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INTERGENERIC HYBRIDIZATION TO INDUCE ALIEN GENETIC TRANSFERS INTO *TRITICUM AESTIVUM*

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Abstract

Intergeneric hybridization investigations in cereals, particularly the Triticeae, have gained greater research interest since the late 1960's. Embryo recovery has remained alarmingly low, and at times has only been possible after utilizing special pre-and/or post-pollination manipulative procedures in attempts to enhance crossability. This paper describes efforts to improve *Triticum aestivum* L. (2n=6x=42, AABBDD) by utilizing the alien genetic variation of diverse genera for incorporation of disease resistance or tolerance to soil and environmental stresses. Some intergeneric hybrids between *Agropyron* species, *Elymus* species, *Haynaldia villosa, Hordeum vulgare, Secale cereale, T. turgidum,* and *T. aestivum* are described. Additionally are described hybrids of potential agricultural gain and those with limitations of practicality.

Introduction

World population continues to increase at a phenomenal pace. The last doubling – the fourth – occurred by 1975, and was achieved in 45 years since the third doubling, bringing the world population to 4 billion. The next population doubling if we keep up the prevalent birth rates will be by year 2015 (Borlaug, 1978), throwing caution to the agricultural scientists and food management sector.

The struggles for increased food production are universal, and plant breeders are many times stymied by lack of appropriate germplasm to incorporate into the existent food crops. Such genetic resources may either be unknown, do not exist in the cultivated or wild species, or reside in the secondary or tertiary gene pools (Harlan & deWet, 1971). This prevents a rapid genetic flow or transfer, and expressivity mechanisms to operate.

Associated with the aspect of genetic resources, researchers have since the late 1960's ingeniously attempted to resolve crossability barriers (Kruse, 1969, 1973, 1974). The accomplishments of over a decade have shed light on future promise and exemplified the limiting facets of intergeneric hybridization (Sharma & Gill, 1983a; Mujeeb-Kazi & Kimber, 1985). Special emphasis in the present consideration is attached to cereals, that undoubtedly are the structural base essentials of world food consumption. It is fortuitous that a majority of the intergeneric hybridization investigative studies have included the *Triticum* species with greater emphasis attached to bread wheat; *T. aestivum* (2n=6x=42, AABBDD); improvement for several agronomic traits that are located in the genetically diverse hard to combine alien genera.

The status of our intergeneric hybridization research is discussed keeping agricultural practicality as the research goal. It may be at least another decade before the impact of this program is felt. Can the bread wheat plant type be so modified to express in its background the alien desired characters associated with: 1) high lysine, 2) barley yellow dwarf resistance, 3) salt plus drought tolerance or 4) *Fusarium* plus *Helminthosporium* resistance, 5) rust resistance and freedom of leaf spotting complex diseases, 6) powdery mildew resistance, and 7) Karnal bunt resistance, etc. The question just posed and our research effort to address these problems form the basis of this paper.

Materials and Methods

Growth Condition of Parents: Hordeum vulgare (2n=2x=14, HH), *Secale cereale* (2nx=2x=14, RR), *Triticum turgidum* (2n=4x=28, AABB), *T. aestivum* (2n=6x=42, AABBDD) plants were grown in pots and kept under field conditions in Ciudad Obregon and El Batan, Mexico. This constituted the two field crossing cycle locations. Species of these genera were also grown in pots, as were those of *Aegilops, Agropyron, Elymus* and *Haynaldia*, and maintained under greenhouse conditions of 26.6°C/16.5°C (14h day/10h night) with approximately 45% to 50% relative humidity for each of the four additional crossing cycles in 1979 and 1980. The effort was for producing new F_1 combinations that could not be attempted in the field due to: 1) inavailability of *Agropyron* and *Elymus* species pollen at our location in Mexico, or 2) having the ideal environment for achieving the fertilization processes, or 3) a need for environmental buffering to support the hybrid embryo development prior to embryo culture.

Production of Hybrids: Spikes of the plants to be used as female parents were emasculated and pollinated the next morning with pollen of the desired male parent. A second pollination was occasionally made the following morning where poor pollen producing alien species were the male parents. Gibberellic acid (75 ppm, aqueous) was applied as an injection treatment into the floret cups 8 hours after pollination. The detail procedures are discussed by Mujeeb-Kazi & Rodriguez, (1984) Mujeeb-Kazi & Kimber, (1985).

Embryo Extraction and Culture: The embryos were allowed to develop, excised 20 days after pollination, and cultured on a special medium for small embryos (Taira & Larter, 1978). The embryos either differentiated or merely increased in size. If it was a size increase, the embryos were transferred to the MS medium (Murashige & Skoog, 1962) and allowed to differentiate. Upon differentiation the plantlets were transferred to peat pots, and maintained in the growth chamber under high humidity (70%), before ultimate transfer to potted soil and the greenhouse growth environment. The growth conditions of the growth chamber were 15°C/10°C, 14h day/10h night and approximately 70% relative humidity. The greenhouse conditions were similar to those earlier mentioned for the growth of the parental genera.

Confirmation of Hybridity: Root tips were sampled from each potential hybrid plant. This allowed the hybrids to be identified on the basis of the somatic chromosome number. The analytical procedure was that of Mujeeb-Kazi & Miranda, (1985).

Spikes for meiotic analyses were then sampled from the somatically confirmed hybrids, fixed in 6:3:1 (ethanol: chloroform: acetic acid) for 24 hours, then transferred to 70% ethanol and refrigerated until use. Anthers were hydrolyzed in lN HCl for 4 minutes at 58°C, rinsed in deionized distilled water and stained with feulgen. Alcoholic acid carmine was also used as an alternate stain. Squashes in both cases were made in 45% acetic acid or 2% propionic orcein and chromosome relationships analyzed at metaphase I.

Clonal Propagation and Induction of Amphiploidy: Depending upon plant vigor the hybrids were cloned and first grown under growth chamber conditions of 3°C–8°C, 20h night/4h day, and approximately 45% relative humidity for six weeks. They were then moved to the earlier mentioned greenhouse environment, and resumed vigorous growth. For inducing amphiploidy a mixture of 0.2% colchicine + 2.0% dimethylsulfoxide aqueous solution was used for 4 hours by the capping procedure, or for 6 hours by the aerated root treatment. Confirmation of amphiploidy was by somatic and meiotic cytology.

Production of Backcross I (BCI) Progeny: Because of complexities in obtaining amphiploids for the majority of the hybrids, self-sterile spikes of these hybrids were backcrossed to desired parents. The seeds set were allowed to develop for 20 days, embryos were then excised and cultured on the MS Medium (Murashige & Skoog, 1962). When endosperm was well developed in backcross I (BCI) seed production embryo culturing was eliminated for all subsequent backcrosses. Pollination and post-pollination gibberellic acid treatments were similar to those used for F_1 hybrid production, as were the plantlet growth and cytological procedures.

Development of Addition Lines, Substitution Lines and Subtle Genetic Transfers: Pollinations of the amphiploids (after emasculations), or of the self-sterile F_1 hybrids with desired male parents were the sources of BCI, or BCII populations. Repeated backcrossing and cytology was the basis of developing alien addition lines, then substitution lines, with prospects through both of attaining chromosome arm translocations or subtle gene transfers. The schematic of Fig. 1 of *T. aestivum* x *E. giganteus* elaborates this further, and can be extended for most of the other hybrids (Table 1) maintained in CIMMYT at El Batan, Mexico, under greenhouse conditions.

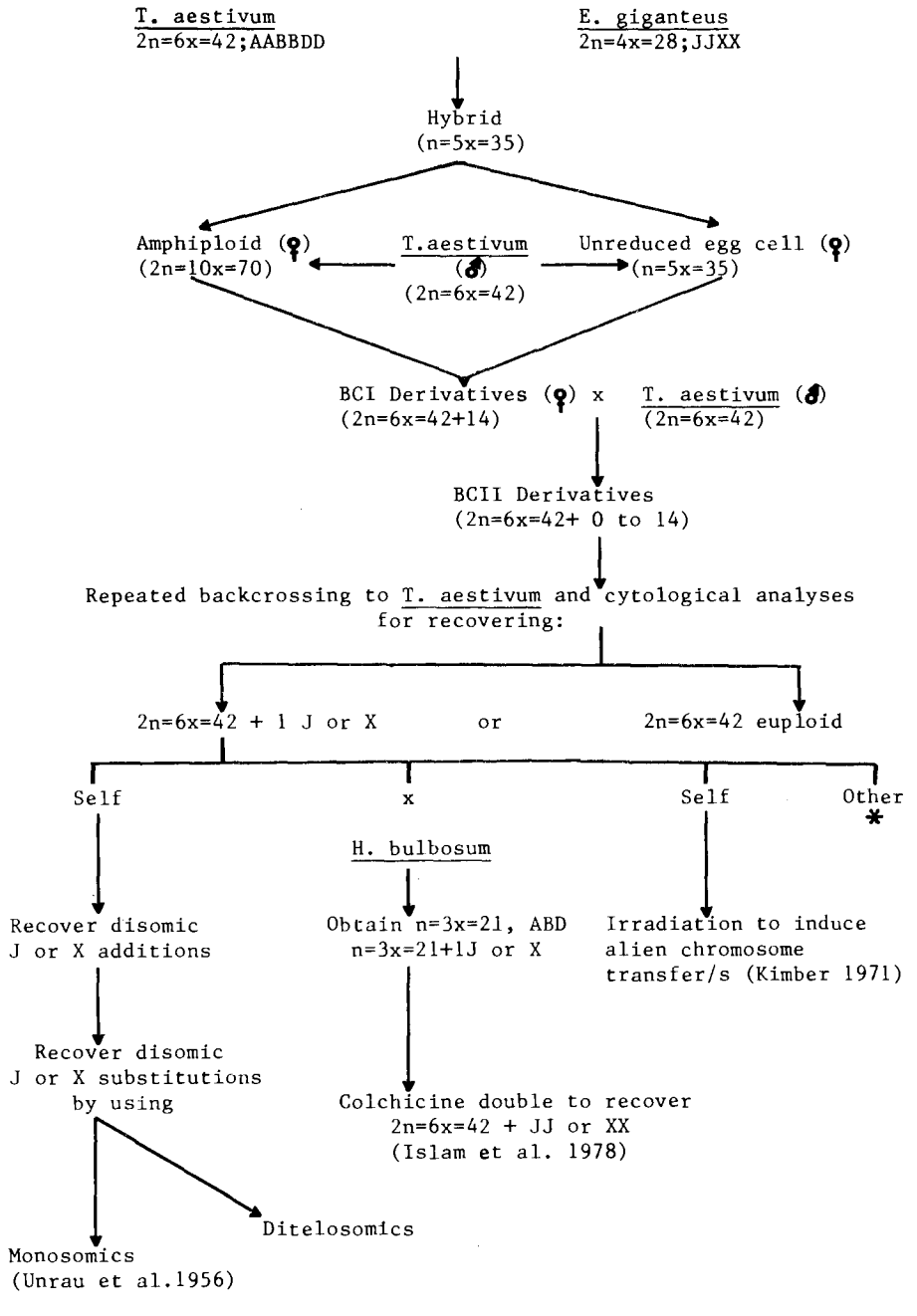

Fig. 1. Schematic showing sequential advance of an F_1 hybrid aimed at recovering alien chromosome addition lines, substitution lines or subtle gene transfers. *Manipulations including 5B locus, tissue culture or chromosome arm-translocations are not included.

Table 1. Some perennial intergeneric and trigeneric hybrids maintained in CIMMYT, El Batan, Mexico, under greenhouse and/or field conditions

Cross Number	Cross Combination	Chromosome number
	A. *T. aestivum*/ *Agropyron* species	
B82-10824	Chinese Spring/ *A. acutum*	n = 6x = 42
B82-11004	Fremont/ *A. acutum*	n = 6x = 42
B82-11058	Nacozari 75 / *A. acutum*	n = 6x = 42
B82-10692	Chinese Spring/ *A. caespitosum*	n = 5x = 35
B82-10759	Chinese Spring/ *A. campestre*	n = 7x = 49
B82-10939	Chinese Spring/ *A. curvifolium*	n = 5x = 35
B81-1084	Chinese Spring/ *A. elongatum* (10x)	n = 8x = 56
B81-1176	Chinese Spring-Cno (E)/ *A. elongatum* (10x)	n = 8x = 56
B81-1194	Nyu Bay/ *A. elongatum* (10 x)	n = 8x = 56
B81-1064	Pavon 76/ *A. elongatum* (10x)	n = 8x = 56
B81-1065	Zaragoza/ *A. elongatum* (10x)	n = 8x = 56
B82-10516	Chinese Spring/ *A. intermedium*	n = 6x = 42
B82-10848	Glennson 81/ *A. intermedium*	n = 6x = 42
B82-10656	Nacozari 75/ *A. intermedium*	n = 6x = 42
B82-5063	Chinese Spring/ *A. podperae*	n = 6x = 42
B82-10643	Chinese Spring/ *A. pulcherrimum*	n = 6x = 42
B82-10840	Chinese Spring/ *A. junceum* (2x)	n = 4x = 28
B82-10780	Chinese Spring/ *A. junceum* (4x)	n = 5x = 35
B82-10990	Fielder/ *A. junceum* (4x)	n = 5x = 35
B82-10910	Fremont/ *A. junceum* (4x)	n = 5x = 35
B82-10995	Pavon 76/ *A. junceum* (4x)	n = 5x = 35
B82-11049	Chinese Spring/ *A. junceum-mediterranean* (6x)	n = 6x = 42
B79-1006	Tobari 66/ *A. junceum-mediterranean* (6x)	n = 6x = 42
B82-10682	Chinese Spring/ *A. rechingeri*	n = 5x = 35
B82-10669	Pavon 76/ *A. rechingeri*	n = 5x = 35
B82-5049	Chinese Spring/ *A. repens*	n = 6x = 42
B82-10559 to 10585	Chinese Spring/ / *A. repens*/*A. desertorum* (C-3)	n = 35 –57
B82-11042	Chinese Spring/ *A. scirpeum*	n = 5x = 35
B82-10865	Chinese Spring/ *A. scythicum*	n = 5x = 35
B82-10861	Fremont/ *A. scythicum*	n = 5x = 35
B82-10602	Chinese Spring/ *A. trichophorum*	n = 6x = 42
B82-10899	Chinese Spring/ *A. varnense*	n = 6x = 42
B82-10948	Nacozari 75/ *A. varnense*	n = 6x = 42

Cross Number	Cross Combination	Chromosome number
B82-10975	Pavon 76/ *A. varnense*	n = 6x = 42
B82-11008	Fielder/ *A. varnense*	n = 6x = 42
B83-4630	Chinese Spring Ph Ph/ *A. acutum*	n = 6x = 42
B83-4614	Chinese Spring Ph Ph/ *A. caespitosum*	n = 5x = 35
B84-5984	Chinese Spring Ph Ph/ *A. elongatum*	n = 8x = 56
B84-5995	Chinese Spring Ph Ph/ *A. intermedium*	n = 6x = 42
B84-6002	Chinese Spring Ph Ph/ *A. trichophorum*	n = 6x = 42
B83-4626	Chinese Spring Ph Ph/ *A. varnense*	n = 6x = 42
	B. *T. aestivum*/ *Haynaldia* sp	
B32-2528	Chinese Spring/ *H. villosa*	n = 4x = 28
	C. *T. aestivum*/ *Elymus* species	
Log82-135	Fremont/ *E. angustus*	n = 9x = 63
B82-10694	Chinese Spring/ *E. cinereus*	n = 5x = 35
B79-1002	Chinese Spring/ *E. giganteus*	n = 5x = 35
B82-10652	"	n = 5x = 35
B82-10653	Chinese Spring/ *E. triticoides*	n = 5x = 35
	D. *Agropyron* species/ *T. aestivum*	
B81-1058	*A. elongatum* (10x)/Bonza	n = 8x = 56
B80-1054	*A. elongatum* (10x)/Jupateco 73	n = 8x = 56
B81-1037	*A. fibrosum*/ Pavon "S"	n = 5x = 35
B81-1038	*A. fibrosum*/ Pavon 76	n = 2x= 14
	E. *Elymus* species/ *T. aestivum*	
B81-1012A	*E. agropyroides*/Chinese Spring-Ciano (E)	n = 6x = 42
B79-1018	*E. agropyroides*/Nyu Bay	n = 6x = 42
B79-1019	*E. agropyroides*/ Zaragoza 75	n = 6x = 42
B81-1009A	*E. dahuricus*/ Pitic 66	n = 6x = 42
	F. Other combinations	
B79-1009	*A. elongatum* (4x)/*H. vulgare*	n = 3x = 21
B84-5982	*A. junceum* (2x)/ *A. junceum* (4x)	n = 3x = 21
B79-1008	*A. elongatum* (4x)/ *S. cereale*	n = 3x = 21
Log-80-70	*A. trachycaulum*/*E. giganteus*	n = 4x = 28
Log 80-22	*E. agropyroides*/*E. giganteus*	n = 5x = 35
B79-1027	*E. canadensis*/*H. vulgare*	n = 3x = 21

Cross Number	Cross Combination	Chromosome number
B81-1008	*Elymus* sp./*S. cereale* (4x)	n = 4x = 28
B79-1031	*H. vulgare/E. canadensis*	n = 3x = 21
B79-1015	*H. vulgare/E. patagonicus*	n = 4x = 28
	G. *T. turgidum/Agropyron* species	
B83-4316	Cocorit 71/ *A. acutum*	n = 5x = 35
B83-4604	G-803/ *A. acutum*	n = 5x = 35
B83-4297	Yavaros 79/ *A. acutum*	n = 5x = 35
B83-4337	Cocorit 71/ *A. littorale-campestre*	n = 6x = 42
B83-4346	Cocorit 71/ *A. intermedium*	n = 5x = 35
B83-4438	Mexicali 75/ *A. intermedium*	n = 5x = 35
B83-4309	Yavaros 79/ *A. intermedium*	n = 5x = 35
B83-4373	Cocorit 71/ *A. junceum* (4x)	n = 4x = 35
B79-1004	Cocorit 71/ *A. junceum-mediterranean* (6x)	n = 5x = 35
B81-5036	Cocorit 71/ *A. podperae*	n = 5x = 35
B83-4416	Mexicali 75/*A. podperae*	n = 5x = 35
B83-4385	Cocorit 71/ *A. pulcherrimum*	n = 5x = 35
B83-4470	Mexicali 75/ *A. pulcherrimum*	n = 5x = 35
B81-5040	Mexicali 75/ *A. scythicum*	n = 4x = 28
B83-4524	Mexicali 75/ *A. trichophorum*	n = 5x = 35
B83-4536	Mexicali 75/ *A. varnense*	n = 5x = 35
B83-4572	G-803/ *A. varnense*	n = 5x = 35
B83-4552	Cappelli Ph Ph/ *A. acutum*	n = 5x = 35
B83-4545	Cappelli Ph Ph/ *A. intermedium*	n = 5x = 35
B83-4546	Cappelli Ph Ph/ *A. varnense*	n = 5x = 35
	H. *T. timopheevii/ Agropyron* sp.	
B81-1241	*T. timopheevii/A. elongatum* (10x)	n = 7x = 49
	I. *Agropyron* species/ *T. turgidum*	
B79-1012	*A. elongatum*/ Cocorit 71	n = 3x = 21
B81-1040	*A. fibrosum*/ Cocorit 71	n = 4x = 28
B80-1046	*A. fibrosum*/ Mexicali 75	n = 4x = 28
B80-1050	*A. fibrosum*/ Quilafen	n = 4x = 28
L80-1765B	*A. scabrifolium*/ Mexicali 75	
L80-1062	*A. sibericum*/ Cocorit 71	n = 4x = 28
B80-1033	*A. trachycaulum*/ Cocorit 71	n = 4x = 28
B80-1032	*A. trachycaulum*/ Mexicali 75	n = 4x = 28

Cross Number	Cross Combination	Chromosome number
	J. *Elymus* species/ *T. turgidum*	
B81-5035	*E. virginicus*/ Cocorit 71	n = 4x= 28
	K. *Trigeneric hybrids*	
L80-1758B	*A. fibrosum/ T. turgidum/ /S. cereale*	n = 5x = 35
B84-6025	*E. canadensis/ T. aestivum/ / S. cereale*	n = 6x = 42
B83-6112	*T. aestivum/ A. curvifolium/ /S. cereale*	n = 6x = 42
B83-6153	*T. aestivum/ A. intermedium/ / S. cereale*	n = 7x = 49
B83-5269	*T. aestivum/ A. junceum* (4x)/ / *S. cereale*	n = 6x = 42
B84-6023	*T. aestivum/ A. pulcherrimum/ / S. cereale*	n = 7x = 49
B81-1255	*T. aestivum/ E. giganteus/ / A. elongatum*	n =10x= 70
B81-1259	*T. aestivum/ E. giganteus/ / T. aestivum*/3/ *A. elongatum.*	n =59 – 66
B81-1270	*T. aestivum/ E. giganteus/ / S. cereale*	n = 6x = 42
B81-5109	*T. timopheevii/ H. bogdanii* / / S. cereale*	n = 4x = 28

* F_1 source G. Kimber (obtained as amphidiploid).

Results and Discussion

Barley x Wheat Hybrids (Potential source of barley yellow dwarf virus resistance and protein quality)

1) *H. vulgare* (2n=2x=14, HH) x *T. turgidum* (2n=4x=28, AABB). The hybrid had a n=3x=21 HAB chromosome composition, with a meiotic association of 19.26_{I} 0.39_{II} 0.46_{II} 0.02_{III} and a 1.21 mean chiasmata frequency per cell. The hybrid resembled *T. turgidum* phenotypically and its cytology expressed the 1B and 6B satellite details, completely suppressing the secondary constrictions of the barley chromosomes.

The backcross I combination *H. vulgare/T. turgidum/./T. turgidum* gave progeny that remained either maternal in cytological composition (n=3x=21, HAB) and considered apomictic (Mujeeb-Kazi, 1981a), or had the expected n=5x=35, HAABB composition. The mean meiotic relationship of this BCI plant was 16.61_{I} 5.08_{II} 3.4_{II} 0.34_{III} 0.114_{IV} with a 12.914 mean chiasmata frequency per cell, suggesting an interference in the AABB genome associations. The BCI plant was both male and female sterile and did not set BCII seed when it was pollinated by *T. turgidum*. This has complicated the practical gain objectives to be derived from alien transfers in a durum background.

The combination of several manipulative procedures is in progress and presumably by producing the reciprocal combination the chances of practical success may be significantly different.

2) Interesting results were also obtained from the cross *H. vulgare* (2n=14, HH) /*T. aestivum* (2n=6x=42, AABBDD). The self-sterile F_1 hybrids (n=4x=28, HABD) of *H. vulgare* cv. Manker with *T. aestivum* L. cvs. Bonza, Chinese Spring, and Pavon had a mean chromosome pairing relationship of $24.3_{I}\,1.33_{II}\,0.38_{II}\,0.15_{III}\,0.028_{IV}\,0.033_{VI}$ with a mean chiasmata frequency of 2.57 per cell (Mujeeb-Kazi & Rodriguez, 1980, 1981a, 1984). In *H. vulgare* L. cv. Betzes/*T. aestivum* cv. Chinese Spring, Fedak (1977) reported a chiasmata frequency of 1.84 per cell, and also observed heteromorphic bivalent formation. These observations were inferred to be due to i) the influence on the Ph locus of the barley genome, and ii) intergeneric barley-wheat chromosome pairing. The high chiasmata frequency of 2.57 and the heteromorphic bivalents observed in the hybrids we have obtained is interpreted otherwise. This is based on the random association of the HABD genomes, i.e. six, that would normally permit a chiasmata frequency of 2.57 per cell and even slightly more. The heteromorphic bivalents may also be a consequence of the homoeologous pairing of the wheat chromosomes due to inherent size differences, instead of being exclusively attributed to pairing between barley and wheat chromosomes (Mujeeb-Kazi, 1981b).

Precocious separation of up to six chromosomes was observed during meiotic analysis of the F_1 hybrids. These were speculated to be *Hordeum* chromosomes, and were later so confirmed when a similar separation was observed in the meiocytes of the BCI plants produced by pollinating the *H. vulgare/T. aestivum* hybrids with *T. aestivum*. Here the wheat chromosomes paired as 21_{II} in several meiocytes and up to six of the seven barley univalents showed this precocious separative tendency (Mujeeb-Kazi & Rodriguez, 1984). It was speculated (Mujeeb-Kazi & Rodriguez, 1983a, b) that chromosome arm fold-back coupled with chromatid separation may be partial factors contributing to this observation of precocious separation.

The BCI *H. vulgare/T. aestivum/ /T. aestivum* derivatives were pollinated with several commercial *T. aestivum* cultivars to produce BC_{II} progeny. Additional pollinations of the BCII plants with *T. aestivum* produced BCIII seeds. Selfed fertile progeny was not obtained from any BCII plant and the barley maternal parent apparently has been the principal cause of sterility due to pistilloidy, similarly observed earlier (Islam *et al.*, 1975; 1978). Hence the reciprocal cross was attempted between a commercial wheat variety and a high protein/lysine barley variety that proved successful. This reciprocal *T. aestivum* cv. Tesia/*H. vulgare* hybrid after recurrent backcrossing and cytology is to serve for the goal of developing barley addition lines, substitution lines, or subtle genetic transfers in a wheat background similar to the Fig. I schematic for *T. aestivum* x *E. giganteus*. Limits to practical applicability for wheat/barley crosses is envi-

sioned based upon lack of barley genetic expressivity at the phenotype level in hybrids and early backcross derivatives as observed in the combinations described above, and also from other findings (Fedak 1977, 1980; Islam *et al.*, 1978, 1981). Presumably, the ideal check to this constraint would come from the transfer of the yd_2 gene for barley yellow dwarf resistance, located on chromosome 3H of some *H. vulgare* varieties, to *T. aestivum.* Such a program is currently being pursued in USA (Qualset, *Pers. Comm.).*

Barley x Elymus Hybrids

The barley x *Elymus* species hybrids were produced for accomplishing gene transfers via F_1 recombination from *Elymus* sp. to barley based upon the genetic information concerning the H genome homology between *Hordeum* and *Elymus* species. The *Elymus* species used were *E. canadensis* (2n=4x=28, SSH_1H_1) and *E. patagonicus* (2n=6x=42, $S_1S_1H_2H_2H_3H_3$) where the S genome is derived from *Agropyron spicatum*, and the $H_1H_2H_3$ genomes from the H genome of barley.

1) *E. canadensis* x *H. vulgare* hybrid. The hybrid with n=3x=21, SH_1H chromosomes was both male and female sterile, setting no backcross I seed after pollination attempts with either parent. It has not been possible to induce fertile amphiploids either. The phenotypic resemblance is intermediate, and the hybrid spikes partially maintain the nodding characteristic of *E. canadensis.* Meiotic relationships in the hybrid suggest no homology between the H and H_1 genomes. An occasional rod bivalent was observed with a mean chiasmata frequency of 0.81 per cell (Mujeeb-Kazi & Rodriguez, 1982).

2) *H. vulgare* x *E. patagonicus* hybrid. In this hybrid; n=4x=28, $HS_1H_2H_3$; the chiasmata frequency was lower than expected should there have been close homology between the HH_2H_3 genomes. The frequency of 4.77 chiasmata per cell was a manifestation of few trivalents and a very scarce occurrence of ring bivalents. The open bivalents and trivalents were attributed to autosyndetic paring and/or partial genome homology (Mujeeb-Kazi, 1985). It does not appear that transfers from *Elymus* to improve barley may be easily accomplished, but the promise definitely exists and needs addressing to. There seems considerable merit in the proposed taxonomic revision (Dewey, *Pers. Comm.*) where *H. vulgare* genomically is designated "I" and "H" is attributed to the *Critesion* species. This would then logically separate the genomes of *H. vulgare* and *Elymus* species to account for the low pairing we have observed.

T. aestivum and Elymus Species Hybrids

1) The *T. aestivum* x *E. giganteus* hybrid with n=5x=35 chromosomes led to BCI derivatives (*T. aestivum/E. giganteus/ /T. aestivum*) that were either 2n=8x=56 AABBDDJX or AABBDD (JX-1). The meiosis of the BCI plants was predominantly $21_{II}14_I$ or $21_{II}13_I$ (Mujeeb-Kazi & Rodriguez, 1981b; Mujeeb-Kazi, *et al.*, 1983b).

Pollinating the BCI plants with *T. aestivum* cultivars produced BCII progeny that should expectedly possess the 42 AABBDD wheat chromosomes, plus 0 to 14 JX or 0 to 13 (JX-1) chromosomes from *E. giganteus*. The chromosome range observed for the BCII plants was from 44 to 54. Some BCII plants were partially self-fertile setting seeds up to 47.8%. When the BCII plants were further pollinated by *T. aestivum* seed setting for the BCIII derivatives varied from 45.2% to 81.8% according to the *T. aestivum* cultivar used for backcrossing (Table 2). The BCII selfed and BCIII progeny have been analyzed cytologically and advanced by additional selfing or BCIV seed production for developing disomic addition lines of *E. giganteus* chromosomes to *T. aestivum*.

Deriving disomic substitutions may require either use of 1) monosomics or 2) ditelosomics. The monosomic procedure (Unrau *et al.*, 1956) would give progeny of 42 chromosome plants whose meiotic relationships shall be (1) 21_{IIW} or (2) $20_{IIW}1_{1W}1_{1(J/X)}$ or (3) $20_{IIW}1_{II(J/X)}$. If the addition chromosome does not express macromorphologically to facilitate visual selection, an added backcross to *T. aestivum* and meiotic analysis may be required for confirming the substituted lines with a configuration of $20_{IIW}1_{1W}1_{1(J/X)}$. The use of ditelosomics appears as an alternative procedure where the ditelosomic x *E. giganteus* line combination shall yield a 40_W t_W 1_W $1_{J/X}$ progeny. A cytological study of all selfed progeny seeds obtained from 40_W t_W1_W $1_{J/X}$ shall enable selection of plants having a chromosomal constitution of 42 and include the telocentric chromosome. The composition of plants carrying the telocentric chromosome shall be: 40_W 1_W t_W or 40_W t_W $1_{(J/X)}$. The 40_W 1_W t_W plants would be identified at meiosis by the presence of a heteromorphic bivalent, while the 40_W t_W $1_{J/X}$ should meiotically associate as 21_{II} 1_I $1t_I$. The latter plants would upon selfing produce the desired substitution type, i.e., $40_W + 1_{J/X}+1_{J/X}$.

Table 2. Percentage seed set data in backcross and selfed derivatives from the *Triticum aestivum* cv. Chinese Spring (CS)/ *Elymus giganteus* hybrid using different *T. aestivum* varieties in backcrosses to the F_1 hybrid

Cross Combination	Generation	Percentage seed set
CS/ *E. giganteus* / / 2* CS (1)	$BCIIF_1$	47.3
CS/ *E. giganteus* / / 2* CS /3/ Bza (E)*	BCIII	70.0
CS/ *E. giganteus* / / 3*CS	BCIII	65.8
CS/ *E. giganteus* / / 2* CS /3/ Pvn 76*	BCIII	81.8
CS/ *E. giganteus* / / 2* CS /3/ Za 75*	BCIII	70.0

* Bza (E) = Bonza (dwarf); Pvn 76 = Pavon 76; Za 75 = Zaragoza 75.

E. giganteus is an exceptionally coarse, strongly rhizomatous, Asian grass that commonly grows on sandy sites along river banks and seashores. It is an allotetraploid (2n=4x=28), with two distincly different genomes (JJXX), Dewey 1972a, b, Petrova 1960. The practical utility of the species lies in its potential for being moderately salt tolerant, drought tolerant, resistant to leaf and stem rust, free of leaf spotting diseases, and more promising as a resistance source for *Helminthosporium sativum* and *Fusarium graminareum*. The addition lines and advanced BCII selfed or BCIII progeny are being tested for the expression of these characteristics of *E. giganteus* in the *T. aestivum* cultivar backgrounds.

For the purpose of identifying the *Elymus* chromosomes we have developed the giemsa C-banded karyotype of *E. giganteus*, 2n=4x=28, JJXX. The species exhibits terminal heterochromatic regions and interstitial bands and can be readily identified (Mujeeb-Kazi, 1981b; Mujeeb-Kazi & Jewell, 1984), for most chromosomes. Where such is not possible due to insignificant chromosome arm ratio differences compounded by identical telometric heterochromatic banding, biochemical assays will prove particularly helpful and are being utilized.

2) *E. canadensis* x *T. aestivum* hybrid. The F_1 hybrid possessed a n=5x=35, SHABD chromosomal composition, with a mean meiotic relationship of 34.85_I 0.072_{II} and a chiasmata frequency of 0.072 per cell (Mujeeb-Kazi & Bernard, 1985). This is suggestive of the lack of genome homology among *E. canadensis* and *T. aestivum*, and maintenance of the diploidizing mechanism of the 5B locus of *T. aestivum*.

The BCI seeds possessed 52 to 61 chromosomes as a consequence of maternal aneuploidy. Such DCI progeny are common in intergeneric hybrids and are produced when the unreduced egg cell instead of possessing n=5x=35 chromosomes carries built in duplications, deletions, etc., that are randomly distributed over all F_1 chromosomes when little chromosome pairing exists in the F_1. Other instances of such events have been reported by Jewell & Mujeeb-Kazi, (1982), Mujeeb-Kazi & Bernard, (1982), Mujeeb-Kazi & Rodriguez, (1982, 1983a, b) and Rodriguez & Mujeeb-Kazi, (1981).

The meiotic data of the F_1 hybrid is suggestive of the complexities to expect in obtaining direct genetic transfers from *E. canadensis* because of the lack of intergenomic homology with *T. aestivum*. Similar non-homologous genome trends were also observed for hybrids between *H. vulgare* x *T. aestivum* (Mujeeb-Kazi & Rodriguez, 1980, 1981a), *H. vulgare* x *T. turgidum* (Mujeeb-Kazi & Rodriguez, 1983a), *T. aestivum* x *E. giganteus* (Mujeeb-Kazi & Rodriguez, 1981b), *E. canadensis* x *H. vulgare* (Mujeeb-Kazi & Rodriguez, 1982), and *H. vulgare* x *E. patagonicus* (Mujeeb-Kazi, 1985). These observations impose limitations on obtaining subtle alien genetic transfers and restrict the methodology to the development of alien addition lines, substitution lines, inducing transfers by irradiation of the addition lines or by suppression of 5B locus by *Ae. spel-*

toides either when the BCI progeny is normal as for *T. aestivum/E. giganteus/ /T. aestivum*, or is aneuploid as for the above *E. canadensis* BCI derivatives where aneuploidy may present cytogenetically systematic advanced progeny development associated with addition line production.

It may hence be advantageous to incorporate into distant hybridization the manipulative procedures that relate to the 5BL loci of *T. aestivum* wherever possible, preferably at the initial cross. This shall allow intergeneric recombinations to function more effectively than what has so far been possible for several hybrids.

Hybrids Involving Agropyron Species with T. turgidum, T. timopheevii and T. aestivum

Resistance to scab and/or *Helminthosporium* is much needed in the wheat growing areas of S. America, People's Republic of China, and in tropical environments. Similarly, incorporation of salt tolerance or drought tolerance will be an asset for several countries where wheat cultivation is limited by such soil stresses. Though *Elymus* species are being hybridized with *T. aestivum, Agropyron* species are also being hybridized with *Triticum* (Sharma & Gill, 1981, 1983a, b; Mujeeb-Kazi, *et al.*, 1983a, 1984) and several hybrids have been obtained. A few hybrid combinations of special mention are: the combinations of *T. turgidum, T. timopheevii, T. aestivum* with *A. elongatum* (2n=10x=70). The decaploid *A. elongatum* was collected in Argentina in a locale where the soil was encrusted with salt. An accession of this species has been previously hybridized with *T. aestivum* cv. Chinese Spring, (Dvorak, 1976). Our approach differed that in addition to hybridizing with cv. Chinese Spring, other commercial *T. aestivum* cultivars were also utilized. Where the F_1 hybrid had Chinese Spring as the female wheat parent, the BCI derivates produced incorporated leading commercial *T. aestivum* cultivars as the backcross pollen donors.

T. timopheevii and *T. turgidum* were also hybridized with *A. elongatum* for evaluating crossability, and having a durum background available should the pentaploid breeding route be felt necessary for inducing wheat/alien chromosome translocations or for obtaining unique segregates for plant type.

2) *Agropyron* species other than *A. elongatum* (2n=10x=70) were hybridized with *T. turgidum* and *T. aestivum*, in efforts to incorporate scab and *Helminthosporium* resistance. While our pathologists are screening the various *Agropyron* and *Elymus* species for resistance, we have indiscriminately produced intergeneric hybrids without waiting for the pathological screening results considering the complexities of hybridization. Based upon the eventual resistance data the hybrids shall be selectively advanced and tested for tolerance expressivity. The hybrids in general did not exhibit intergeneric pairing nor did they express high autosyndetic pairing, presumably a consequence of the

active 5B locus. The low chiasmata frequency per cell supports this interpretation, and is suggestive that the wheat genetic manipulation systems be utilized for attaining subtle alien genetic transfers.

3) *A. distichum* (2n=4x=28) found in South Africa is a salt tolerant grass and its lower polyploidy offers advantage over *A. elongatum* (2n=10x=70) both in hybridization and practicality with *T. aestivum* or *T. turgidum*. Dr. Pienaar provided the C-1 and BCI seeds of these combinations to CIMMYT and we have now started to incorporate other durum and bread wheat varieties as BC parents instead of *T. turgidum* cv. Nordum or *T. aestivum* cv. Inia that were used originally (Pienaar 1980; Pienaar, *et al.*, 1977). The advanced BCII (5) material (Inia/*A. distichum*/ /Inia/3/Genaro(5) now has a desirable agronomic level for field testing for salt and has also shown promise for *H. sativum* resistance. This combination is unique since recombination occurs in the F_1 hybrid and complex gene transfer procedures are not needed to exploit its potential in breeding programs.

4) *A. junceum* (2n=6x=42) a rust resistant and salt tolerant source was hybridized with *T. turgidum* and *T. aestivum*. An amphiploid was produced for the *T. aestivum* x *A. junceum* combination with 2n=12x=84 chromosomes. The amphiploid was partially fertile and produced C-2 progeny with 74 to 82 chromosomes. Backcross I progeny derived from the C-1/*T. aestivum* was expected to possess 2n=9x=63 chromosomes had BCI derivatives of 59 to 63 chromosomes with telocentrics, characteristics of univalent or multivalent misdivisions at meiosis. Backcross II and C-3 seed formation is in progress. Some other sources with salt tolerance potential are *A. junceum* (2n=2x=14; 2n=4x=28) and *A. scirpeum* (2n=4x=28). These are being exploited (Miranda *et al.*, 1984).

Trigeneric Hybrids

1) *H. vulgare* x *T. aestivum* hybrids despite high mean chiasmata frequencies per cell (Mujeeb-Kazi and Rodriguez, 1980, 1983b) and the presence of heteromorphic bivalents, provide inconclusive evidence of intergeneric gene transfer. Consequently, a manipulation of crossing procedures may assist in surmounting the problems ensuing from gene penetrance and possible lack of gene expressivity in alien genetic backgrounds. The use of trigeneric hybrids is one such manipulative procedure. Hybrids obtained are listed in Table 1. Fedak and Armstrong, 1980, 1981, reported a trigeneric *T. aestivum*/ *H. vulgare*/ /*S. cereale* combination. When *H. vulgare*/*T. aestivum*/ /*T. aestivum* plants with 2n=7x=49 HAABBDD chromosomes were pollinated by *S. cereale* (2n=14, RR), we obtained trigeneric hybrids that possessed either 29 or 32 chromosomes. Using BCI progeny as the maternal source provides a two-fold recombination probability. It may be more prone to reflect cytogenetic variations (if indeed there are any) under the influence of the H genome chromosomes; additionally, it may be complemented by the incorporation of the R genome.

Whether the trigeneric hybrids possessed 29 or 32 chromosomes, the presence of the seven rye chromosomes was detected with C-banding. This fitted the expected model of the trigenerics possessing 21 ABD + 0 to 7H + 7R chromosomes. The mean meiotic relationship expressed chromosome associations with a 3.739 chiasmata frequency per cell. It may be worthwhile to study the *T. aestivum/H. vulgare/ /S. cereale* and *T. aestivum/H. vulgare/ /T. aestivum/3/S. cereale* in order to assess the meiotic exchanges in each combination, which is in progress.

2) In considering the trigeneric *T. aestivum/E. giganteus/ /A. elongatum* hybrid, the F_1 between *T. aestivum/E. giganteus* indicated no possibility of a direct alien gene transfer due to lack of pairing between *T. aestivum* and *E. giganteus* chromosomes (Mujeeb-Kazi & Rodriguez, 1981b). To explore whether the trigeneric route would be beneficial, the *A. elongatum* (2n=10x=70) salt tolerant source was the germplasm choice. The trigeneric hybrids have 70 chromosomes i.e., 21 ABD + 14JX + 35(Ag). Additionally a *T. aestivum/E. giganteus/ /T. aestivum* BCI plant with 56 chromosomes (42AABBDD + 14JX) was also pollinated by *A. elongatum* (2n=10x-70) to yield trigeneric hybrid seeds. These would have a 21 ABD + 0 to 14 JX + 35(Ag) composition. The somatic range observed was from 59 to 65 and 3 to 9 *E. giganteus* chromosomes were present as detected by C-banding of the *E. giganteus* chromosomes. The hybrids are vegetative and meiotic analyses are awaited. All trigenerics will follow a backcross to wheat procedure and any beneficial event that occurs shall be ascribed as fortuitous.

3) In the *T. aestivum/E. giganteus/ /S. cereale* combination, the somatic count was 42, i.e., 21 ABD + 14JX + 7R. The seven rye chromosomes were identified by C-banding. The F_1 hybrid between *T. aestivum/E. giganteus* possessed upto 1.02 rod bivalent formation (Mujeeb-Kazi & Rodriguez, 1981b). It will be interesting to observe meiosis in the trigeneric combination and determine whether the intergeneric genome pairing has been altered which then may resolve the complexities of alien genetic transfers. Were this indeed to occur producing trigeneric hybrids may have more rewards than the current academic pursuit.

Complexities of intergeneric hybridization

It has not been a problem to obtain intergeneric hybrid combinations among *Agropyron, Elymus, Hordeum, Secale* and *Triticum* species. A routine procedure has been developed for advancing the self sterile F_1 hybrids to eventually test for agricultural practicality, complemented by cytology. However, despite the promising results of the past decade the inherent complexities of intergeneric hybridization have been elucidated, that could prevent practical agricultural gain. The observations that influence this interpretation are derived from cytological analyses of several F_1 hybrids and BC progenies that involve some Triticeae genera, and are for convenience categorized as follows:

1) F_1 hybrids of somatic and/or meiotic instability that are comprised of some *Agropyron* species, *E. canadensis, H. vulgare, T. aestivum*, and *T. turgidum* (Fedak, 1977, 1980; Islam *et al.*, 1975, 1978, Mujeeb-Kazi & Rodriguez, 1983a, b; Rodriguez & Mujeeb-Kazi, 1981; Sharma & Gill, 1981).

2) BC_I progenies with somatic variations e.g. progenies from *Ae. variabilis, Agropyron* species, *Elymus* species, *H. vulgare, T. aestivum* and *T. turgidum* (Mujeeb-Kazi & Bernard, 1982; Jewell & Mujeeb-Kazi, 1982; Pienaar, 1980; Rodriguez & Mujeeb-Kazi, 1981).

3) F_1 hybrids and BC progenies that are normal with lack of intergenomic pairing (Mujeeb-Kazi & Rodriguez, 1981a, b; Mujeeb-Kazi, 1981b).

Excluding the hybrid combinations with normal cytology and intergenomic homology from the discussion of this paper, categories 1) and 2) may eventually lead to novel combinations of chromosomes through selfing, for example, several homoeologous and non-homoeologous substitutions of alien chromosomes in the one plant (Jewell & Mujeeb-Kazi, 1982). Selfing of mono 5B BCI plants is expected to give rise to plants deficient for chromosome 5B and a potential source for allowing exchange of genetic material between wheat and alien chromosomes (Jewell & Mujeeb-Kazi, 1982). To alleviate the complexities of category (3) it is fortuitous that the plant systems offer enough flexibility to allow the use of cytological manipulative techniques. Such techniques may relate to alien genetic transfers and genetic expressivity by utilizing the Ph mutant or aneuploids of chromosome 5B (Mujeeb-Kazi & Bernard, 1982).

The authors feel that a codominant F_1 plant phenotype is an initial index of evaluating the limits of alien genetic expressivity. If codominance exists in F_1 the remaining genetic constraints of achieving success from a intergeneric hybridization program can presumably be overcome by utilizing several manipulative techniques, incorporate other genera (*Aegilops* sp.), coupled by cytology of F_1, the BCI, and to a certain extent advanced BC progenies. Though complex to initially combine genera, the wide crossing procedure offers significant potential for the not too distant a future of improving bread wheat (*T. aestivum* L.) for disease, stress and quality characters. It is another means of providing a more diverse genetic base to wheat breeders, different from what currently exists in the gene pool, and also a new base in some respects where the genetic variability may be totally lacking (Mujeeb-Kazi, 1984).

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