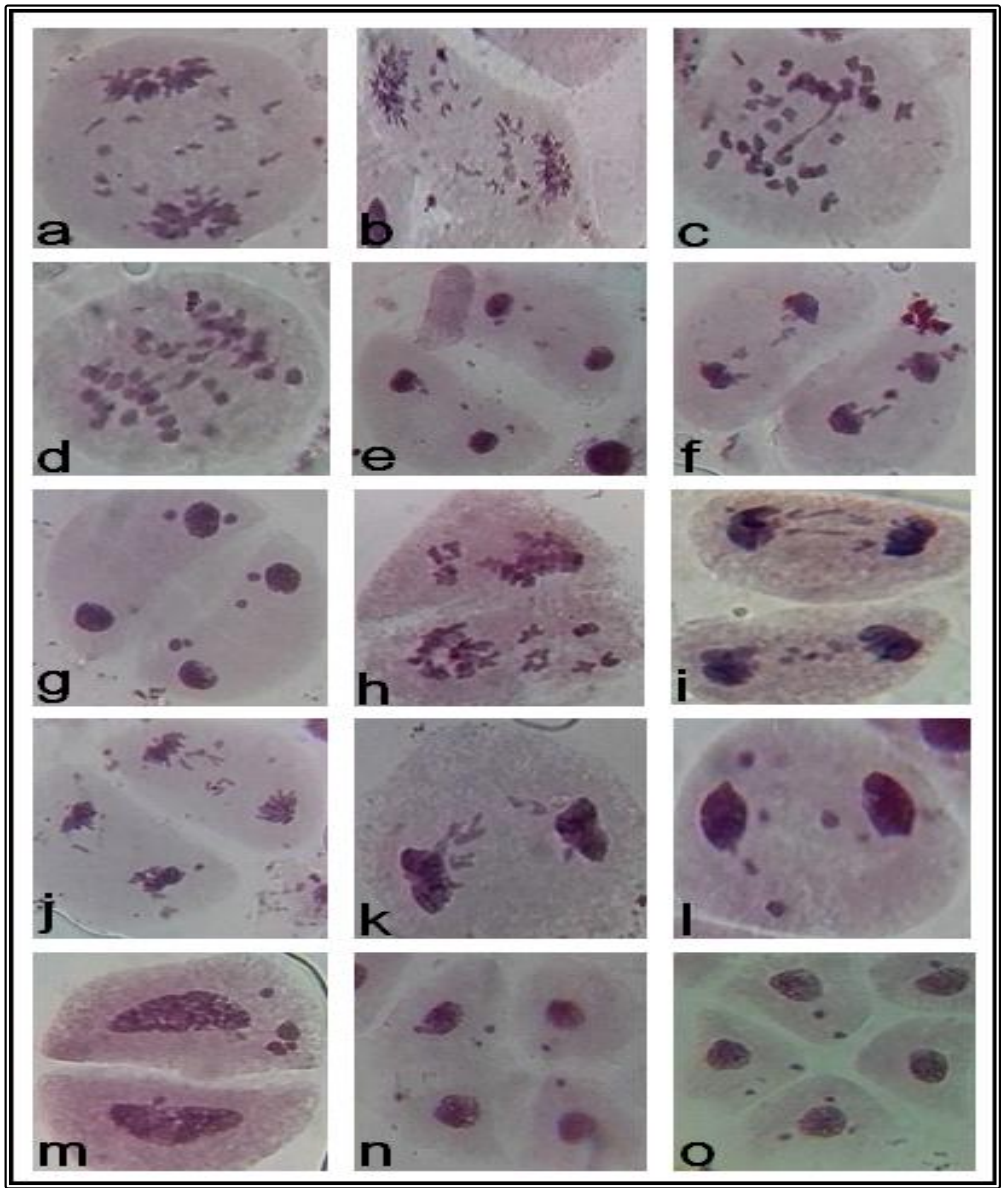

Fig. (3): Laggards and micronuclei formation of interspecific hybrids of the bread and durum wheat cultivars at anaphase I , anaphaseII, telophase I , telophase II and quartet stages. Figs (a, b, c and d) show meiotic behavior of microsporocytes at anaphase I. a, b and c) show 18, 21 and 6 laggards + 1 chromatid bridge in Shandweel 1 × Benisouef 5 , respectively and d) shows 10 laggards in Misr 2 × Benisouef 5. Figs (e, f, g) show meiotic behavior at telophase II. e and f) show 9 and 11 laggards in Shandweel 1 × Gemmiza 11 and g) and 6 laggards in Misr × Benisouef 5. Figs (h, I and j) show meiotic behavior at anaphase II. h) shows 17 laggards in Shandweel 1, i) shows 8 laggards in Shandweel 1 × Benisouef 6 and j) shows l2 forwards + 7 laggards in Shandweel 1 × Benisouef 5. Figs (k, l, m) show micronuclei at telophase I as 9 in Shandweel 1 × Benisouef 6, 6 in Misr 2 × Benisouef 5 and 5 in Shandweel 1, respectively. Figs (n, o) show 5 and 7 micronuclei in Misr 2 × Benisouef 5 and Misr 2 × Benisouef 5, respectively .