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Interspecific Hybrids from Wild x Cultivated *Triticum* Crosses - A Study on the Cytological Behaviour and Molecular Relations

Kari Bhagyalakshmi[1,2], Kunnummal Kurungara Vinod[1,3], Mahadevan Kumar[1], Samudrakani Arumugachamy[1], Amala Joseph Prabhakaran[2,4], Thondikulam Subramanian Raveendran[1]

[1] *Centre for Plant Breeding and Genetics, Tamil Nadu Agricultural University, Coimbatore 641003, India*
[2] *Indian Agricultural Research Institute, Regional Station, Wellington, The Nilgiris, India*
[3] *Indian Agricultural Research Institute, Rice Breeding and Genetics Research Centre, Aduthurai 612101, Tamil Nadu, India*
[4] *Directorate of Oilseeds Research, Hyderabad 500030, Andhra Pradesh, India*

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Abstract

Genetic diversity of cultivated wheat is narrowing down and is increasingly becoming non-complacent in tackling new pathogenic races and adverse environmental situations. Wild relatives of wheat are rich repositories of beneficial genes that are capable of defying adverse situations. However, these wild species are not readily crossable with cultivated ones. The present study attempted to cross three wild wheat species as females with three cultivated species of varying ploidy to understand the intricate behaviour of hybrids in relation to cytology, morphology, and molecular recombination. Post-fertilization barriers caused hybrid recovery in wild species in contrast to cultivated species. *Triticum monococcum* did not produce hybrids in any of the crosses. Various degrees of chromosome anomalies and hybrid sterility were seen with hybrids of *T. timopheevi* and *T. sphaerococcum*. Cytoplasmic factors were suspected to add more to the abnormality. G genome from *T. timopheevi* could enhance more pairing between B and D of cultivated species. Precocity of certain chromosomes in laggard formation was evident, pointing towards evolutionary self balance of the genomes which prevented homeologous pairing. They are eliminated in hybrids. Molecular diversity clearly corroborated with genetic proximity of the species, which distinguished themselves by maintaining the genome homeology.

Key words: wide hybridization, *Triticum*, molecular diversity, meiotic anomalies, cytoplasmic factors

Introduction

Wheat exceeds all other cereal grain crops in acreage and production. The genetic variability within cultivated wheat is rapidly diminishing, primarily due to the replacement of the highly variable landraces with pure line varieties (Frankel 1970). Wheat breeders have been targeting immediate progenitors of wheat (*Triticum and Aegilops*) and more distantly related genera (*Secale*, *Agropyron*, *Aegilops*, *Haynaldia*, *Elymus*, *Hordeum*, etc.) as supplementary sources to harness beneficial genes.

Different species belonging to the genus *Triticum* and its congeners are diverse in their phenotypic adaptation to a wide range of environments. They hold a rich pool of genetic heterogeneity viz., resistance to pathogens and pests, drought tolerance, winter hardiness, adaptability to poor soil, and high protein content besides other qualities and yield traits. Furthermore, diploid, tetraploid, and hexaploid wild wheat share one or more genomes with cultivated wheat. They play a major role in wheat improvement through introgression of genes. Specific level utilization, however, depends on the production of successful interspecific hybrids with adequate fertility.

Attempts of intra 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 cytogenetics of wild and domesticated species. This has further aided in the utilization of exotic gene pools for wheat improvement. Interspecific crosses still remain a major challenge to wheat breeders. The complex

* **To whom correspondence should be addressed**
Kunnummal Kurungara Vinod
E-mail: kkvinodh@gmail.com
Tel: +91-94430-81539

fertilization behaviour of different wheat species needs to be understood in detail in order to transfer desirable genes from the wild to the cultivated.

In the present study, three wild species of genus *Triticum* with different ploidy levels, viz., *T. monococcum* (2n=14), *T. timopheevi* (2n=28), and *T. sphaerococcum* (2n=42) were crossed with three cultivated species viz., *T. dicoccum* (2n=28), *T. durum* (2n=28), and *T. aestivum* (2n=42). The study focused on the crossability of the species, cytogenetic behaviour of the hybrids, their pollen and spikelet fertility as well as genetic diversity.

Materials and Methods

Interspecific hybridisation

The crossing and field evaluation of the parents and interspecific hybrids were done at the Regional Station of Indian Agricultural Research Institute, Wellington, The Nilgiris. The parent materials used were wild *Triticum* collections viz., *T. monococcum*, *T. timopheevi*, and *T. sphaerococcum* as female parents and cultivated wheat viz., *T. aestivum* cv. Agra local, *T. durum* cv. MACS 2864 and *T. dicoccum* cv. NP200 as males. Direct crossings were done in all nine possible combinations.

Morphology of interspecific hybrids

The hybrid seeds were germinated *in vitro* and were transplanted to the field on day 15 along with the parents. The parents and the hybrids were studied for morphological characters viz., plant height (cm), tillering habit, leaf colour, days to heading, length of panicle (cm), and for the presence of awns. At the time of anthesis, pollen fertility was determined using 1% acetocarmine mixed with glycerol (1:1).

Cytology of interspecific hybrids

Young spikes of appropriate size were fixed in Carnoy's fluid for 24 h before storing in 70% ethanol at 4 °C. Temporary smears of microsporocytes were prepared with 1% acetocarmine and examined after destaining the smears with 45% acetic acid.

Pre-fertilization barriers

To investigate pollen-pistil interactions at pre-fertilization levels, epifluorescence technique was used to detect pollen tube growth and fertilization (Parani 1998). The pollinated pistils were fixed in Carnoy's fluid at hourly intervals for first eight h and then at 12, 24, and 48 h after pollination. The pistils were dissected out and softened with 8N NaOH for 8 h at room temperature, washed thoroughly in distilled water, and stained overnight in 0.1% Aniline Blue in 1 N Tribasic potassium phosphate. The pistils were mounted in glycerol (50%) and examined under ultraviolet illumination using a 320-400 nm excitation filter and a 470 nm barrier filter using Olympus BX 60 microscope.

Molecular marker analysis

Genomic DNA was extracted from young leaf tissues using cetyl trimethyl ammonium bromide (CTAB) procedure. Random amplified polymorphic DNA (RAPD) markers were used to fingerprint parents and hybrids. Of the ten random primers (OPBA series; Operon Inc.) three which produced polymorphic bands (OPBA-01, OPBA-03, and OPBA-07) were used for the analysis. The amplified fragments were resolved in 1.5% agarose gel electrophoresis and imaged under ultraviolet transillumination following ethidium bromide staining. The polymorphic bands were scored for molecular diversity, and similarity matrix was constructed using Dice similarity coefficient. The dendrogram was obtained using the unweighted pair group method using arithmetic averages (UPGMA). The tree construction followed bootstrapping of 10,000 times.

Results

Interspecific hybridization

All the crosses attempted with *T. monococcum* failed. No seed set was obtained from the 640 florets pollinated (Table 1). The cross between *T. timopheevi* with *T. dicoccum* yielded 74 seeds with a success of 58.7% of which only 23 had germinated. In the other two crosses viz., *T. timopheevi* x *T. durum* and *T. timopheevi* x *T. aestivum*, the seed sets observed were 20.9 and 37.7% respectively. *T. timopheevi* x *T. durum* hybrids yielded 48.3% viable hybrids while *T. timopheevi* x *T. aestivum* produced 47.8% viable hybrids (22 numbers). Crosses made of *T. sphaerococcum* with *T. dicoccum*, *T. durum*, and *T. aestivum* produced seed sets of 28.5, 26.2, and 37.8% in that order. Only nine out of 53 seeds germinated (17.0%) for the *T. sphaerococcum* x *T. dicoccum* cross. Viability of the hybrids was 28.2% for the cross with *T. durum* and 12.3% with *T. aestivum*. The seeds obtained were very small in size and shrivelled in nature.

Table 1. Crossability of the wild and cultivated species of *Triticum*

Ovule parent	Pollen parent	No. of florets pollinated	No. of seeds obtained	Seed set (%)	Viable hybrids obtained	Viability percent
T. monococcum	*T. dicoccum*	215	0	0	0	0
	T. durum	203	0	0	0	0
	T. aestivum	222	0	0	0	0
T. timopheevi	*T. dicoccum*	126	74	58.73	23	31.08
	T. durum	139	29	20.86	14	48.28
	T. aestivum	122	46	37.70	22	47.83
T. sphaerococcum	*T. dicoccum*	186	53	28. 49	9	16.98
	T. durum	149	39	26.17	11	28.21
	T. aestivum	172	65	37.79	8	12.31

Morphology of interspecific hybrids

All the hybrids of *T. timopheevi* were bushy with an average height ranging from 97 (*T. timopheevi* x *T. aestivum*) to 115 cm (*T. timopheevi* x *T. dicoccum*). The leaves of hybrids were

pubescent except for *T. timopheevi* x *T. dicoccum* which had glabrous leaves. The hybrids had started to produce spikes from day 78 (*T. timopheevi* x *T. durum*) up to day 96 (*T. timopheevi* x *T. dicoccum*). The average panicle length varied from 7.8 to 10.4 cm which was longer than both the parents. The awns were more prominent among hybrids. The peduncle was more similar to the male parent and longer than the female. Hybrids produced white coloured anthers with sterile pollen. They were fully sterile and set no seeds on selfing (Table 2).

Table 2. Morphology of parents and hybrids

Material	Plant height (cm)	Tillering	Leaf nature	Days to heading	Presence of awns	Panicle length (cm)	Pollen fertility (%)	Seed set on selfing (%)
T. timopheevi	112 ±5	Profuse	Dark green;	110	Present	6.1 ±0.5	100.0	96.3
T. sphaerococcum	76 ±5	Medium	Green	65	Absent	5.9 ±0.5	99.1	97.0
T .dicoccum	130 ±5	Medium	Green	58	Present	6.9 ±0.5	100.0	100.0
T. durum	62 ±5	Low	Green	46	Present	7.4 ±0.5	100.0	99.5
T. aestivum	105 ±5	Low	Green	45	Present	7.2 ±0.5	100.0	100.0
T. timopheevi x T. dicoccum	115 ±5	Profuse	Dark green; glabrous	89	Present	9.5 ±0.5	0.0	0.0
T. timopheevi x T. durum	105± 5	Profuse	Dark green; hairy	78	Present	7.8 ±0.5	0.0	0.0
T. timopheevi x T. aestivum	97 ±5	Profuse	Dark green; hairy	96	Present	10.4±0.5	0.0	0.0
T. sphaerococcum x T. dicoccum	79 ±5	Medium	Green	69	Present	8.5 ±0.5	73.8	1.6
T.sphaerococcum x T. durum	72 ± 5	Medium	Green	68	Present	9.8 ±0.5	75.1	3.2
T. sphaerococcum x T. aestivum	74 ±5	Medium	Green	64	Present	8.7±0.5	65.0	2.1

Hybrids of *T. sphaerococcum* had plant height (72 to 79 cm) that was closer to the female parent (76 cm). Tillering was medium resembling that of the female parent. Colour of the leaves was normal. Flowering started on day 64 in *T. sphaerococcum* x *T. aestivum* hybrids. Awns were prominent in all progenies. The length of the panicle varied between 8.5 and 9.8 cm, which were longer than both the parents. The anthers contained both fertile and sterile pollen. The percentage of seed set was low for all the hybrids on selfing.

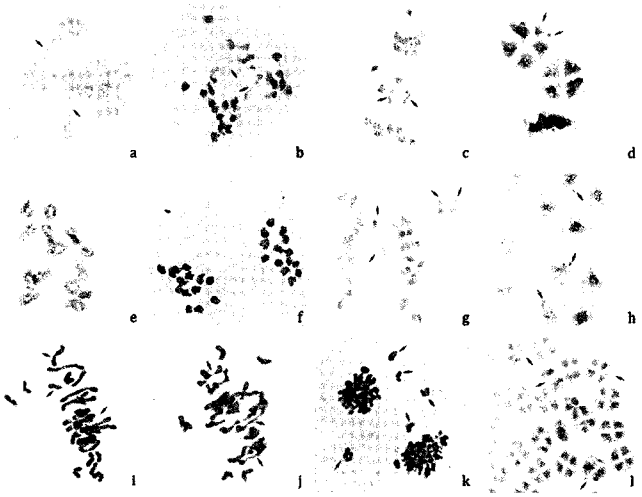

Fig. 1. Cytological behaviour of interspecific hybrids of *T. timopheevi*. Arrow points indicate locations of abnormalities. Figures (a-d) show meiotic behaviour of microsporocytes in the hybrids of *T. timopheevi* x *T. dicoccum*. a) metaphase with rod chromosomes (3I + 8II + 3III, x600); b) anaphase I - bridge formation (x600); c) anaphase I - laggards (x600); d) sporad formation - hexad and tetrad (x400). Figures (e-f) show cytology of microsporocytes of the hybrid *T. timopheevi* x *T. durum*. e) diakinesis (14 II, x600); f) anaphase I - normal separation (x600); g) anaphase I - laggards (x600); h) tetrads with micronuclei (x400). Figures (i-k) show meiotic behaviour of microspore mother cells of the hybrid *T. timopheevi* x *T. aestivum*. i) metaphase (exclusion of certain bivalents, 10I + 5II + 5III, x600); j) early anaphase (x600); k) anaphase I - laggards and normal division (x600) and l) sporad formation -dyad, triad, tetrad, and pentad (x 400).

Meiotic behaviour of interspecific hybrids

Hybrids of *T. timopheevi* with *T. dicoccum* and *T. durum* were of 2n=28, while the hybrids with *T. aestivum* were 2n=35. The microsporocyte cytology of these hybrids showed univalents, trivalents, and quadrivalents at diakinesis / metaphase I, except in the hybrids of *T. timopheevi* x *T. durum* (Table 3; Figure 1). The average number of univalents ranged from 5.2 (*T. timopheevi* x *T. dicoccum*) to 11.4 (*T. timopheevi* x *T. aestivum*). Hybrids of *T. durum* produced 14 bivalents. Trivalents ranged from 1.8 to 4.5. Quadrivalents were seen only in the *T. aestivum* cross. Metaphase showed presence of rod bivalents in *T. dicoccum* hybrids. Abnormal anaphase separation and bridge formation were common and many laggards were seen in hybrids of *T. dicoccum* and *T. aestivum*. The number and frequency of laggards varied in different crosses. Abnormal tetrad formation and

Table 3. Meiotic chromosome association and behaviour at diakinesis/ metaphase I and formation sporad and micronuclei in different interspecific hybrids

Cross	Chromosome association at diakinesis / metaphase*					Most frequent association	Frequency of laggards									No. of bridges	Frequency of sporads						Total no. of micronucle
	I	II	III	IV	Total		0	1	2	3	4	5	6	11	Total		2	3	4	5	6	Total	
T. timopheevi x T. dicoccum	2-6 (5.2)	8-10 (8.7)	1-3 (1.8)	-	96	6I+8II+2III	-	5	9	16	19	23	8	-	80	2	15	18	23	36	8	100	-
T. timopheevi x T. durum	-	14 (14.0)	-	-	90	14II	23	-	2	-	-	-	-	-	25	-	-	-	100	-	-	100	1-5
T. timopheevi x T. aestivum	5-12 (11.4)	4-11 (4.5)	1-5 (4.5)	1 (0.6)	112	11I+4II+4III+1IV	3	7	13	36	20	33	4	4	120	1	26	27	12	35	-	100	1-3
T. sphaerococcum x T. dicoccum	1-5 (2.3)	9-15 (12.3)	2 (1.1)	3 (1.2)	110	1I+12II+2III+1IV	7	-	37	3	53	-	-	-	100	-	-	-	100	-	-	100	2-4
T. sphaerococcum x T. durum	1-4 (2.2)	13-15 (13.8)	1 (0.1)	2 (1.3)	100	3I+14II+1IV	4	-	64	-	32	-	-	-	100	-	-	-	100	-	-	100	1-7
T. sphaerococcum x T. aestivum	2-4 (2.7)	16-19 (17.4)	1 (0.3)	2 (0.9)	112	2I+16II+2IV	14	-	36	-	-	-	-	-	50	-	-	-	100	-	-	100	3

*Figures in the parentheses denote weighted mean of the chromosome association.

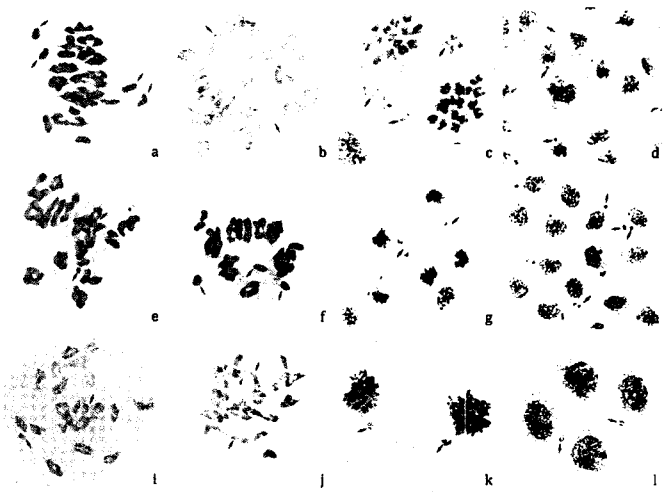

Fig. 2. Cytological behaviour of interspecific hybrids of *T. sphaerococcum*. Arrow points indicate locations of abnormalities. Figures (a-d) show meiotic behaviour of microsporocytes in the hybrids of *T. sphaerococcum* x *T. dicoccum*. a) Metaphase (non-orientation of univalents, 4I + 12II + 1III + 1IV, x600); b) diakinesis (1I + 10II + 2III, x600); c) anaphase I - laggards (x600); d) tetrads with micronuclei (x400). Figures (e-f) show cytology of microsporocytes of the hybrid *T. sphaerococcum* x *T. durum*. e) diakinesis (with univalents, 2I + 13II + 1III + 1IV, x600); f) diakinesis (3I + 13II + 2III, x600); g) anaphase II - laggards (x600); h) tetrads with micronuclei (x400). Figures (i-k) show meiotic behaviour of microspore mother cells of the hybrid *T. sphaerococcum* x *T. aestivum*. i) diakinesis (2I + 17II + 2III, x600); j) diakinesis (3I + 16II + 1III +1 IV, x600); k) anaphase I - laggards and a normal cell (x600) and l) tetrads with micronuclei (x400).

frequent formation of dyad, triad, pentad, and hexad were observed. Formation of micronuclei was seen in the hybrids with *T. durum* and *T. aestivum*, which was absent in that of *T. dicoccum*. The shape of the pollen grains showed polymorphism except in the case of hybrids with *T. durum*.

Interspecific hybrids of *T. sphaerococcum* with *T. dicoccum* and *T. durum* were of 2n=35. The hybrids with *T. aestivum* were 2n=48. Chromosome associations such as univalents, bivalents, trivalents, and quadrivalents in varying frequencies were observed in all the crosses (Table 3; Fig. 2). The average number of univalents ranged from 2.2 (*T. sphaerococcum* x *T. durum*) to 2.7 (*T. sphaerococcum* x *T. aestivum*). Bivalents were most common in the cross with *T. aestivum* (17.4). Occurrence of trivalents was more in *T. sphaerococcum* x *T. dicoccum* hybrids (1.1) and quadrivalents in hybrids with *T. durum* (1.3). Two pairs of precocious chromosomes were found in anaphase I of the *T. sphaerococcum* x *T. dicoccum* cross. A preponderance of two and four laggards in the interspecific hybrids with *T. durum* (64 and 32% respectively) as well as with *T. dicoccum* (37 and 53%) were seen. Laggards were rarely seen in hybrids with *T. aestivum*. Occasional bridge formation was noticed in *T. sphaerococcum* x *T. dicoccum* and *T. sphaerococcum* x *T. aestivum* hybrids. Normal tetrad formation was observed in all the cases, but with a varying number of micronuclei.

Pre-fertilization barriers

The pollen growth observed on the pollinated stigmas of the wild species including *T. monococcum* showed that the pollen germination was normal and occurred 1-2 h after pollination. The pollen tubes grew normally and entered the ovule by about 38 h in all the cases (data not shown).

Molecular marker analysis

Fifty-two amplified DNA fragments were produced in parents and hybrids in the RAPD analysis. There were 33 polymorphic bands producing average polymorphism of 63.5%. The RAPD markers had an average polymorphism information content ranging from 0.435 (OPAB 1) to 0.450 (OPAB 7) (Table 4).

Table 4. Details of the polymorphic markers used

Particulars	OPAB 1	OPAB 3	OPAB 7
Primer sequence	TTCCCCACCC	GTGCGAGAAC	GGGTCGCATC
No. bands produced	19	15	18
No. polymorphic bands	13	9	11
Polymorphism %	68.4	60.0	61.1
Average PIC* value	0.448	0.435	0.450

*PIC: Polymorphic information content

Discussion

Cytology and morphology of interspecific hybrids

T. monococcum (diploid einkorn wheat, A^mA^m) was the donor of A genome to the cultivated wheat (Sears 1948). It harbours many genes conferring resistance against many diseases (Cadle et al. 1997; Gill et al. 1988; Hussien et al. 1998; McIntosh et al. 1984; Miranda et al. 2007), high protein content (Vallega 1978) and adaptability to wide environments. In this study, crosses with *T. monococcum* were not successful and post-syngamic hybridization barriers resulted in embryo abortion and failure of endosperm development. Since *T. monococcum* harboured a dominant multi-allelic gene *L* which induced lethality in inter-

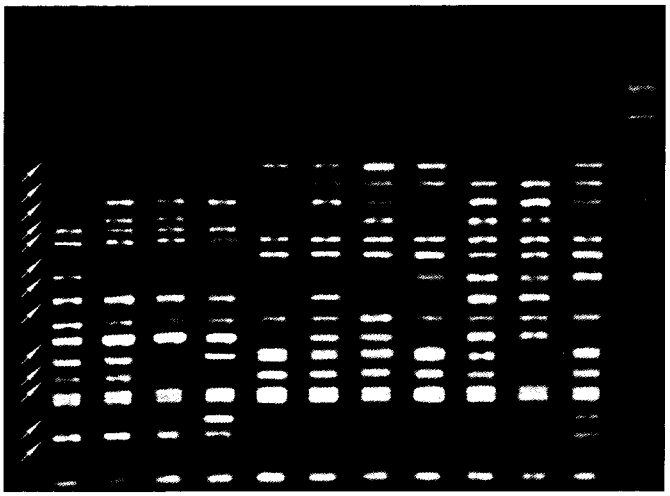

Fig. 3. RAPD profiles of interspecific hybrids of *Triticum* for the primer OPAB 1. On lane 1 - *T. timopheevi*, lane 2 - *T. timopheevi* x *T. dicoccum*, lane 3 - *T. timopheevi* x *T. durum*, lane 4 - *T. timopheevi* x *T. aestivum*, lane 5 - T. sphaerococcum, lane 6 - *T. sphaerococcum* x *T. dicoccum*, lane 7 - *T. sphaerococcum* x *T. durum*, lane 8 - *T. sphaerococcum* x T. aestivum, lane 9 -T. dicoccum, lane 10 - *T. durum*, lane 11 - *T. aestivum* and lane M shows ladder.

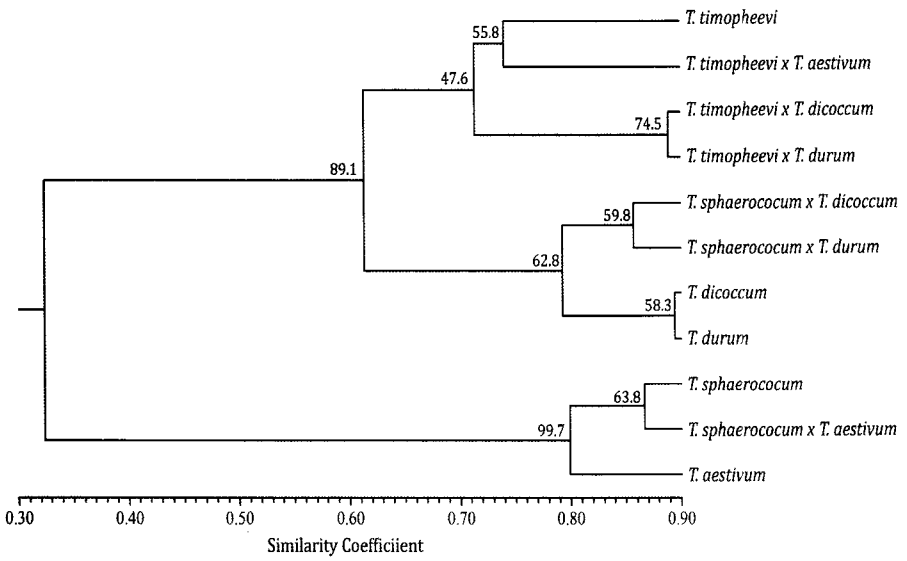

Fig. 4. Consensus tree showing the genetic relationship of *Triticum* species and their interspecifc hybrids used in the study as revealed by RAPD markers. The numbers at the forks show the percentage of times the group consisting of the species which are to the right of that fork occurred while bootstrapping 10,000 times.

specific hybrids (Sears 1948), it was not easily crossable with cultivated wheat (The and Baker 1975).

The cultivated and wild forms of *T. timopheevi* (A^tA^tGG) are known to provide disease resistance genes (Dyke 1992; Perugini et al. 2008). *T. timopheevi* is distinguished from other species by the presence of G genome inherited from *Aegilops speltoides* (Suemoto 1973). Furthermore, a founder translocation involving chromosomes 6A, 1G, and 4G distinguishes *T. timopheevi* from cultivated tetraploids (Jiang et al. 1994). In the present study, microsporocyte cytology revealed meiotic abnormalities exhibiting chaotic chromosome pairing culminating in abnormal chromosome separation and predisposed laggard formation (Fig. 1), caused by genomic imbalances between the species. The hybrids of *T. timopheevi* x *T. durum* were the exception to this. The multivalent formation suggested a homeological relationship between these species. The homeology between the B and G genomes has been reported earlier (Tomar and Vari 1995). This was evident from the normal pairing observed in *T. timopheevi* x *T. durum* hybrids, wherein possible homeological pairing could have been accelerated by some specific enhancer genes from the G genome. Furthermore, the observations led to conclude that the G genome could be fostering multivalent formation among B and D genomes in other crosses because such types of pairings were normally absent in hexaploid wheat in the absence of the G genome. These meiotic anomalies resulted in the formation of anomalous pollen precursor cells, resulting in polymorphic sterile pollen grains. Despite producing uniform pollen in *T. timopheevi* x *T. durum* hybrids, all the F_1s were sterile. Disharmonious interactions between cytoplasm and nucleus might also have resulted in hybrid sterility. These observations gain importance especially in the crosses involving *T. timopheevi* as female parent, where *timopheevi* cytoplasm can be a source of cytoplasmic male sterility.

T. sphaerococcum (AABBDD) is one of the sources for disease resistance gene against powdery mildew (Hsem et al. 2001). Even though it shared two genomes A and B with all male parents used, the seed set was limited. No significant improvement was seen either in the cross between *T. sphaerococcum* and *T. aestivum*, despite both being hexaploids carrying the same set of genomes A, B, and D. This implied that genome stabilization that occurred independently during the course of evolution could be inducing incompatibility. These genomes, though homeological, are incorporated with specific homeologous pairing supressors similar to *Ph1* allele on the long arm of chromosome 5B (Jauhar et al. 2004). The presence of precocious chromosomes of about 1-2 pairs possibly points to this evidence. They tend to get eliminated in the hybrid combinations to maintain their exclusive affinity to the whole genome they harbour. These laggards were leading to the formation of micronuclei affecting the pollen fertility. It was interesting to note that in the hybrids of *T. sphaerococcum*, a smaller number of laggards was observed unlike those of *T. timopheevi*, possibly referencing the more probable chromosome pairing between the genomes involved.

Interspecific hybrids of *T. timopheevi* had many of the morphological characters similar to that of female parent. The quantitative traits such as plant height and heading date were intermediate but skewed towards the maternal parent. It has been reported in wheat that substitution of nuclear components into the background of alien cytoplasm, caused morphologically inferior phenotypes in terms of plant height, vigour, biomass, changes in ear traits, and prolongation of heading time (Tomar et al. 2004). Similar results were seen in the case of *T. sphaerococcum* hybrids, except for the awnness which was dominant and was inherited from the pollen parents. In most of the earlier studies, the wild parents have been used as male to introgress the desirable genes into cultivated species without contaminating the cytoplasmic background of the cultivated species. In this study, we have deliberately used the wild parents as female to incorporate the effect of alien cytoplasm into the hybrids. Our results are indicative of significant effect of maternal origin, as seen in leaf and floral traits.

Genetic diversity

Molecular marker distribution showed hybrids flanked between the parents confirming their hybridity. The dendrogram obtained was particularly interesting, which revealed more genetic proximity of the hybrids towards maternal parents as described by the inherited amplicons. Friebe and Gill (1994) reported that translocation polymorphisms between wheat

species play a key role determining the DNA similarities, which might in turn hamper the production of normal chromosome pairing. In this context, it was interesting to note that the cultivated tetraploid species *T. dicoccum* and *T. durum* had more genetic closeness, similar to the case of hexaploid species, *T. aestivum* and *T. sphaerococcum*. These species are reported to have a common ancestral origin. The interspecific hybrids of these species showed varying degrees of meiotic anomalies. This highlights the presence of similar genomic fragments in their chromosomes, probably distributed in a rearranged fashion transpired by translocations and inversions during the course of evolution. The A, B, and D genomes in cultivated wheat are homeologues, but they differ considerably with respect to the distribution of highly repeated DNA sequences (Tomar et al. 2004).

Though wide hybridization is a challenging task, there is always a need to mobilize genes from wild species to the cultivated. The use of wild species as female had been thought of as an alternate to retrieve viable recombinants and there had been always a possibility of subsequent backcrossing to cultivated species so that the unwanted wild genome can be naturally eliminated in due course except for the genes introgressed.

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