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Cytogenetics of a *Hordeum vulgare–Triticum turgidum* hybrid and its backcross progenies with *T. turgidum*

ABSTRACT: A *H. vulgare* L. cv. Manker (HH, $2n = 14$)/*T. turgidum* L. cv. Cocorit 71 (AABB, $2n = 4x = 28$) hybrid is described. The hybrid was somatically stable with a $n = 3x = 21$, HAB composition. Mean meiotic relationships were 19.26 univalents, 0.39 bivalent rods, 0.46 bivalent rings, 0.02 trivalents, and with a 1.21 chiasma frequency per cell. Meiocytes possessed hyper- and hypoploid compositions with a unique separation of up to five chromosomes. When the self-sterile F_1 hybrid was pollinated by *T. turgidum*, backcross-1 seed sets. These seed produced BC_1 plants with $n = 3x = 21$ and an expected $2n = 5x = 35$, HAABB pentaploid. The pentaploid BC_1 plant was completely sterile and did not survive. Pollination of the five apomictic BC_1 plants by *T. turgidum* resulted only in $n = 3x = 21$, HAB, apomictic plants. Subsequent backcrosses with *T. turgidum* produced BC_5 progeny with a range of chromosome numbers from 20 to 35. None of the advanced backcross plants is self-fertile. The complexity of advancing the *H. vulgare–T. turgidum* hybrid and the backcross progeny for agricultural use is discussed.

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INTERGENERIC *Hordeum vulgare–Triticum turgidum* hybrids have been reported by Mujeeb et al.[19], and Thomas et al.[29]. The hybrids in all cases resembled the *T. turgidum* phenotype more than *H. vulgare*, and were a source of information on 1) apomixis[20], 2) presence of somatic/gametic instability[19], and 3) documentation of hybridity[29]. Exploiting the genetic potential of *H. vulgare–T. turgidum* hybrids for practical use has received little consideration, whereas the combination of *H. vulgare* with *T. aestivum* has received wide attention[2–10,13,22–25,27]. Theoretically, the self-sterile F_1 *H. vulgare–T. turgidum* hybrids should offer a working schematic similar to that of *T. aestivum–H. vulgare*[23], particularly if the reciprocal combination is produced.

This paper reports the results of further hybridization of the *H. vulgare* cv. Manker–*T. turgidum* cv. Cocorit 71 combination of Thomas et al.[29], to reanalyze the chromosomal instability observed by Mujeeb et al.[19], in light of the stability reported by Martin and Laguna[15], for *H. chilense–T. turgidum*. Also discussed is the production and cytology of the backcross-1 (BC_1) seed (*H. vulgare–T. turgidum* × *T. turgidum*) together with a consideration of the complexities of further advancing the BC_1 progeny in order to achieve alien genetic transfers and self-fertile progeny.

Materials and Methods

Intergeneric *Hordeum vulgare* L. cv. Manker–*Triticum turgidum* L. cv. Cocorit 71 hybrids were obtained using embryo culture[26,28] and a crossing technique similar to that described by Thomas et al.[29]. The hybrids were cloned and maintained in a growth chamber under a 14-hour day, 20°C/15°C (day/night) and approximately 45 percent relative humidity. Spikes were sampled for meiotic analysis, and the remaining spikes were pollinated by *T. turgidum* cv. Cocorit 71. Early pollinations on two successive mornings, with gibberellic acid (75 ppm) injected into the floret cups each afternoon, assisted backcross-1 seed setting. No embryo culture was necessary. The BC_1 seed were refrigerated at 4°C for 10 days to break dormancy, and then germinated under room temperatures of 18°C to 20°C.

Somatic cytology procedures followed the schedule of Mujeeb et al.[18]. The meiotic samples were fixed in 6:3:1 (alcohol: chloroform: acetic acid) for 24 hours and stored in

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70 percent ethanol under refrigeration until use. The anthers were stained with Feulgen or 2 percent propionic-orcein and observed for metaphase I meiotic relationships.

All BC_1 plants, whether with the 21 HAB or 35 HAABB composition, were backcrossed to *T. turgidum* cv. Cocorit 71 to obtain 1) 35, HAABB types, and 2) BC_2 plants with the potential for *Hordeum* genetic information transfer. Advanced backcross progenies were similarly obtained by pollinations with *T. turgidum* varieties.

Results and Discussion

The *H. vulgare–T. turgidum* hybrid possessed 21 chromosomes that were meiotically associated as 19.26 univalents, 0.39 bivalent rods, 0.46 bivalent rings, 0.02 trivalents, with a 1.21 mean chiasma frequency per cell. There was no somatic instability in the cells analyzed, but meiotic instability was hyper- or hypoploid, (Figure 1*C*, *E*, and *F*). Aneuploid cells were scored with extreme caution in that the unique separation of certain chromosomes received due consideration. It appears that several mechanisms are germ-plasm specific. The aneuploidy that Mujeeb et al.[19] observed was again seen more explicitly using the same parental combination. Martin and Laguna[15] did not observe this instability when they used *H. chilense* instead of *H. vulgare*. The mean meiotic relationships may be another index of germ-plasm influence. Martin and Laguna[15] reported 20.39 univalents, 0.30 bivalents; and 20.06 univalent, 0.466 bivalent chromosome associations when *H. chilense* was hybridized with two cultivars of *T. turgidum*. No ring bivalents were observed. However, in the present data (Table I) the bivalent frequency is considerably higher with the rod and ring bivalents ranging from 0–5, suggestive of a germplasm influence.

Some chromosome pairing relationships are illustrated in Figure 1*A–D*. A trivalent association was observed in one normal meiocyte with 21 chromosomes, but trivalent and quadrivalent associations were more frequent in aneuploid cells. Several cells (62.1 percent) had 21 univalents, and many expressed chromosomal separation characteristics similar to those observed in *H. vulgare–T. aestivum* and *H. vulgare–T. aestivum* × *T. aestivum*[23,24]. This characteristic chromosome separation trend was observed in the F_1 hybrid (Figure 1*A–D*) as well as in the BC_1 progeny (*H. vulgare–T. turgidum* × *T. turgidum*). The meiotic relationships of the BC_1 plant indicate that the uniquely separated chromosomes may belong to the barley genome. Mujeeb-Kazi and Rodriguez[22,23] made a similar interpretation for such chromosomes in *H. vulgare–T. aestivum* and its BC_1 progeny with *T. aestivum*. Under those conditions the BC_1 plant had enough meiocytes expressing 21 bivalents, 7 univalents, with 5 to 6 univalents showing uniqueness of chromosome separation to be designated as those of *Hordeum*. We speculate that these chromosomes may have undergone synapsis without forming chiasma. Should this be followed by a centromeric break coupled with normal metaphase I separation, the configurations seen in Figure 1*A* and *C* may result. This does not preclude the concept that there also may occur a chromosome arm foldback leading to a similar configuration as described above. Since *H. vulgare* chromosomes can be differentially stained this unique separation is being studied further. In the BC_1 progeny (*H. vulgare–T. turgidum* × *T. turgidum* with $2n = 5x = 35$ chromosomes) six meiocytes expressed the theoretical expected fit of 14 bivalents, 7 univalents for the HAABB genomes (Table II) but with a higher occurrence of rod bivalents. The meiocytes with cumulative numbers other than 21 and 35 were excluded from the data of Tables I and II. Those variations merely substantiate the instability phenomenon with possible germ-plasm specificity.

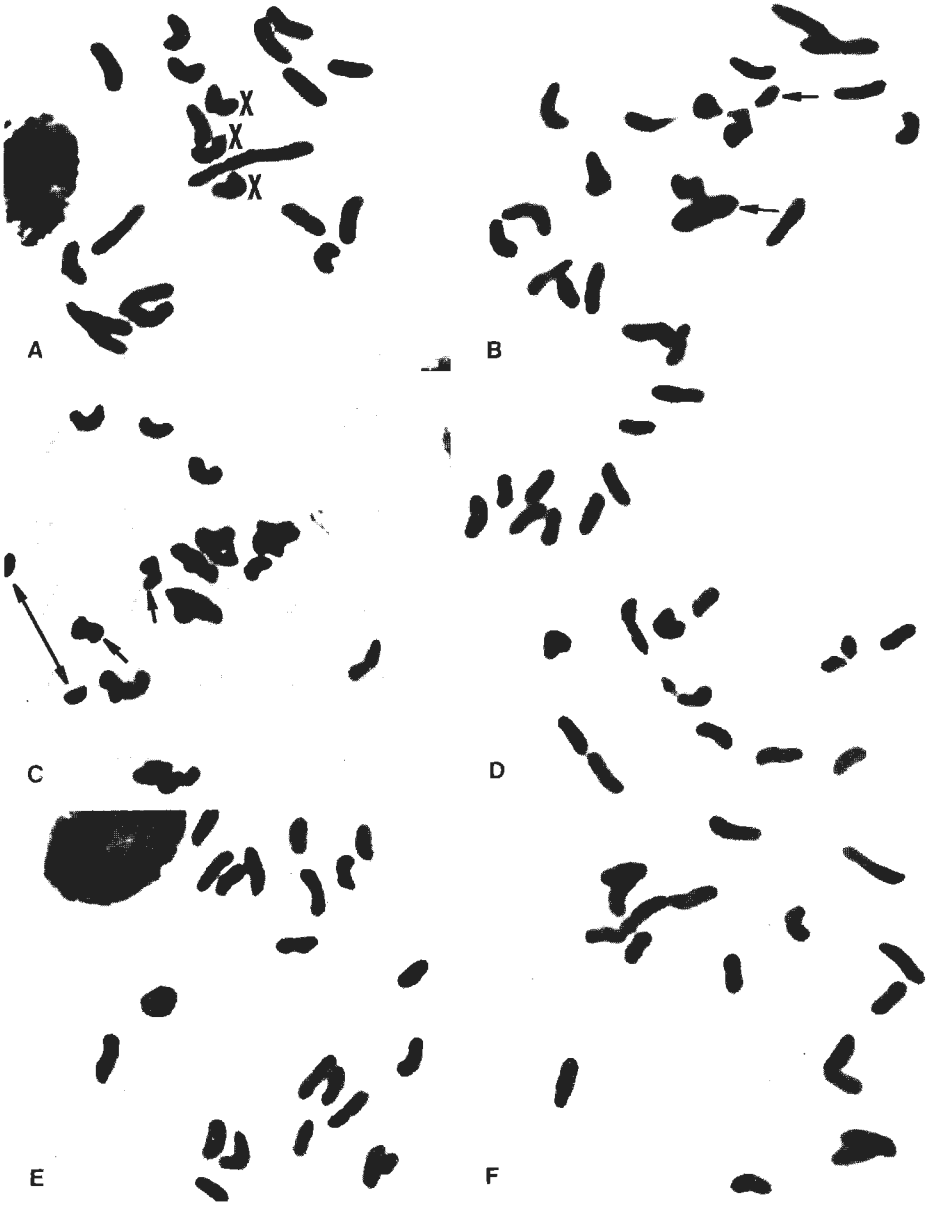

FIGURE 1 Mean metaphase I meiotic relationship in a *H. vulgare–T. turgidum* hybrid: *A*—19 univalents, 1 bivalent rod; note separation of chromosomes marked with X. *B*—17 univalents, 1 bivalent rod, 1 bivalent ring; arrows indicate bivalents. *C*—4 bivalent rings, with separation of three chromosomes (arrows). *D*—19 univalents, 1 bivalent rod. *E*—22 univalents. *F*—aneuploid meiocyte with univalents.

Heteromorphic bivalents were frequently observed but their presence is not solely attributed to pairing between *Hordeum* and *Triticum* chromosomes, since chromosomal size variations among the *Triticum* chromosomes also may reflect a heteromorphic bivalent expression as a consequence of homoeologous chromosome pairing. The pollen grains expressed both polymorphism in size and shape and variations in pore numbers. It seems highly probable that these polymorphic trends are a consequence of the distribution of the chromosomal information in anaphase I and II. The chromosomes may undergo 1) complete separation in anaphase I, or 2) have preferential separation. They likewise determine whether the end-product is to be a diad, triad, or a polymorphic tetrad. It was commonly observed that the product size was positively correlated with the amount of chromatin that it received. The more pronounced such polymorphic developmental trends, the greater may appear the chances to obtain backcross progeny, since transmission is notably higher on the maternal side. This proposition is supported by the relative ease of obtaining BC_1 (*H. vulgare–T. turgidum* × *T. turgidum*) seed without resorting to embryo culture. The plump seed type does not resemble Cocorit 71, and has excellent germination. These BC_1 seed were expected to produce pentaploid ($2n = 5x = 35$, HAABB) BC_1 plants, but the progeny possessed more $n = 3x = 21$, HAB types. For the recovery of $n = 3x = 21$, HAB types, apomixis may be considered as an influencing phenomenon. This was earlier concluded[20] as being the sole phenomenon when self-sterile F_1 hybrids of *H. vulgare–T. turgidum* or *H. vulgare–T. aestivum* were pollinated by *T. turgidum* or *T. aestivum* to give rise to progeny that maintained the maternal F_1 chromosome number, i.e., 21 HAB, or 28 HABD. There remained the possibility of elimination of the *Triticum* genomes (AB or ABD) on the maternal side, followed by true fertilization by the respective *Triticum* species pollen to produce the 21 HAB or 28 HABD seed. If the backcross *Triticum* variety was identical to that which entered the F_1 hybrid combination it may be quite impossible to discern between apomictic development and true fertilization. Based upon more detailed investigations on *H. vulgare–T. turgidum* and *H. vulgare–T. aestivum* hybrids that have utilized genetic markers, and N-banding polymorphisms as criteria for mixing varieties on the backcrosses, we do conclude that apomixis is the operating phenomenon in the above crosses. Additional support is derived from a trigeneric combination of *T. aestivum–Elymus giganteus* × *Agropyron elongatum* (unpub.) where the hybrids would possess 70 chromosomes: 21 ABD + 14 JX of the unreduced egg fertilized by 35 of pollen from *A. elongatum*. While such trigeneric plants were obtained, one embryo produced a plant with 35 chromosomes. This resembled both the morphology and cytology of the *T. aestivum–E. giganteus* self-sterile F_1 that was used as the female for the trigeneric combination, and appears to be the result of apomictic development.

All BC_1 plants were pollinated with *T. turgidum*. The apomictic $n = 3x = 21$ plants set seed, whereas the pentaploid $2n = 5x = 35$ produced no seed and developed five weak tillers. It appears that the complexity of obtaining BC_2 progeny is much greater with *T. turgidum* than with *T. aestivum*. The 15 seed that set when the apomictic ($n = 3x = 21$, HAB) plants were pollinated by *T. turgidum* gave rise to vigorous seedlings. All were $n = 3x = 21$. A plant with the $2n = 5x = 35$ combination was not obtained until this stage (BC_2). The F_1 hybrids, and BC_1 plants (apomicts or of 35 chromosome composition) were poor in tillering. Although the one BC_1 plant with 35 chromosomes could not be maintained, it was encouraging to at least have apomictic seed as a partial source of maintaining the hybrid progeny as $n = 3x = 21$, HAB. Efforts to utilize the hybrids as sources for practical agricultural application at this stage received greater attention considering the complexity encountered in recovering pentaploid ($2n = 5x = 35$, HAABB) germplasm for facilitating possible alien genetic transfer from *H. vulgare* to *T. turgidum*.

By repeated backcrossing the apomict BC_1 plants were advanced up to BC_5. Some of these plants have set BC_6 seed after pollination by *T. turgidum*. None of the BC_5 plants was self-fertile. It was not until BC_4 that a product of true backcross fertilization was obtained (Table III). This plant had 33 chromosomes instead of the expected 35, i.e., BC_3 with $n = 3x = 21$, HAB + 14 AB from pollen = 35 HAABB. The other BC_4 plants with 21 chromosomes when backcrossed to *T. turgidum* varieties produced BC_5 progeny ranging from 20 to 35 chromosomes. Plants with 20 and 23 chromosomes may be considered apomicts and derived as products of maternal aneuploidy. Those with 33 chromosomes are presumably a consequence of the aneuploid egg cell being fertilized by the normal 14 AB pollen. We need, however, also to interpret a chromosome loss that occurred after normal 35 chromosome backcross seed was produced. Aneuploid egg cells were observed in several intergeneric combinations that has led to variable backcross progenies[21]. The backcross variations have been accurately understood through N-banding applications in the *T. aestivum–Aegilops variabilis* × *T. aestivum* combination where the BC_1 progeny ranged from 39 to 63, instead of 56 chromosomes. Since *T. aestivum* and *Ae. variabilis* were amenable to N-banding, Jewell and Mujeeb-Kazi[11] made the following observations: 1) backcross fertilization did indeed occur; 2) the loss of chromosomes on the maternal side occurred in both *T. aestivum* and *Ae. variabilis;* and 3) this chromosome loss was random due to the lack of chromosome pairing in the F_1 hybrid. This may well be the mechanism that

Table I. Mean chromosome associations in *Hordeum vulgare–Triticum turgidum* L. hybrid ($n = 3x = 21$, HAB)

No. cells	Chromosome association I	II rods	II rings	III	% of total	Mean chiasma frequency/cell
41	21				62.1	
3	19		1		4.6	
10	19	1			15.2	
2	17	1	1		3.0	
2	17	2			3.0	
1	15	1	2		1.5	
1	15		3		1.5	
2	13		4		3.0	
1	11	2	3		1.5	
1	11	1	4		1.5	
1	9	1	5		1.5	
1	8	5		1	1.5	
Total 66	1271*	26*	30*	1*		
Mean chromosome relationship	19.26_{I}	0.39_{II} rods	0.46_{II} rings	0.02_{III}		1.21

* Derived as (21 × 41) + (19 × 3) + . . . + (8 × 1) = 1271 for I. Similarly estimated for II and III

Table II. Mean chromosome associations in a *H. vulgare–T. turgidum* × *T. turgidum* BC_1 plant (2n = 5x = 35, HAABB)

No. cells	Chromosome associations I	II rods	II rings	III	IV	% of total	Mean chiasma frequency/cell
1	35					2.86	
1	29	3				2.86	
1	29	2	1			2.86	
1	28	2				2.86	
1	27	4				2.86	
1	27	3	1			2.86	
1	26	3		1		2.86	
1	25	5				2.86	
3	23	6				8.57	
1	21	7				2.86	
1	19	7	1			2.86	
1	19	5	3			2.86	
1	18	8	4			2.86	
1	17	3	4		1	2.86	
1	16	8		1		2.86	
1	16	7	1	1		2.86	
1	16	6	2	1		2.86	
1	15	4	6			2.86	
1	15	6	4			2.86	
1	13	8	3			2.86	
1	13	5	6			2.86	
1	11	6	6			2.86	
1	10	2	9	1		2.86	
1	10	7	4	1		2.86	
1	8	4	1	3	2	2.86	
1	7	10	4			2.86	
1	7	9	5			2.86	
1	7	8	6			2.86	
1	7	6	8			2.86	
1	7	5	9			2.86	
1	7	1	10	2		2.86	
1	7	1	13			2.86	
1	4	5	7	1	1	2.86	
Total 35	585*	178*	119*	12*	4*		
Mean chromosome relationship	16.71_{I}	5.09_{II} rods	3.4_{II} rings	0.34_{III}	0.114_{IV}		12.914

* Derived as: (35 × 1) + (29 × 1) + . . . + (4 × 1) = 585 for I. Similarly estimated for II, III, and IV

Table III. Chromosome number and origin details of backcross progenies (BC) of *H. vulgare–T. turgidum*/n/*T. turgidum*

BC_5 progeny	Plant nos.	Somatic no.	BC_4 origin	Somatic no.	BC_3 origin	Somatic no.	BC_2 origin	Somatic no.
M16*/Ct. 71[3]/GG/Mex./GG[†]	12708	29	5731	33	2308	21	1301	21
〃	12708	30	〃	33	〃	21	〃	21
〃	12710	31	〃	33	〃	21	〃	21
〃	12711	31	〃	33	〃	21	〃	21
〃	12712	29	〃	33	〃	21	〃	21
M16*/Ct. 71[4]/GG/Mex.[+]	12713	33	5734	21	2309	21	1303	21
〃	12714	35	〃	21	〃	21	〃	21
M16*/Ct. 71[4]/GG[2+]	12715	35	5735	21	2309	21	〃	21
M16*/Ct. 71[4]/GG/Mex.[+]	12716	20	〃	21	〃	21	〃	21
〃	12717	23	5738	21	〃	21	〃	21
〃	12719	35	5746	21	2312	21	1307	21

* M16 = *H. vulgare* cv. Manker
† *T. turgidum* varieties: Ct. 71 = Cocorit 71; GG = Grano Grande; Mex. = Mexicali 75

influences the production of plants with 33, 23, and 20 chromosomes in BC_4 and BC_5 (Table III). It is our intention to resolve this speculation by using N-banding on BC_6 material produced from BC_5 plant nos. 12716 and 12717 (Table III).

The *H. vulgare–T. turgidum*/n/*T. turgidum* backcross combinations described above seem to have little practical utility since none was self-fertile. Pistilloidy[9,22] commonly observed in *H. vulgare–T. aestivum*/n/*T. aestivum* has been a major factor for *H. vulgare–T. turgidum*/n/*T. turgidum*. The pistilloidy problem was overcome in the *H. vulgare–T. aestivum* crosses by obtaining the reciprocal combination, i.e., *T. aestivum–H. vulgare* and backcrossing the self-sterile F_1 to *T. aestivum*. Self-fertile backcross progenies have resulted[22], and *H. vulgare* chromosome additions to *T. aestivum* were successfully accomplished[7–9]. Presumably the *T. turgidum–H. vulgare* cross combination direction may lead to self-fertile backcross plants as obtained for *T. aestivum* based progenies[22]. Should efforts be so directed the two most important factors to consider are: 1) the phenotypic dominance of *T. turgidum;* 2) the possible difficulty of obtaining fertile amphiploids. The former may offset any practical advantage from desirable *H. vulgare* gene transfers because of a lack of their genetic expressivity. Since the lack of expression is yet to be critically demonstrated it may justify the research effort. Inducing amphiploidy has been elusive for *T. aestivum–H. vulgare*, *H. vulgare–T. aestivum*, and *H. vulgare–T. turgidum*. It may well include *T. turgidum–H. vulgare* when the combination is produced. Only in three instances have fertile amphiploids been produced between species of *Triticum* and *Hordeum*, i.e., *T. timopheevii–H. bogdanii*[12], *H. chilense–T. aestivum*[1,16,17], and *H. chilense–T. turgidum*[14,15]. Martin and Laguna[14] considered the *H. chilense–T. turgidum* amphiploid to have the potential of a new crop. Such anticipation for *T. turgidum–H. vulgare* may be less optimistic, but worth considering if agricultural practicality is to be achieved specifically from this cross. It is our contention that intergeneric hybridization efforts shall contribute to wheat improvement principally through procedures that allow engineering of subtle gene transfers or via utilization of induced or spontaneously occurring alien chromosomal translocations.

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