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Meiotic Instability in *Hordeum vulgare* × *Triticum aestivum* hybrids



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ABSTRACT: *Hordeum vulgare* × *Triticum aestivum* hybrids ($n = 4x = 28$, HABD) expressed meiotic instability, with meiocytes possessing a hyper- or hypoploid composition. Meiotic restitution aided backcross-1 (BC₁) seed formation when the hybrids were pollinated by the respective *T. aestivum* cultivars. The BC₁ seed-set range was (*H. vulgare* cv. Manker × *T. aestivum* cv. Bonza) × cv. Bonza < (cv. Manker × cv. Pavon) × cv. Pavon < (cv. Manker × cv. Chinese Spring) × cv. Chinese Spring. Gibberellic acid (75ppm) applied twice to the florets as a post-pollination treatment assisted BC₁ seed set. Apart from the expected BC₁ heptaploid somatic count of $2n = 7x = 49$, HAABBDD, BC₁ plants also possessed a somatic range from 27 to 50. These variations are attributed to apomixis and F₁ meiotic instability. Pollinating the self-sterile BC₁ plants with *T. aestivum* produced BC₂ progeny. Chromosome composition of the BC₂ plants was within the normal limits of expectation based on random loss of barley chromosomes. The BC₂ progeny advanced to BC₃ did not produce any self-fertile plants. Self-sterility was resolved by producing the reciprocal (*T. aestivum* × *H. vulgare*) hybrid and advancing it to BC₂ where all plants were self-fertile. The wheat phenotype was dominant.

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INTERGENERIC *Hordeum vulgare* × *Triticum aestivum* hybridization has received considerable interest^{5-8,10-15,17,19,22,24,27,29,32,34} among researchers. Chromosome instability is a common occurrence among hybrids as observed in: *H. vulgare* × *T. aestivum*⁷, (*H. vulgare* × *T. aestivum*) × *T. aestivum*¹⁴, (*T. aestivum* × *H. vulgare*) × *T. aestivum*¹⁵, *H. vulgare* × *T. turgidum*²⁴, (*E. canadensis* × *T. aestivum*) × *T. aestivum*²⁶, (*T. aestivum*/*Elymus giganteus*) × *T. aestivum*²⁸, and *E. canadensis* × *H. vulgare*³⁰. Meiotic restitution leading to F₁ fertility in *Aegilops helldreichii* × *T. durum* was demonstrated by Mann and Sasakuma¹⁸, and by Islam and Shepherd¹¹ in wheat-barley hybrids. These apparently have influenced the findings of others^{7,14,15,27,30}, and contributed to the production of backcross-1 (BC₁) progeny that is derived from self-sterile F₁ hybrids²⁶.

We have various intergeneric hybrid combinations involving some Triticeae^{26,27,29}. Of these, the hybrids of *H. vulgare* with three *T. aestivum* cultivars were reported separately³². This paper reports the meiotic instability that occurred in these *H. vulgare* × *T. aestivum* hybrids. It discusses the BC₁ cytological variations, BC₂ seed production with *T. aes-*

tivum cultivars, and the somatic cytology of some BC₂ and BC₃ progeny.

Materials and Methods

The production of intergeneric hybrids of *Hordeum vulgare* L. cv. Manker with *Triticum aestivum* L. cvs. Bonza, Chinese Spring, Pavon was described previously³². The hybrids were vegetatively cloned and maintained in two growth chambers. The growing conditions were 14 hours of light, 15°C and 10°C, day and night temperatures, respectively, and approximately 45 percent relative humidity.

Representative spikes of these hybrids were meiotically analyzed while some of the self-sterile spikes were pollinated by the respective *T. aestivum* cultivars. Early pollinations when stigma receptivity was not apparent on two successive mornings, with gibberellic acid (75ppm) treatment injected into the floret cups each afternoon, assisted backcross seed setting. Embryos were excised 20 days after pollination and cultured in a special media for small embryos³⁵. The embryos in culture tubes were kept in the dark at 20°C for about two weeks, then transferred for differentiation and

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growth to Murashige and Skoog's³³ media. When the plantlets were 2 cm in size, they were transferred to peat pots and kept in a greenhouse under approximately 70 percent relative humidity. Natural light conditions were 14 hours, with day and night temperatures 20°C and 15°C, respectively. The plantlets grew vigorously and were finally transplanted in the greenhouse to 23 cm clay pots containing soil. Some BC₁ seed were allowed to mature on the F₁ plants, since the embryos earlier excised from BC₁ seed possessed copious starchy endosperm. These BC₁ seed were germinated on moist filter paper in a petri-dish under room conditions of 18° to 20°C after 4°C refrigeration for 10 days to break dormancy.

Root tips from the BC₁ progenies were periodically sampled and processed for somatic counts²³. All meiotic samples were fixed in 6:3:1 (alcohol: chloroform: acetic acid) for 24 hours, and stored in 70 percent ethanol under refrigeration until use. Anthers were stained with feulgen or 2 percent propionic orcein, and observed for metaphase I meiotic relationships.

The BC₁ plants were backcrossed to several *T. aestivum* cultivars to realize the practical incorporation of *Hordeum* characters into *T. aestivum* via addition lines, substitution lines, or genetic transfers³². BC₂ and BC₃ seed production was identical to BC₁ production except that for BC₃ no GA₃ was applied as a post-pollination treatment, and in neither backcross was embryo culturing necessary.

Results and Discussion

F₁ hybrids, BC₁ progeny, and chromosome variations

The *H. vulgare* × *T. aestivum* hybrids possessed 28 chromosomes ($n = 4x = 28$, HABD), meiotically associated as 26.3 univalents, 1.33 bivalents, 0.38 ring bivalents, 0.15 trivalents, 0.021 quadrivalents, and 0.033 hexivalents with a mean chiasma frequency of 2.57 per cell³². The hybrids were somatically stable. The meiotic stages showed a unique separation of one to five chromosomes, and the chromosome univalents were absent from the anaphase I separation phase (Figure 1A-C, E, and G). The separation appears to be initiated earlier in three chromosomes (Figure 1A and G). This chromosome separation rate difference is apparent in Figure 1E where chromosomes X₁ and X₂, although separated, lag behind X₃, X₄, and X₅. Such separated chromosomes were counted as one, before expressing meiotic instability as hyperploidy or hypoploidy (Figure 1A-G).

Frequently, meiocytes exhibited chromo-

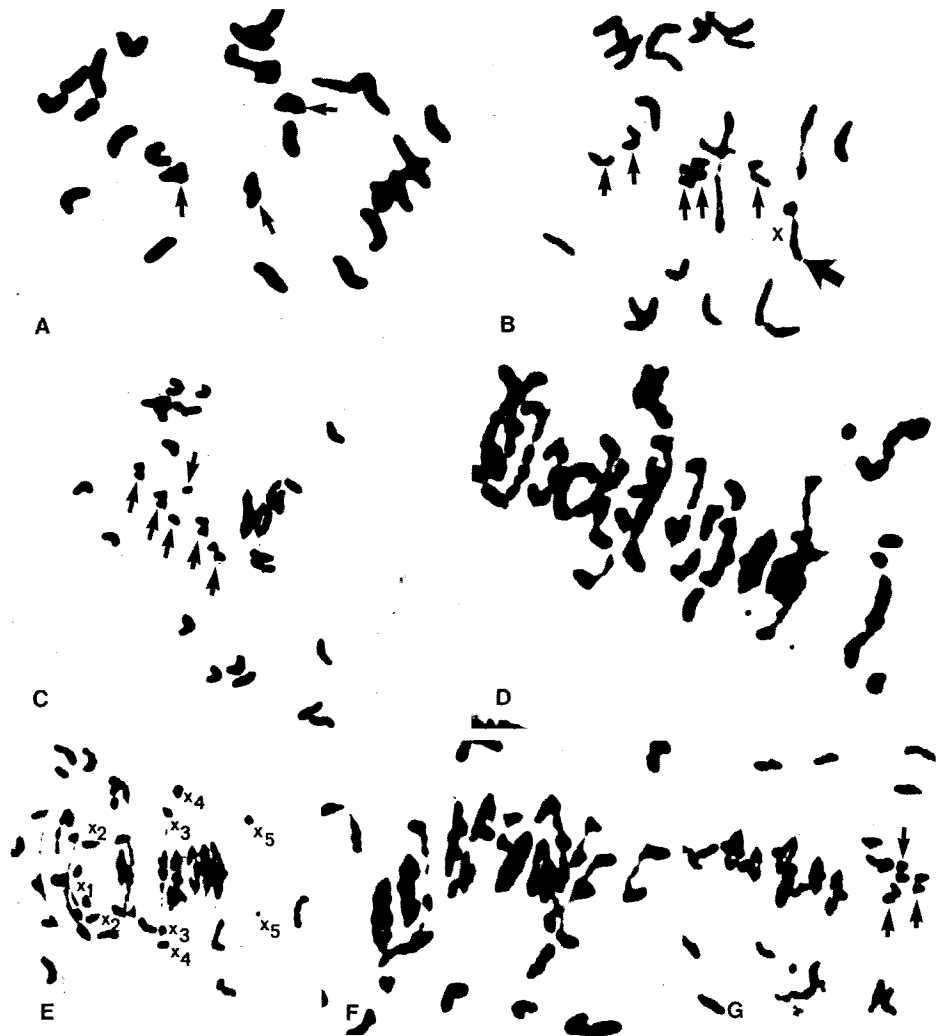


FIGURE 1 Metaphase I chromosome pairing relationships in *Hordeum vulgare* × *Triticum aestivum* hybrids showing meiotic instability. A—1 rod bivalent, 25 univalents; separation of three chromosomes is initiated (arrows). B—1 rod bivalent, 1 bivalent (heteromorphic with X and large arrow), 23 univalents; separation of 5 chromosomes initiated (small arrows). C—2 ring bivalents, 26 univalents; five chromosomes with unique separation area shown (arrows); one has already separated (arrow). D—15 bivalents, one quadrivalent, 8 univalents. E—6 ring bivalents, 5 rod bivalents, and univalents; early separation of five chromosomes completed, (marked X₁, X₂, X₃, X₄, X₅). F—6 ring bivalents, 3 rod bivalents, 2 trivalents, and 13 univalents. G—6 ring bivalents, 18 univalents; early separation of three chromosomes marked with arrows.

some separations suggestive of meiotic non-reduction. Presumably, frequency of unreduced cells is higher for the egg cells. Thus, the self-sterile hybrid spikes were pollinated with *T. aestivum* for backcross BC₁ seed production. This yielded the BC₁ seed that theoretically should possess $2n = 7x = 49$, HAABDD chromosomes. The BC₁ plants, however, showed somatic variations ranging from chromosome counts of 27 to 50^{25,29}. The presence of BC₁ plants with 28 chromosomes, or near aneuploidy, seems to be a function of apomixis²⁵. The meiotic pairing relationships of these apomictic plants were remarkably similar to the F₁ *H. vulgare* × *T. aestivum* hybrids from which they originated. The

backcross plant with 50 chromosomes resulted from an unreduced egg that carried 29 chromosomes and was fertilized by *T. aestivum* pollen. Although mitotic instability was not observed in the F₁ hybrid in the cells analyzed, it is logical to assume its existence because of the aneuploid progeny that appeared in BC₁. The somatic instability observed in the BC₁ progeny is consistent with several earlier reports^{7,14,15,25} for *H. vulgare* × *T. aestivum* or the reciprocal cross ($n = 4x = 28$, HABD or ABDH), and for *H. vulgare* × *T. turgidum* ($n = 3x = 21$, HAB).

Failure to observe chromosome instability in *H. chilense* × *T. turgidum*²⁰ presumably is due to *H. chilense*, since the durum variety

(cv. Cocorit 71) was identical to that used by Mujeeb et al.²⁴. This supports the view of Thomas et al.³⁶ that the genetic mechanism effecting intergeneric hybrid production resided not only in *Triticum* sp., but also is under *Hordeum* germplasm control. It is further supported by the ability of the *H. chilense* genome to substitute partially for the 5B effect²¹. Further evidence can be extrapolated from observations with *H. bulbosum*¹, and with *H. vulgare* cv. Betzes^{7,13,14}. Recently, Mujeeb-Kazi and Rodriguez³¹ demonstrated that F₁ hybrids between *H. vulgare* × *T. turgidum* cv. Cocorit 71 exhibit meiotic instability and chromosomal relationships that differ from the earlier report²⁰ for *H. chilense* × *T. turgidum*. The *H. vulgare* cv. Manker seems to be the influencing factor in the variation observed by Mujeeb-Kazi and Rodriguez³¹. Somatic instability in intergeneric hybrids between *Hordeum*, *Triticum*, and *Elymus* species also has been reported²⁸⁻³⁰. The F₁ hybrid of *T. aestivum* × *E. giganteus* was mitotically stable with a $n = 5x = 35$, ABDJX composition, and BC₁ plants were generally $2n = 8x = 56$, AABDDJX, although elimination of one chromosome did occur. This was an *Elymus* chromosome, since the meiosis of regular BC₁ plants was 21 bivalents, 14 univalents, and the plant with 55 chromosomes was 21 bivalents, and 13 univalents²⁸. The F₁ *E. canadensis* × *H. vulgare* hybrid had meiocytes predominantly with a cumulative chromosome count of 21, but meiotic instability was observed and meiocytes possessed up to 25 univalents³⁰. Thus, we can infer that chromosomal instability is fairly well extended within intergeneric hybrids among the Triticeae, especially among *H. vulgare*, *T. turgidum*, *T. aestivum*, and some *Elymus* species. More recently, Jewell and Mujeeb-Kazi¹⁶ and Mujeeb-Kazi and Bernard²⁶, have demonstrated that several BC₁ hybrids of wheat with *Aegilops variabilis*, and *Agropyron* species express a high degree of instability. Using routine chromosome counting and N-banding they demonstrated that chromosome variations in BC₁ were a consequence of the

fertilization of aneuploid egg cells with normal ($n = 3x = 21$) wheat pollen. The aneuploidy of the egg cells resulted from a random loss of chromosomes from both genera that entered the F₁ combination.

The separation of at least five chromosomes (Figure 1B, C, E, and G) may be attributed to barley chromosomes. It may be a consequence of the altered meiotic developmental rate of *H. vulgare* as compared with *T. aestivum* in the F₁. By extrapolation from earlier findings^{2-4,9} the meiotic duration of *H. vulgare* and *T. aestivum* is 39.4 and 24.0 hours, respectively. Assuming coordinated division among the HABD genomes, the *H. vulgare*, H genome should have maintained a slower meiotic rate than the *T. aestivum*, ABD genomes. Bennett and Kalsikes⁴ estimated the meiotic duration of *S. cereale* to be about 51 hours, 31 hours for *T. turgidum*, and 37 hours for the hexaploid 6A190 triticale derived from their combination. The rate in 6A190 is somewhat slower than that of *T. turgidum*. We do not have satisfactory evidence as to why in the *H. vulgare* × *T. aestivum* F₁ and its BC₁ hybrid with *T. aestivum* the *H. vulgare* chromosomes express the degree of disjunction that causes them to separate at par or even somewhat earlier than the paired *T. aestivum* chromosomes or the univalents. This timing observation and separation is consistent with meiotic relationships expressed in *H. vulgare* × *T. turgidum* hybrids and their backcross progeny with *T. turgidum*³¹, and the “unique separation” of chromosomes in this case is under further study.

In subsequent analyses a sixth chromosome also was observed to have the disjunction characteristic. That the “unique” chromosomes may be barley is tentatively inferred after meiotic analysis of the BC₁ plants with $2n = 7x = 49$, HAABDD. A relationship of 21 bivalents, 7 univalents was expected but univalency was rampant in the meiocytes. However, there were many cells with the expected 21 bivalents and 7 univalents. Five chromosomes clearly expressed the disjunction seen in the F₁ hybrid (Figure 1B, C, E, and

G), and a sixth chromosome was frequently observed. It was encouraging to observe transfer of these subtle F₁ cytological effects to BC₁ progeny. Instability and univalency are generally expressed in pollen grain polymorphism for size, shape, and pore numbers, and were observed in our barley-wheat material. The variations of pollen grains are characteristic of chromosome separation at anaphase I or II, coupled with the lack of chromosome orientation and aberrant spindle function. Pollen grain size seems positively correlated with the chromatin content, presumably governed by the amount of chromatin distributed to the microspores during meiotic development.

BC₂ and BC₃ progeny

None of the BC₁ plants were self-fertile and pollinating them with *T. aestivum* cultivars produced BC₂ seed in varied frequencies²⁹. That data²⁹ did not include the BC₂ progeny of the BC₁ plant (1124B) obtained later. Pollinating this BC₁ plant with *T. aestivum* cv. Zaragoza gave 14 seed of 117 florets, and pollination by cv. Pavon gave 53 seed of 187 florets.

The BC₂ progeny was totally self-sterile but set seed when pollinated by *T. aestivum*. Some of the BC₂ combinations whose plants were advanced to the BC₃ generation are included in Table I. The selected BC₂ plants ranged in chromosome number from 28 to 48. These self-sterile BC₂ plants resulted from a high degree of pistilloidy, a finding that Islam et al.^{13,14} had earlier noted for a similar hybrid combination, but of a different varietal constitution. BC₃ seed set and cytological data are included in Table II, and in general all BC₂ plants set BC₃ seed irrespective of the pollen parent cultivar. The cultivar mixing in the backcross generations was an attempt to obtain self-fertility in later generations, but this was not successful. All plants in BC₃ remained self-sterile and expressed variations in somatic chromosome numbers together with aberrations observed as dicentrics, isochromosomes,

Table I. *Hordeum vulgare* cv. Manker/n/*Triticum aestivum* cultivar combinations forming BC₂ progeny, with selections of BC₂ plants advanced for BC₃ progeny

BC ₂ combination <i>H. vulgare</i> × <i>T. aestivum</i> × <i>T. aestivum</i>	Florets pollinated	BC ₂ seed set	BC ₂ plants obtained	Chr. and (id. nos.) of BC ₂ plants advanced for BC ₃ progeny
Manker × Pavon × Pavon × C.Spring	225	25	18	47(1704) 46(1707) 45(1708) 44(1709) 44(1713) 44(1714)
Manker × Pavon × Pavon × C.Spring	108	17	8	43(1721) 46(1724)
Manker × Pavon × Pavon × C.Spring	62	3	2	28(1726)
Manker × C.Spring × C.Spring × Zaragoza	117	14	10	47(1811) 48(1812) 43(1813) 45(1815) 43(1816) 43(1817) 43(1820)

or telocentrics. The BC₃ progeny expressed *T. aestivum* phenotype and the segregation observed was attributed to cultivar mixing in the backcrosses. The variation was for days-to-heading, spike morphology, and awn characteristics, and seemed to be little influenced by the number of *H. vulgare* chromosomes present in the progeny.

The range in chromosome numbers for the BC₃ progeny was within the normal limits observed for other hybrids (unpub. data), based on the random incorporation of alien chromosomes, spontaneous substitution, and chromosomal structural changes. Apart from practical aspects, the barley-wheat hybrids and their backcross progenies with wheat have been excellent material for evaluation of genome relationships and related basic genetic functions. Chromosomal instability in BC₁ has helped to develop an understanding of apomictic seed formation in a self-sterile intergeneric system²⁵. It may explain to some degree how euploids, which are believed to result from cross contamination, could arise during F₁ intergeneric hybrid production. The cytological detail has aided in assessing the manner of barley chromosomal disjunction. F₁ instability represented as aneuploidy has offered a precise developmental sequence that is cytologically detectable and rigidly transmitted. This precision in *H. vulgare*, *Triticum* spp., or *Elymus* hybrids may well be applied to other distant hybridization areas within the Gramineae. The detectable chromosomal behavior, albeit an offshoot of instability mechanisms, is an asset when the practical objectives focus

on developing addition-substitution lines or inducing genetic transfers via translocations. An en-bloc unaccountable loss of alien genetic information in initial cell division cycles would be hazardous to intergeneric hybridization, unless it leads to the production of haploids as in *T. aestivum* × *H. bulbosum*¹. Fortunately, these circumstances do not prevail in our current investigations. We are, however, concerned about our failure to obtain self-fertile plants in BC₃, and we need to know how to incorporate alien genetic information into a stable cytogenetic system. Despite the instability at the BC₁ levels, unlike most other intergeneric hybrids, the cytogenetic system offers considerable normality. The alien chromosomes (*H. vulgare*) do not significantly alter the pairing of the wheat genome chromosomes either in BC₁ or in advanced backcross generations. This is deduced from the findings of Islam et al.¹⁰ where the alien barley additions when tested by crosses to wheat formed 21 bivalents, and one univalent, and from our current study where normalcy was observed in backcrosses-2 and-3 (unpub. data).

The F₁ *T. aestivum* × *H. vulgare* hybrid possessed 28, ABDH chromosomes and phenotypically resembled wheat cv. Tesia. The BC₁ progeny somatic count ranged from 46 to 49. The BC₂ plants were all self-fertile despite their chromosome composition. No barley characters were expressed in BC₁ or BC₂ progenies. A critical cytology study to identify the *H. vulgare* chromosomes has yet to be initiated. It shall be particularly interesting to

observe the addition lines of chromosome 3 (carrying BYDR resistance) and its expression when added to wheat.

References

1. BARCLAY, I. R. High frequencies of haploid production in wheat (*Triticum aestivum*) by chromosome elimination. *Nature* 256:410-411. 1975.
2. BENNETT, M. D. The duration of meiosis. *Proc. Roy. Soc. London. Ser. B.* 178:277-299. 1971.
3. ——— and R. A. FINCH. The duration of meiosis in barley. *Genet. Res.* 17:209-214. 1971.
4. ——— and P. J. KALTSIKES. The duration of meiosis in diploid rye, a tetraploid wheat and the hexaploid triticales derived from them. *Can. J. Genet. Cytol.* 15:671-679. 1973.
5. CHAPMAN, V. and T. E. MILLER. The amphiploid of *Hordeum chilense* × *Triticum aestivum*. *Cer. Res. Comm.* 6:351-352. 1978.
6. FEDAK, G. Production, morphology, and meiosis of reciprocal barley-wheat hybrids. *Can. J. Genet. Cytol.* 22:117-123. 1980.
7. ———. Increased homoeologous chromosome pairing in *Hordeum vulgare* × *Triticum aestivum* hybrids. *Nature* 266:529-530. 1977.
8. ———. Barley-wheat hybrids. In *Interspecific Hybridization in Plant Breeding Proc. 8th Eucarpia Congress, Madrid, Spain.* p. 261-267. 1977.
9. FINCH, R. A. and M. D. BENNETT. The duration of meiosis in diploid and autotetraploid barley. *Can. J. Genet. Cytol.* 14:507-515. 1972.
10. ISLAM, A. K. M. R. and K. W. SHEPHERD. Production of disomic wheat-barley chromosome addition lines using *Hordeum bulbosum* crosses. *Genet. Res.* 37:215-219. 1981.
11. ——— and ———. Meiotic restitution in wheat-barley hybrids. *Chromosoma* 79:363-372. 1980.
12. ———, ———, and D. H. B. SPARROW. Isolation and characterization of euplasmic wheat-barley chromosome addition lines. *Heredity* 46:161-174. 1981.
13. ———, ———, and ———. Production and charac-

Table II. Backcross-3 seed set and cytological data of the *H. vulgare* × *T. aestivum* × *T. aestivum* combination

BC ₂ parent	BC ₂ chr. no.	BC ₃ seed	BC ₃ % seed set	No. BC ₃ plants	Range BC ₃ chr. nos.	BC ₃ plants with isochr. and/or telocent. and/or dicent.
1704	47	16	24.6	11	42 to 45	2
1707	46	2	7.1	2	43 and 68	1
1708	45	2	4.8	2	42 and 42	1
1709	44	56*	30.9	26	39 to 46	2
1713	43	29	13.2	10	41 to 55	1
1714	44	30*	27.3	5	41 to 44	2
1721	43	16	8.8	2	41 and 41	1
1724	46	4	7.4	2	44 and 45	
1726	28	21	15.9	16	41 to 79	2
1811	47	129*	31.9	57	41 to 49	22
1812	48	16	11.3	10	42 to 45	2
1813	43	2	4.0	2	41 and 41	
1815	45	33	23.1	26	41 to 45	9
1816	43	148*	31.1	50	41 to 46	15
1817	43	48*	17.5	16	42 to 44	3
1820	43	34	19.0	22	41 to 43	5

* Not all seed were germinated

- terization of wheat-barley addition lines, Proc. 5th Int. Wheat Gen. Symp., (New Delhi, India) p. 365-371. 1978.
14. ———, ———, and ———. Addition of individual barley chromosomes to wheat. Barley Gen. III., Proc. 3rd Int. Barley Gen. Symp. Garching, p. 260-270. 1975.
 15. JAN, C. C., J. DVORAK, C. O. QUALSET, and C. W. SCHALLER. Hybridization between *Triticum aestivum* L. and *Hordeum vulgare* L. Agr. Abstracts 71st Ann. Meetings, Fort Collins, CO. p. 64. 1979.
 16. JEWELL, D. and A. MUJEEB-KAZI. Unexpected chromosome numbers in backcross-1 generations of F₁ hybrids between *Triticum aestivum* and related alien genera. *Wheat Inf. Serv.* 55:5-9. 1982.
 17. KRUSE, A. *Hordeum* × *Triticum* hybrids. *Hereditas* 73:157-161. 1973.
 18. MANN, S. A. and T. SASAKUMA. Fertility of amphiploids in Triticeinae. *J. Hered.* 68:87-94. 1977.
 19. MARTIN, A. and V. CHAPMAN. A hybrid between *Hordeum chilense* and *Triticum aestivum*. *Cer. Res. Comm.* 5:365-368. 1977.
 20. ——— and E. S. LAGUNA. A hybrid between *Hordeum chilense* and *Triticum turgidum*. *Cer. Res. Comm.* 8:349-353. 1980.
 21. ——— and ———. Effects of the 5B system on control of pairing in *Hordeum chilense* × *Triticum aestivum* hybrids. *Z. Pflanzenzuchtg.* 85:122-127. 1980.
 22. ——— and ———. Cytology and morphology of the amphiploid *Hordeum chilense* × *Triticum turgidum*. CONV. Durum. *Euphytica* 31:261-267. 1982.
 23. MUJEEB, K. A., J. B. THOMAS, R. R. RODRIGUEZ, R. F. WATERS, and L. S. BATES. Chromosome instability in F₁ hybrids of *Hordeum vulgare* L. with *Triticum turgidum* L. and *T. aestivum*. *J. Hered.* 69:179-182. 1978.
 24. ———, R. F. WATERS, and L. S. BATES. A mitotic schedule for somatic counts in cereal root tips and embryos. *Cytologia* 43:339-343. 1978.
 25. MUJEEB-KAZI A. Apomictic progeny derived from intergeneric *Hordeum-Triticum* hybrids. *J. Hered.* 72:284-285. 1981.
 26. ——— and M. BERNARD. Somatic chromosome variations in backcross-1 progenies from intergeneric hybrids involving some Triticeae. *Cer. Res. Comm.* 10:41-45. 1982.
 27. ——— and R. RODRIGUEZ. Some intergeneric hybrids in the Triticeae. *Cer. Res. Comm.* 8:469-475. 1980.
 28. ——— and ———. An intergeneric hybrid of *Triticum aestivum* L. × *Elymus giganteus*. *J. Hered.* 72:253-256. 1981.
 29. ——— and ———. Cytogenetics of intergeneric hybrids involving genera within the Triticeae. *Cer. Res. Comm.* 9:39-45. 1981.
 30. ——— and ———. Cytogenetics of hybrids of *Elymus canadensis* × *Hordeum vulgare*. *J. Hered.* 73:77-79. 1982.
 31. ——— and ———. Cytogenetics of a *Hordeum vulgare* × *Triticum turgidum* hybrid and its backcross progeny with *T. turgidum*. *J. Hered.* 74:109-113. 1983.
 32. ——— and ———. *Hordeum vulgare* × *Triticum aestivum* hybrids. *Cytologia* in press. 1983.
 33. MURASHIGE, T. and F. SKOOG. A revised medium for rapid growth and bioassays with tobacco tissue cultures. *Physiol. Plant.* 15:473-497. 1962.
 34. SHEPHERD, K. W. and A. K. M. R. ISLAM. Wheat: barley hybrids—the first eighty years. In *Wheat Science: Today and Tomorrow*. Evans and Peacock, Eds. Camb. Univ. Press. p. 107-128. 1981.
 35. TAIRA, T. and E. N. LARTER. Factors influencing development of wheat-rye hybrid embryos in vitro. *Crop Sci.* 18:348-350. 1978.
 36. THOMAS, J. B., K. A. MUJEEB, R. RODRIGUEZ, and L. S. BATES. Barley-wheat hybrids. *Cer. Res. Comm.* 5:181-188. 1977.