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Production and cytogenetics of *Triticum aestivum* L. hybrids with some rhizomatous *Agropyron* species

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Summary. Intergeneric hybrids between *Triticum aestivum* L. and conventional rhizomatous *Agropyron* species were produced in variable frequencies. They were recovered in high percentage frequencies for *T. aestivum* cultivars with *A. acutum* (14.6%), *A. intermedium* (48.0%), *A. pulcherrimum* (53.3%), and *A. trichophorum* (46.6%). The crossability percentages with the highly crossable cultivar 'Chinese Spring' for these *Agropyron* species accessions were 33.12%, 65.0%, 53.3%, and 65.4%, respectively. Autosyndetic associations of two of their three genomes gave mean meiotic chromosome association data of 17.0 I (univalents) +1.53 II (ring bivalents) +7.04 II (rod bivalents) +1.43 III (trivalents) +0.05 IV (quadrivalents) +0.01 IV (pentavalents) for *A. acutum* and of 21.8 I +1.56 II (rings) +7.22 II (rods) +0.84 III +0.04 IV for *A. intermedium*. Chromosome pairing at metaphase I was comparatively lower for *A. pulcherrimum* (34.4 I+0.2 II (rings) +3.4 II (rods) +0.14 III) and *A. trichophorum* (36.7 I+0.35 II (rings) +2.26 II (rods) +0.04 III) hybrids with *T. aestivum*. Hybrids of wheat with *A. campestre* and *A. repens* were obtained in low frequency. Direct crossing did not permit *T. aestivum*/*A. desertorum* hybridization. However, by utilizing the $2n=10x=70$ *A. repens*/*A. desertorum* amphiploid as the pollen source, hybridization with *T. aestivum* did indeed occur. Aneuploidy was prevalent in this hybrid combination while all other hybrid combinations were apparently normal.

Key words: *Triticum aestivum* – *Agropyron* – (*Elytrigia, Thinopyrum*) – Intergeneric hybridization – Crossability – Wide crosses

Introduction

Intergeneric hybrids between *Triticum aestivum* and the traditional *Agropyron* species have been rather limited, despite the apparent genetic potential of disease resistance and/or stress tolerance that abounds in these alien species. A vast range of intergeneric hybrids have been recently produced (Mujeeb-Kazi and Bernard 1985; Mujeeb-Kazi and Kimber 1985; Mujeeb-Kazi et al. 1987; Sharma and Gill 1983a; Sharma and Baenziger 1986) that serve as excellent germplasm stock for wheat improvement. In this paper, seven intergeneric hybrid combinations are described, of which a few are unique. Those combinations repeated here belong to the *A. intermedium* and its synonymous species complex, which we reproduced in order to obtain access to F_1 hybrid germplasm. The findings with the synonymous *A. intermedium* species were cytogenetically quite variable and consequently each species hybrid – *A. intermedium, A. acutum, A. trichophorum* and *A. pulcherrimum* – is described in detail. Additionally, the above species crossed readily with the wheat cultivar Chinese Spring, thus prompting us to hybridize them with commercial wheat cultivars and, hence, imparting practical significance to the study.

In the process of hybrid production, aspects of crossability, cytogenetics, phenotypic detail, and genome composition impact are exemplified which, for all the reported hybrids, are unique research contributory sources.

Materials and methods

The traditional *Agropyron* species with their new nomenclature (Dewey 1984) were maintained in the rhizomatous range grass nursery in Logan, Utah, USA.

The details of the germplasm utilized are listed in Table 1, with Dewey's (1982) field book as the source of the categories mentioned in the table. Three dates of wheat cultivar plantings adjacent to the range grass nursery were made at bi-weekly intervals starting March 15, 1982. The wheat cultivars were 'Chinese Spring', 'Fielder', 'Fremont', 'Glennson 81', 'Nacozari

Table 1. Details of some rhizomatous *Agropyron* species used as pollen sources for hybridization with *Triticum aestivum* varieties

Species	Chromosome no.	Field location		Collection no., source or origin*
		Row	Plant no.	
A. acutum (*T. acutum*)	42	1	1–10	PI-202727, Belgium
A. campestre (*El. pungens*)	56	3	33	Cauderon 485, France
A. intermedium (*T. intermedium*)	42	2	31–40	Cauderon 690, via Australia
A. pulcherrimum (*T. pulcherrimum*)	42	1	43	PI 401308, Iran
A. repens (*El, repens*)	42	1	41–43	WS-31-24, Utah, USA
A. repens/A. desertorum (*El. repens/A. desertorum*)	70	12	19	A-11-48, Utah, USA
A. trichophorum (*T. trichophorum*)	42	6	3	Jaaska, USSR

* Source: Dr. D.R. Dewey's 1982 field book of planting at Evans Farm, Logan, Utah

76', and 'Pavon 76'. These were located at Evans Farm, Logan, Utah, and planted by Dr. W. Dewey.

Two of us (A. Mujeeb-Kazi and S. Roldan) visited Logan in June 1982 to make wheat/alien species crosses according to procedures described by Mujeeb-Kazi and Rodriguez (1984), with embryo rescue similar to processes reported by Mujeeb-Kazi et al. (1987). If, during embryo excision, a well-developed endosperm was observed, the subsequent spikes with potential hybrid seeds set on them were allowed to reach maturity on the plant.

All potential hybrid embryos in culture tubes and mature dry hybrid seeds were transferred to El-Batan, CIMMYT, Mexico. The plantlet differentiation, growth, and maintenance conditions were identical to those reported earlier for caespitose hybrids (Mujeeb-Kazi et al. 1987). Root tip somatic cytology was according to the procedure of Mujeeb-Kazi and Miranda (1985). Anthers were scored for mean meiotic metaphase I associations after staining in alcoholic carmine or 2% aceto-orcein and smearing in 45% acetic acid.

Spikes from hybrid plants and the 'Chinese Spring' progenitor were studied for morphological details at complete emergence and photographed. The cytological photography film was Kodak Technical pan 2415 with a special green filter (Collins Microscope Company, Kansas City, Missouri, USA).

Results and discussion

Crossability

The seed setting was in extremely high frequencies for *Agropyron acutum*, *A. intermedium*, *A. pulcherrimum* and *A. trichophorum*. The seed set percentages varied from 14.6%–53.3% over all *Triticum aestivum* cultivars (Table 2). All wheat cultivars were hybridized with the alien species, though the seed setting rate varied between them.

T. aestivum hybrids with *A. campestre*, *A. repens* and *A. repens/A. desertorum* were obtained in a low frequency (Table 2) and were predominantly produced with the cultivar 'Chinese Spring'. The highly successful role of 'Chinese Spring' is attributed to the $kr_1kr_1kr_2kr_2kr_3kr_3$ crossability genes it possesses (Falk and Kasha 1981; Fedak and Jui 1982) for its crossability with rye (Riley and Chapman 1967). The loci kr_1, kr_2 and kr_3 are located on chromosomes of homoeologous group 5, i.e., 5B, 5A, and 5D, respectively, and interact in a complementary manner with kr_1 locus contributing most to the crossability frequencies.

Hybrid identification and stability

All hybrids possessed the stable chromosome number comprising half the chromosomal complement of each parent involved in the hybrid combination except for *T. aestivum* cv. 'Chinese Spring'//*A. repens/A. desertorum*. In this combination, the range in chromosome number was from 35–57 with a telocentric chromosome. Though meiotic data are the absolute criteria for hybrid identification and genome relationships, superior somatic preparations can provide accurate hybrid identification plus confirmation, with the technique of Mujeeb-Kazi and Miranda (1985) convincingly facilitating the identification of the hexaploid ($n=6x=42$) hybrids. In all 42 chromosome hybrids, a single dosage of the satellited wheat chromosomes (1B, 6B, and 5D) would be present if an euploid wheat is involved in the crosses. If a 1B/1R euploid wheat is involved (such as 'Glennson' 81), one dose of the 6B and 5D satellited chromosomes will be present, since the satellite on 1RS remains unexpressed. The secondary constrictions of the alien chromosomes are generally not observed due to amphiplasty but, if observed, are readily identifiable as those of the alien species. The technique has been put to more effective use by range grass cytogeneticists (Hsiao et al. 1986; Wang 1985) and its merits have been further described by Mujeeb-Kazi and Kimber (1985).

Aneuploidy in F_1 hybrids has been extensively observed in intergeneric hybrids among the Triticeae (Mujeeb-Kazi et al. 1987). In the present study, it was restricted to the hybrids of wheat with the amphiploid of *A. repens/A. desertorum* ($2n=10x=70$). A normal intergeneric hybrid would possess 56 chromosomes: 21 of wheat + 21 of *A. repens* + 14 of *A. desertorum*. A few hybrids with 56 chromosomes were indeed observed but there were several hyper- and hypoploid F_1 hybrids with

Table 2. Some intergeneric hybrids of *Triticum aestivum* L. ($2n = 6x = 42$) varieties with rhizomatous *Agropyron* species indicating details of chromosome number, florets pollinated (a), seeds set (b), percent seed setting (c), embryos excised + seeds with embryos that reached maturity on the plant (d), and plants differentiated (e)

Pollen source	Female *T. aestivum* cultivar	F_1 *Chromosome* no.	Crossability category				
			a	b	c	d	e
A. acutum	Ch. Spring	42	788	261	33.1	261	*
	Fielder	42	440	26	5.9	26	*
	Fremont	42	582	12	2.1	12	*
	Glennson-81		108	0	0	0	0
	Nacozari-76	42	182	16	8.8	16	*
	Pavon-76	42	94	6	6.4	6	*
	Total		2,194	321	14.6	321	58*
A. campestre	Ch. Spring	49	38	4	10.5	4	3
A. intermedium	Ch. Spring	42	660	443	67.1	429	*
	Glennson 81	42	182	19	10.4	19	*
	Nacozari-76	42	228	75	32.9	75	*
	Pavon	42	190	82	43.2	82	*
	Total		1,260	619	49.1	605	92*
A. pulcherrimum	Ch Spring	42	749	399	53.3	399	27*
A. repens	Ch. Spring	42	64	1	1.6	1	1
	Glennson 81		250	0	0	0	0
	Pavon-76		100	3	3.0	2	0
	Total		414	4	1.0	3	1
A. repens/A desertorum	Ch. Spring	35–57 (t)	288	51	17.7	51	29
A. trichophorum	Ch. Spring	42	892	583	65.4	583	*
	Glennson-81	42	100	4	4.0	2	*
	Nacozari-76	42	58	4	6.9	4	*
	Pavon-76	42	206	1	0.5	1	*
	Total		1,256	592	47.1	590	49*

* Accessions where hybrids possessed endosperm and all embryos were not excised. Those excised, differentiated into plants as indicated in the total over varieties column while mature F_1 seed was stored

t telocentric chromosome

Table 3. Mean spike characteristics of intergeneric hybrids of *Triticum aestivum* L. cv. 'Chinese Spring' with some rhizomatous *Agropyron* species

Wheat control, *Agropyron* species (Male parent) and F_1 chromosome no.		Spike character[a]												
		1	2	3	4	5	6	7	8	9	10	11	12	13
Chinese Spring		7.9	0.7	25.0	0.3	0.9	0.7	25.0	4.0	0.7	0	0.9	0.1	0.3
A. acutum	(42)	13.1	0.6	14.3	0.9	1.9	0.5	14.3	5.9	0.9	0	1.1	0.3	0.3
A. campestre	(49)	20.7	0.7	21.0	1.0	1.6	0.8	19.0	7.7	1.0	0	1.0	0	0.4
A. intermedium	(42)	11.8	0.7	18.7	0.6	1.2	0.5	18.7	4.7	0.8	0	1.0	0	0.4
A. pulcherrimum	(42)	13.6	1.4	11.0	1.3	1.6	1.4	11.0	5.9	1.1	0	1.2	0	0.4
A. repens	(42)	10.6	0.7	20.0	0.5	1.3	0.4	20.0	5.2	0.8	0.1	0.9	0.3	0.3
A. repens/A. desertorum														
(i) no. 10558	(54)	8.9	0.4	16.0	0.5	1.6	0.6	16.0	5.2	0.9	0.1	1.1	0.1	0.3
(ii) no. 10563	(54t)*	8.6	0.5	22.0	0.3	1.2	0.4	22.0	3.9	0.7	0.1	0.9	0.1	0.3
(iii) no. 10565	(35)	12.2	0.7	19.0	0.6	1.1	0.5	18.0	4.6	0.7	0	0.9	0	0.4
(iv) no. 10573	(56)	8.0	0.4	17.0	0.5	1.3	0.4	17.0	4.6	0.8	0.1	0.9	0.1	0.3
(v) no. 10585	(35)	13.5	0.8	23.0	0.6	1.5	0.7	23.0	5.9	0.8	0	0.9	0	0.3
A. trichophorum	(42)	16.8	0.7	15.0	1.2	1.6	0.8	15.0	5.7	0.1	0	1.1	0	0.4

[a] 1 Spike length (cm); 2 Spike width (cm); 3 Nodes per spike; 4 Internode length (cm); 5 Spikelet length (cm); 6 Spikelet width (cm); 7 Spikelets per spike; 8 Florets per spikelet; 9 Glume body length (cm); 10 Glume awn length (cm); 11 Lemma body length (cm); 12 Lemma awn length (cm); 13 Anther length (cm)

* t telocentric chromosome included in number

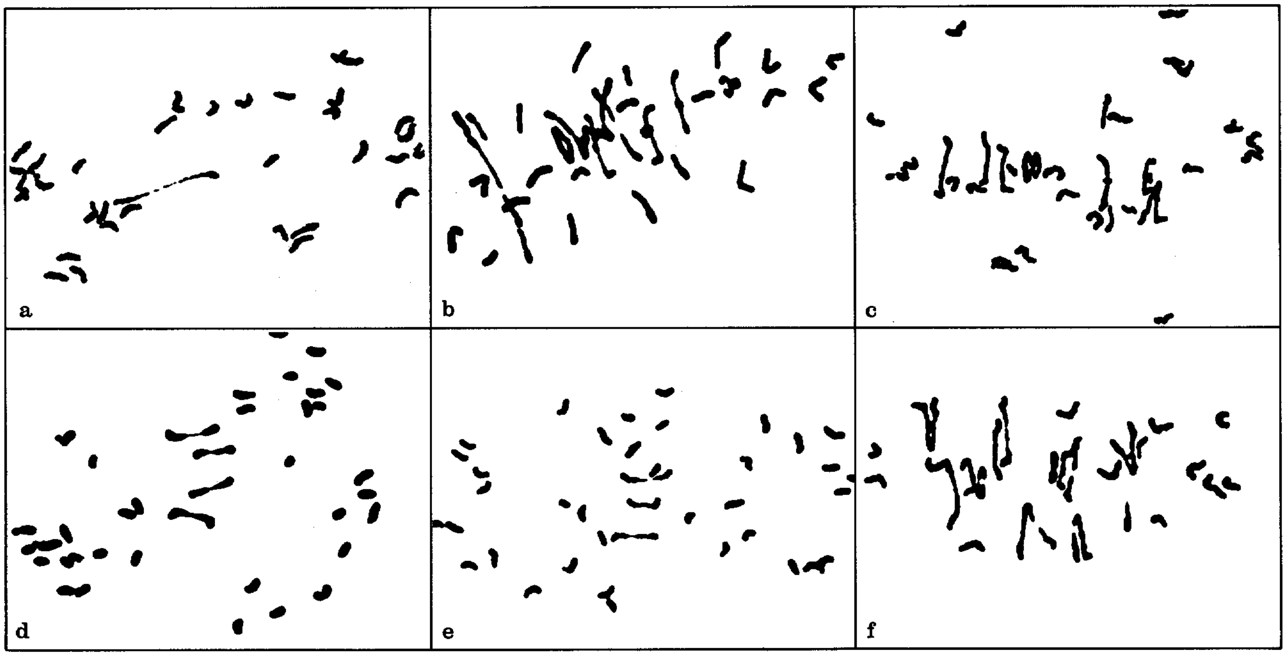

Fig. 1a–f. Representative pollen mother cells (PMC) at metaphase I of *Triticum aestivum/Agropyron* species F_1 hybrids showing in: **a** *T. aestivum//A. repens/A. desertorum;* 35 chromosomes associated as 33 univalents and 1 rod bivalent, **b** *T. aestivum/A. acutum;* 42 chromosomes associated as 21 univalents + 2 ring bivalents + 6 rod bivalents + 1 pentavalent, **c** *T. aestivum/A. intermedium;* 42 chromosomes associated as 23 univalents + 2 ring bivalents + 6 rod bivalents + 1 trivalent, **d** *T. aestivum/A. trichophorum;* 42 chromosome PMC with 34 univalents and 4 rod bivalents, **e** *T. aestivum/A. pulcherrimum;* 42 chromosome PMC with 36 univalents and 3 rod bivalents, **f** *T. aestivum/A. repens;* 42 chromosomes associated as 11 univalents + 2 ring bivalents + 6 rod bivalents + 5 trivalents

telocentric chromosomes, suggesting that the paternal amphiploid source (*A. repens/A. desertorum*) may have undergone asynapsis. There were two F_1 hybrids with 35 chromosomes (Fig. 1a), a situation where preferential losses may have occurred in the *A. repens* genomes (E_1E_2Z). This is an extremely fortuitous event since the resultant 35 chromosome F_1 hybrids may be comprised of the wheat and *A. desertorum* genomes, a hybrid that as yet remains unattainable via direct crossing (Dewey 1984). The above hypothesis is being tested further since it is quite possible that E_1E_2 are the included genomes.

Spike morphology

The hybrids all exhibited a codominant phenotype, possessed lax internodes, and were awnless or tip-awned with related variation in lemma and palea characteristics (Fig. 2 and Table 3). Spikes of all hybrids were glabrous except for hybrids with *A. trichophorum*, where pubescence was significantly apparent. Such a codominant expression in F_1 reportedly has practical agricultural merit (Mujeeb-Kazi et al. 1987). These researchers infer that the alien genome(s) was (were) expressed in the F_1 hybrid, a phenomenon that was lacking in wheat/barley hybrids (Islam et al. 1975, 1978, 1981). The codominant phenotype of the F_1 hybrids is indicative of alien genetic expression as a consequence of epistatic expression and has been a selection sieve for advancing F_1 hybrids for practical use. This modified phenotype is applicable to all the hybrids reported in this study (Fig. 2).

Meiotic analyses

The hexaploid ($2n=6x=42$) species *A. acutum*, *A. intermedium*, *A. pulcherrimum* and *A. trichophorum* have been considered as closely related and synonymous species. They have E_1E_2Z as the genomic complement. These species were hybridized in a very high frequency with *T. aestivum*, particularly with 'Chinese Spring' (Mujeeb-Kazi et al. 1983). This crossability frequency, however, sheds little light on their relationship with one another. Apart from the range in crossability, the meiotic associations of the species in the hybrids with *T. aestivum* were variable (Table 4). It would be expected to observe E_1E_2 autosyndetic associations, as were prevalent for *A. acutum* and *A. intermedium* (Fig. 1b and c) in all synonymous species uniformly, but the low pairing of *A. pulcherrimum* and *A. trichophorum* is suggestive of structural chromosomal changes that may have presumably occurred, associated with evolution among the related

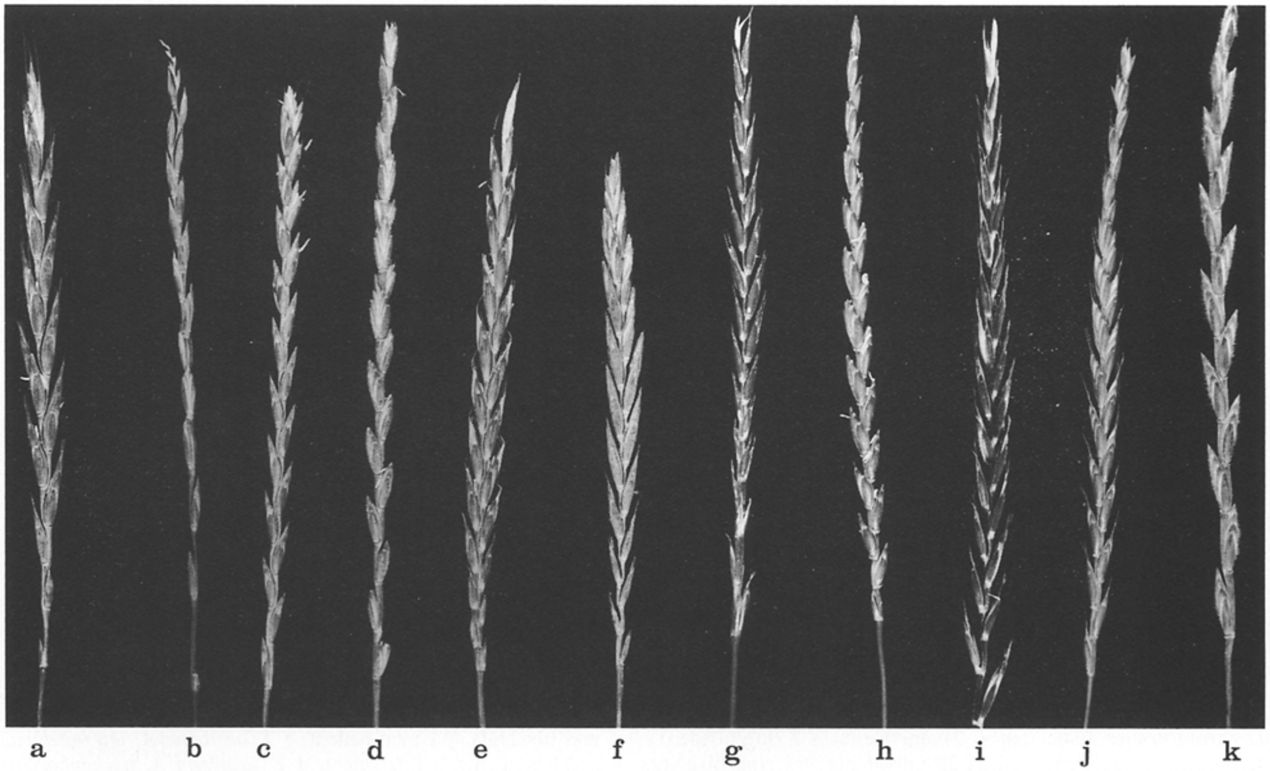

Fig. 2a–k. F_1 spikes of intergeneric hybrid combinations involving *Triticum aestivum* L. cv. Chinese Spring and some rhizomatous *Agropyron* species **a** *A. acutum*, **b** *A. campestre*, **c** *A. intermedium*, **d** *A. pulcherrimum*, **e** *A. repens*, **f** *A. repens*/*A. desertorum* (C-3), 55 chromosome hybrid, **g** *A. repens*/*A. desertorum* (C-3), 54 chromosome hybrid including a telocentric, **h** *A. repens*/*A. desertorum* (C-3), 35 chromosome hybrid, **i** *A. repens*/*A. desertorum* (C-3), 56 chromosome hybrid, **j** *A. repens*/*A. desertorum* (C-3), 35 chromosome hybrid, **k** *A. trichophorum*

Table 4. Mean meiotic associations at metaphase I in intergeneric hybrids of *Triticum aestivum* L. cv. 'Chinese Spring' with some rhizomatous *Agropyron* species

Agropyron species (Male parent) and F_1 chromosome no.		Mean meiotic chromosomal associations					
		I	II Rings	II Rods	III	IV	V
A. acutum	42	17.0	1.53	7.04	1.43	0.05	0.01
A. campestre	49	28.5	4.52	5.13	0.46		
A. intermedium	42	21.8	1.56	7.22	0.84	0.04	
A. pulcherrimum	42	34.4	0.20	3.40	0.14		
A. repens	42	28.1	1.25	5.39	0.19		
A. repens/ *A. desertorum* (C-3)	35	32.9		1.07			
A. trichophorum	42	36.7	0.35	2.26	0.04		

species accessions. Hence, it is reasonable to infer that each hybrid should be treated uniquely and as an individual case rather than agglomerating all species and subspecies into an *A. intermedium* complex, which would provide a simplistic treatment to an otherwise complex group. Our results do not support the *A. intermedium* complex contention. This takes into account the *Ph* gene action and the commonality of the alien species that logically explains differential genomic pairing as a consequence of structural chromosomal changes.

Our results vary to a certain extent from those of other researchers and this is elaborated with data for the 'Chinese Spring'/*A. intermedium* hybrids. Gu and Liang (1984) produced F_1 hybrids from the above cross combination under controlled environmental regimes and incorporated embryo rescue, ultimately achieving a hybrid plantlet differentiation frequency of 0.6%. Sharma and Gill (1983 b) reported a hybrid plantlet frequency of approximately 2.0% and a mean meiotic pairing association of 27.8 univalents +5.71 bivalents (rods) +0.66 bivalents (rings) +0.42 trivalents. We observed a hybrid seed set of slightly over 50% (Table 2), with crossing conducted under field conditions. Endosperm was reasonably well-formed and, subsequently, embryo rescue was not necessary. The meiotic associations (Table 4 and Fig. 1 c) were comprised of 21.8 univalents +7.22 rod bivalents +1.56 ring bivalents +0.84 trivalents +0.04 quadrivalents. Some meiocytes of *T. aestivum*/*A. acutum* hybrids had a similar meiotic association trend and in both cases autosyndetic pairing seems to predominate (Figs. 1 b and c). This trend does not prevail in hybrids of wheat with *A. trichophorum* (Fig. 1 d) or *A. pulcherrimum*

(Fig. 1e), where univalency predominates and the bivalent frequency is significantly reduced. This reduction seems to be more a consequence of evolutionary structural differentiation changes. None of the above four hybrid combinations provides inferential evidence of alien gene transfers via normal wheat/alien chromosome recombination events, in which case established cytogenetic manipulative systems will need to be incorporated. These have been repeatedly discussed in the literature and were more recently commented upon by Mujeeb-Kazi et al. (1987).

The hybrids of *T. aestivum* with *A. campestre*, *A. repens* and *A. repens*/*A. desertorum* were all low-frequency hybrids. The fact that they were new combinations was briefly reported by Mujeeb-Kazi et al. (1983) and Mujeeb-Kazi and Bernard (1985), without any cytogenetic meiotic data. Since these reports, the wheat/*A. repens* hybrid has been produced and cytogenetically analyzed (Fedak et al. 1986). The 42 chromosome hybrids were meiotically associated as 31.95 univalents +1.16 ring bivalents +3.81 rod bivalents +0.03 quadrivalents per cell. The observed pairing was inferred as autosyndetic and probably involved two of the *A. repens* genomes.

In our analyses, the meiotic associations were 28.1 univalents +1.25 ring bivalents +5.39 rod bivalents +0.19 trivalents. The data fit reasonably well to the F_1 $ABDE_1E_2Z$ genomic composition, where the autosyndetic associations adequately account for the chromosome pairing observed, with ample opportunity for projecting an enhanced pairing trend based upon multivalent formation. The hybrid had 42 chromosomes. In the wheat combination with *A. repens*/*A. desertorum* hybrids, a lower chromosome pairing than expected was observed (Table 4 and Fig. 1a for the 35 chromosome hybrid) as was the case for the 56 chromosome hybrid with 10 bivalents. The higher pairing would be a consequence of the autosyndetic pairing of the *A. desertorum* or *A. repens* genomes. It would be possible to observe low pairing as a consequence of the permutations of the *A. desertorum* and *A. repens* genomes. This aspect needs additional study, but the low pairing data of the 56 chromosome hybrid with all the alien genomes are indicative of some lack of autosyndetic associations for the *A. desertorum* genomes as well as for those of *A. repens* for the E_1E_2 genomes. The maximum pairing expected would be 14 bivalents, but in other hybrids with the *E* genomes, low pairing has been present. As a consequence, we are not assured of the genomic constitution of the 35-chromosome F_1 hybrid. In hybrids produced earlier (Mujeeb-Kazi et al. 1987) with *E* genome alien species, variable chromosome pairing trends were observed. For hybrids of *T. aestivum*/*A. curvifolium*, the *E* genomes of the alien species were poorly associated, while some associations (3.5 bivalents per cell) were observed for hybrids involving *A. scirpeum*. The autosyndetic associations of the alien genomes were maximized at backcross I (BCI) (*T. aestivum*/*A. curvifolium*//*T. aestivum* or *T. aestivum*/*A. scirpeum*//*T. aestivum*) (Mujeeb-Kazi, unpublished data) and it may be interesting to observe the BCI derivatives involving the 35-chromosome *T. aestivum*//*A. repens*/*A. desertorum* hybrids.

Practical implications

Production of intergeneric hybrids is only the first step in a series of complex stages that deal with alien genetic transfer(s) leading to improved *T. aestivum* germplasm. The meiotic data are suggestive of a probable lack of gene transfers via direct recombination since most of the F_1 chromosome pairing observed is attributed to autosyndesis. Where this autosyndetic association trend is not apparent, advanced BC derivatives of such hybrids may express it and, if this is the case, the complexity of gene transfers still persists. In general, if wide crosses are to be practically successful, the alien gene of significance should be epistatic to the wheat genetic system, a mechanism that gets complicated if the trait being improved is controlled by complex and recessive polygenes. Sophisticated research avenues promise speedy results that seem far from convincing to this group, where the flexibility of the wheat cytogenetic system will continue to maintain its decided advantage in effecting alien transfers for several decades.

Where F_1 recombination manipulation, even after employing wheat cytogenetic stocks, exhibits gene transfer constraints, avenues exist for exploiting synthetic genomes and interspecific hybridization approaches. The synthetic genome concept elaborated by Mujeeb-Kazi et al. (1987) appears applicable to all except the *A. campestre* intergeneric combinations of this study. Utilizing alien species through this process may presumably assist in effectively working with complex polygenic recessive systems.

Conclusion

The breeding approaches for complex polygenic recessive characters will be long-term and progress slowly. Due to complexity of the character, selection of beneficial plants with alien introgression will be futuristic and will necessitate a delay until production of F_3 or F_4 families. Considering these constraints in intergeneric hybridization primarly associated with en bloc complex recessive polygene transfers that will be long-term, there seems significant merit in exploiting the related germplasm through interspecific hybridization methodologies. The latter have advantages of genome homologies with wheat which would permit recombination events even for complex genetically controlled traits and would provide short term practical benefits (Mujeeb-Kazi and Asiedu 1988).

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