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Production and cytogenetic analysis of hybrids between *Triticum aestivum* and some caespitose *Agropyron* species

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Intergeneric hybrids between *Triticum aestivum* L. cultivars and 12 traditional *Agropyron* species were produced in variable frequencies, lowest being 0.35% for *A. stipaeifolium* to a high of 41.98% for *A. varnense*. The crossing success of *T. aestivum* cultivars ranged from 'Chinese Spring' > 'Pavon-76' = 'Nacozari-75' > 'Fielder' = 'Fremont' > 'Glennson-81'. All F₁ hybrids were somatically stable. The new combinations were with *A. curvifolium* (*Thinopyrum curvifolium*), *A. rechingeri* (*T. sartorii* = *rechingeri*), *A. scythicum* (*T. scythicum*), and *A. stipaeifolium* (*Pseudoroegneria stipaeifolia*). All hybrids were perennial and possessed a modified phenotype that was intermediate between the parents involved in the hybrid combinations with major variation in spike morphology (elongated spikes with lax internodes). High-pairing hybrids, presumably owing to suppression of the *Ph* locus were of *T. aestivum* – *A. scythicum* (15.31 I + 2.25 II rings + 6.92 II rods + 0.32 III) and *T. aestivum* – *A. stipaeifolium* (10.6 I + 7.08 II rings + 4.41 II rods + 0.54 III). In the other combinations, the pairing was either low or high, and if high, pairing was attributed to autosyndetic association of the alien genome chromosomes. Based on the meiotic pairing data, alien species that were segmental allotetraploids or partial autopolyploids, or segmental allohexaploids or autoallohexaploids, may be advantageous in developing backcross derivatives with synthetic genomes. Production of fertile amphiploids was restricted to *T. aestivum* – *A. rechingeri*.

Key words: *Triticum aestivum*, *Agropyron* species, *Pseudoroegneria* species, *Thinopyrum* species, intergeneric hybrids, crossability, wide crosses.

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Des hybrides intergénériques entre des cultivars de *Triticum aestivum* L. et 12 espèces communes d'*Agropyron* ont été produits en fréquences variables, depuis les plus basses avec 0,35% pour *A. stipaeifolium* vers les plus hautes avec 41,98% pour *A. varnense*. Le succès des croisements des cultivars de *T. aestivum* a évolué comme suit: 'Chinese Spring' > 'Pavon 76' = 'Nacozari 75' > 'Fielder' = 'Fremont' > 'Glennson 81'. Tous les hybrides F₁ ont été stables sur le plan somatique. De nouvelles combinaisons ont été faites avec *A. curvifolium* (*Thinopyrum curvifolium*), *A. rechingeri* (*T. sartorii* = *rechingeri*), *A. scythicum* (*T. scythicum*) et *A. stipaeifolium* (*Pseudoroegneria stipaeifolia*). Tous les hybrides se sont avérés vivaces et possédaient un phénotype intermédiaire entre les parents impliqués dans les combinaisons hybrides, mais avec une variation majeure dans la morphologie de l'épi, soit des épis allongés avec des entrenoeuds inégaux. Les hybrides dont les appariements furent élevés, présument en raison de la suppression du locus *Ph*, ont été ceux de *T. aestivum* – *A. scythicum* (15,31 I + 2,25 II (en anneaux) + 6,92 II (en bâtonnets + 0,32) et de *T. aestivum* – *A. stipaeifolium* (10,6 I + 7,08 II (en anneaux) + 4,41 II (en bâtonnets) + 0,54 III). Dans d'autres combinaisons, les appariements ont été faibles ou élevés et, lorsqu'ils étaient élevés, les appariements étaient attribués à des associations autosyndétiques de chromosomes de génomes étrangers. Sur la base d'appariements méiotiques, les données relatives aux espèces étrangères qui constituaient des segments allotétraploïdes ou partiellement autopolyploïdes, des segments allohexaploïdes ou auto-allohexaploïdes, peuvent s'avérer avantageuses pour développer des dérivées de rétrocroisements avec génomes synthétiques. La production d'amphiploïdes fertiles a été restreinte à *T. aestivum* – *A. rechingeri*.

Mots clés: *Triticum aestivum*, *Agropyron* species, *Pseudoroegneria* species, *Thinopyrum* species, hybrides intergénériques, possibilité d'hybridation, croisements étendus.

[Traduit par la revue]

Introduction

As wheat production increases in the warmer, more humid subtropics, scab (*Fusarium graminearum*) and *Helminthosporium sativum* are likely to become major production constraints. Though variation can be incorporated into wheat via inter-specific or intervarietal crosses, alien sources offer additional genetic variation worthy of exploitation. Several complexities, however, exist in accomplishing successful alien genetic incorporation (Mujeeb-Kazi and Kimber 1985), but the prospects of increasing wheat yields substantially compensate for the research constraints.

Different methodologies exist in making intergeneric (wheat–alien species) combinations. Of these, one is based on screening the alien germ plasm for specific resistances and then combining the resistant species with wheat. The alternative approach, so far adopted by us, is to combine the alien species or genera to

several wheat varieties, obtain hybrids, clonally propagate the hybrids, and test the clones for disease or stress tolerance. If clonal testing is not feasible, the F₁ hybrid may be advanced to a backcross self-fertile stage and then tested. Both procedures have their advantages and limitations, and their exploitation has materially and numerically diversified the genetic base available for wheat improvement.

Relatively few *Agropyron* species have been hybridized with wheat (*Triticum aestivum* L.; $2n = 6x = 42$, AABBDD) as the maternal parent. The hybridization successes that we are aware of have been with *A. caespitosum* (Dvořák 1981); *A. distichum* (Pienaar et al. 1977); *A. elongatum* ($2n = 2x = 14$; Jenkins 1958) ($2n = 4x = 28$; Wakar 1935; Peto 1936; Dvořák 1981) ($2n = 10x = 70$, see Cauderon 1979); and *A. intermedium* (Peto 1938; Cauderon 1966), including some synonymous species, i.e., *amurense*, *glaucum*, *trichophorum*; *A. junceum* ($2n = 2x$

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

Species	Chromosome no. and ploidy designation	Field location		Collection no., source or origin*
		Row	Plant no.	
<i>A. caespitosum</i> (<i>T. caespitosum</i>)	$2n = 4x = 28$	28	20 and 22	Jaaska 3 and 4, USSR
<i>A. curvifolium</i> (<i>T. curvifolium</i>)	$2n = 4x = 28$	5	6 and 7	PI-287739, Spain
<i>A. gentryi</i> (<i>T. gentryi</i>)	$2n = 6x = 42$	28	43	PI-228277, Iran
<i>A. junceum</i> (<i>T. bessarabicum</i>)	$2n = 2x = 14$	31	15	Jaaska, USSR
<i>A. junceum</i> (<i>T. junceiforme</i>)	$2n = 4x = 28$	30	30	PI-414667, Greece
<i>A. junceum</i> (<i>T. junceum</i>)	$2n = 6x = 42$	31	31-34	Cauderon 471, France
<i>A. podperae</i> (<i>T. podperae</i>)	$2n = 6x = 42$	6	21-25	PI-228387, Iran
<i>A. rechingeri</i> (<i>T. sartorii</i>) (= <i>rechingeri</i>)	$2n = 4x = 28$	6	26 and 30	CJ-27-10P, Aegean
<i>A. scirpeum</i> (<i>T. scirpeum</i>)	$2n = 4x = 28$	5	26 and 32	Cauderon, via Italy
<i>A. scythicum</i> (<i>T. scythicum</i>)	$2n = 4x = 28$	28	3	Jaaska 15, USSR
<i>A. stipaefolium</i> (<i>T. stipaefolia</i>)	$2n = 4x = 28$	4	36	E-12-30, USSR
<i>A. varnense</i> (<i>T. varnense</i>)	$2n = 6x = 42$	20	29 and 30	PI-282863, Iran

*Source: D. R. Dewey's 1982 Field book of planting at Evans Farm, Logan, UT, U.S.A.

= 14; Alonso and Kimber 1980); *A. junceum* ($2n = 4x = 28$; Mujeeb-Kazi et al. 1983); *A. junceum-mediterranean* ($2n = 6x = 42$, Mujeeb-Kazi and Rodriguez 1980); *A. podperae* (Dewey 1981); *A. scirpeum* (Sharma and Gill 1983a, 1983b).

From these hybrids produced earlier, the successful transfers from a few (wheat - *A. elongatum* and wheat - *A. intermedium*) have been for leaf rust, stem rust, yellow rust, and wheat streak mosaic virus (Browder 1980; Cauderon 1966, 1979; Driscoll 1975, 1981; Knott 1961; Martin 1981; Smith et al. 1981; Weinhues 1965). It is hence logically deduced that a motivation to make wide hybrids is the desire to introduce desirable characteristics from alien sources into wheat. As a consequence, this article reports on several "new" or justifiably "reproduced" hybrids of *Agropyron* species with *T. aestivum*. Apart from their practical utilization in wheat improvement, the hybrids offer promise of basic cytological, evolutionary, or phylogenetic information about the parental species involved in the hybrid. The cytogenetic analyses of the F_1 hybrids help in making interpretations in the latter area which serve to direct the hybrid progeny advance beyond backcross I (BCI) for realizing the breeding objectives though alien genetic transfers.

Materials and methods

Germ plasm

Seeds of *Triticum aestivum* L. (cultivars Chinese Spring, Fielder, Fremont, Glennson-81, Nacozari-75, and Pavon-76) were planted on three dates (March 15, April 1, April 15, 1982) in the field experiment station at Evans Farm, Logan, Utah, U.S.A. The *Agropyron* species were already maintained in the caespitose (CS) field nursery at the same location by D. R. Dewey. Pertinent details of these species as they influence the scope of this study are provided in Table 1.

Hybrid production

Wheat spikes were emasculated, pollinated by the alien species either 3 to 4 days after emasculation (conventional) or 1 day after emasculation (early or bud pollination), and treated with gibberellic acid using the procedure described by Mujeeb-Kazi and Rodriguez (1984) and Mujeeb-Kazi and Kimber (1985). The embryos were excised 14 to 18 days after pollination and cultured on a special medium for small embryos (Taira and Larter 1978). Subsequent procedures associated with embryo differentiation, plantlet growth, transfer to peat pots, and transplanting to a potted soil mix in the greenhouse were routine and similar to those reported earlier (Mujeeb-Kazi and Rodriguez 1983a, 1983b), as were the environmental growth regimes.

F_1 Somatic and meiotic sampling

Root tips were collected for each hybrid combination prior to transferring the young plantlets from the culture tubes to peat pots. They were again periodically sampled from the plants after they were transplanted to soil in pots and maintained in the greenhouse. The cytological procedure of Mujeeb-Kazi and Miranda (1985) was followed for somatic counts. Spikes from each hybrid combination were collected for meiotic determinations, fixed in Carnoy's fixative (6:3:1, absolute alcohol - chloroform - acetic acid) for 48 h, and stored under refrigeration (4 or -10°C) in 70% alcohol until use. Anthers were stained in alcoholic-acid-carmines for 48 h and squashed in 45% acetic acid. Meiotic chromosome associations were analyzed at metaphase I.

Cloning, colchicine treatment, and spike characterization

All F_1 hybrids were cloned to form five plants after 6 months of F_1 plant growth. Colchicine treatment of a few of these cloned plants was carried out by the aerated root treatment procedure using 0.2% colchicine + 2.0% dimethylsulfoxide for 6 h. Fully emerged spikes from all clones and hybrids were characterized for spike details and photographed. Though sampling timings differed for the hybrids, their

TABLE 2. Some intergeneric hybrids of *Triticum aestivum* L. ($2n = 6x = 42$) varieties with caespitose *Agropyron* species indicating details of chromosome number, florets pollinated (*a*), seeds set (*b*), embryos excised + seeds with embryos that reached maturity on the plant when endosperm was present (*c*), and plants differentiated (*d*)

Pollen sources	F ₁ chromosome no.	<i>Triticum aestivum</i> L. varieties												Total over varieties															
		'Chinese Spring'				'Fielder'				'Fremont'				'Glennson-81'				'Nacozari-76'				'Pavon-76'							
		<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>				
<i>A. caespitosum</i> (<i>T. caespitosum</i>)	35	240	105	105	58																					240	105	105	58
<i>A. curvifolium</i> (<i>T. curvifolium</i>)	35	388	27	27	11																					388	27	27	11
<i>A. gentryi</i> (<i>T. gentryi</i>)	42	236	18	18	10									32	0	0	0	88	0	0	0					356	18	18	10
<i>A. junceum</i> (2x) (<i>T. bessarabicum</i>)	28	608	18	15	5					188	0	0	0	66	0	0	0									862	18	15	5
<i>A. junceum</i> (4x) (<i>T. junceiforme</i>)	35	1078	111	111	*	102	4	3	*	150	20	20	*									138	3	3	*	1468	138	137	77 *
<i>A. junceum-mediterranean</i> (6x) (<i>T. junceum</i>)	42	596	37	37	11*																					596	37	37	11
<i>A. podperae</i> (<i>T. podperae</i>)	42	60	1	1	1									62	0	0	0	68	2	0	0					190	3	1	1
<i>A. rechingeri</i> (<i>T. sartorii</i>) (= <i>rechingeri</i>)	35	258	58	56	30									136	0	0	0	392	1	1	1	56	7	7	5	842	66	64	36
<i>A. scirpeum</i> (<i>T. scirpeum</i>)	35	452	9	6	6																					452	9	6	6
<i>A. scythicum</i> (<i>T. scythicum</i>)	35	246	60	56	10					188	6	6	4	120	0	0	0	280	3	2	1	156	0	0	0	990	69	64	15
<i>A. stipaefolium</i> (<i>P. stipaefolia</i>)	35	316	5	2	1																	554	2	2	2	870	7	4	3
<i>A. varnense</i> (<i>T. varnense</i>)	42	477	318	318	*	248	54	54	*	228	4	4	*					52	16	16	*	160	97	97	*	1165	489	489	125 *

*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 F₁ seed was stored.

maintenance remained under a controlled greenhouse environment reported earlier (Mujeeb-Kazi and Rodriguez 1983a, 1983b).

Results and discussion

Germ plasm

A majority of the hybrid combinations listed in Table 2 are unique. The combinations currently reproduced have either differed from combinations produced by other researchers because of the wheat varietal source used or are totally similar where 'Chinese Spring' was the wheat variety used. The reproduced hybrids of the alien species with 'Chinese Spring' have provided us immediate availability of F_1 germ plasm.

In the present study, attempts were not made to make reciprocal crosses (alien species - *T. aestivum*). In several cases, this may be the only way to combine the alien species with wheat. Some species that fit this crossability category include the following: *Agropyron ciliare*,¹ *A. fibrosum*,² *A. scabrifolium*,² *A. scabrigrume*,² *A. trachycaulum*,^{1,2} *A. yezoense*,¹ *E. canadensis*,² *E. virginicus*,² *E. agropyroides*,² and *E. dahuricus*.² For the recently produced hybrids (Table 2), the reciprocal crosses and backcrosses to *T. aestivum* may aid in developing alloplasmic material. Fertile amphidiploids can also be produced, e.g., *A. fibrosum* - *T. turgidum* var. Mexicali (*A. Mujeeb-Kazi*, unpublished), but in other cases the F_1 may be both male and female sterile and remain a biological curiosity. In extreme cases, as an example of the latter, the anthers are totally devoid of pollen mother cells rendering genomic evaluation impossible, e.g., *A. elongatum* - *Secale cereale* (Mujeeb-Kazi and Rodriguez 1980) and *A. scabrigrume* - *T. turgidum* (Mujeeb-Kazi and Bernard 1985a). Because of the unpredictability of success with the reciprocal crosses, such risks were currently avoided; however, their potential was not overlooked. An excellent example of the research complication associated with cross direction is that of hybrids between *Hordeum vulgare* and *Triticum aestivum*, where with *H. vulgare* being maternal, self-fertility was not achieved (Islam et al. 1975, 1978; Mujeeb-Kazi and Rodriguez 1983a, 1983b, 1984).

Hybrid production

Crossing success varied for different combinations and was influenced by the *T. aestivum* variety. The varietal success ranged from high to low as follows: 'Chinese Spring' > 'Pavon-76' = 'Nacozari-75' > 'Fielder' = 'Fremont' > 'Glennson-81'. There were 12 caespitose *Agropyron* species hybridized with one or more of the above *T. aestivum* varieties (Table 2). For the first series of crosses, embryos were excised and cultured. In those crosses where endosperm development was observed during embryo excision, subsequent combinations for each were allowed to mature under field conditions. These were *T. aestivum* varietal combinations with *A. caespitosum*, *A. junceum* ($2n = 4x = 28$), and *A. varnense*. The *T. aestivum* - *A. junceum-mediterranean* ($2n = 6x = 42$) hybrid had endosperm, but because of the low seed set, all embryos were cultured. Seed setting as expressed in Table 2 is a combination of "actual" seed setting plus stimulation, and generally, this equates accurately with actual embryos extracted. The embryo culturing to embryo differentiation ratio was not perfectly correlated, but for each cross a differentiated hybrid plant was obtained. The combinations with an asterisk under the plantlet differentiation category (Table 2) indicate

that, because of endosperm presence as determined during initial embryo excision, the remaining F_1 seeds were left to mature on the plant and all were not germinated after harvesting.

It may be possible to obtain a better ratio of embryo cultured to embryo differentiated frequencies through innovative manipulations bordering on embryo culture media formulations or employing tissue culture micro-propagation techniques. These manipulations are not justified for our practical agricultural objectives where one "normal" vigorous F_1 hybrid of each combination is adequate. However, for those combinations where no embryo differentiation occurred, the culture media and tissue culture manipulations may have merit. Such intergeneric combinations may need greater sophisticated care in our future studies or in those of other researchers with related alien germ plasm utilization research goals. The alien combinations, not considering caespitose or rhizomatous habit that formed this category, were of *T. aestivum* with *A. cristatum* ($2n = 4x = 28$), *A. smithii*, *A. strigosum*, *A. tauri*, *E. salina*, and *E. junceus* (Table 3). These species may combine better with *T. aestivum* in forthcoming studies, but it is doubtful if controlled growth conditions would facilitate the success.

Field crossing with alien grasses is decidedly a factor in crossing frequency variations principally because of the excellent alien pollen supply. In *T. aestivum* - alien species grass crosses that we made earlier in México, successful hybrid production frequencies generally remained low. This may be related to the poor quality and small quantity of pollen obtained when the grasses are grown under controlled greenhouse environments.

Several other factors contribute to crossing success. Investigators may have overestimated the 'Chinese Spring' varietal role in superb hybridization success. The success of 'Chinese Spring' has been attributed to the $kr_1 kr_1 kr_2 kr_2 kr_3 kr_3$ crossability genes it possesses (Falk and Kasha 1981; Fedak and Jui 1982) for its crossability with rye (Riley and Chapman 1967). The loci location on homoeologous group 5 (5B, 5A, and 5D, respectively) act in a complementary manner with the kr_1/kr_1 loci on 5B having the greatest effect. A minor role may also be assigned to the alien species in intergeneric combinations with wheat as elucidated in wheat-barley species crosses, i.e., *H. vulgare*, *H. chilensis*, *H. bogdanii*, or *H. bulbosum*. Additional evidence is supportive of the better combining ability of the varieties of an alien species, i.e., varieties 'Betzes' or 'Manker' of *H. vulgare* (Thomas et al. 1977).

Early pollinations have an advantage over the conventional pollination timings, particularly for those combinations where embryo recovery frequencies were low (e.g., *A. stipaeifolium*). In the future, bud pollinations may contribute as one significant variable in producing difficult to obtain hybrids between *T. aestivum* and the alien species.

The hybrids generally differentiated and grew to 4 cm in approximately 6 weeks after culturing and were transplanted in potted soil at 8 weeks.

Somatic and meiotic sampling

Initial hybrid identification was based on mitotic counts in root tips collected at various growth stages (see sampling stages in Mujeeb-Kazi and Miranda 1985). The high chromosomal metaphase mitotic index, exceptional primary and secondary constriction resolution, and clarity made hybrid identification very accurate even for those combinations where the alien species were hexaploids as *T. aestivum* ($2n = 6x = 42$) is. In such hybrids with 42 chromosomes, only one chromosome of

¹Sharma and Gill 1981, 1983a, 1983c.

²Mujeeb-Kazi and Bernard 1985a, 1985b.

TABLE 3. Some unsuccessful *Triticum aestivum*–alien species combinations where embryo formation occurred but no plants differentiated when embryos were cultured on Taira and Larter's media

<i>T. aestivum</i> cultivar	Alien species	No. of florets pollinated	Seed set	No. of embryos excised	Embryo* and endosperm† detail
Chinese Spring	<i>Agropyron cristatum</i>	74	1	1	iii and 0
Chinese Spring	<i>A. smithii</i>	26	1	1	iii and 0
Chinese Spring	<i>A. strigosum</i>	36	3	3	ii and e
Chinese Spring	<i>A. tauri</i>	53	5	4	ii and e (1) i and E (3)
Chinese Spring	<i>E. salina</i>	18	2	2	ii and E
Nacozari-76	<i>E. junceus</i>	15	1	1	ii and e

*i, normal embryo; ii, small defined embryo; iii, minute and ill-defined.

†0, no endosperm; e, watery endosperm; E, copious endosperm (observation at time of embryo excision).

each of the three satellited pairs of wheat chromosomes was observed; 1B and 6B consistently, and 5D in each hybrid but not in all cells. Satellites of the alien chromosomes expressed inconsistently, and often not at all, a common feature because of amphiplasty. This is exemplified in hybrids of tetraploid or hexaploid wheat with *H. vulgare*, where the barley-satellited chromosomes rarely, if ever, expressed (Mujeeb-Kazi and Miranda 1985). Similarly, in *T. aestivum* varieties with the 1B–1R translocated chromosomes, it is only the 6B-satellited pair that expresses the 6BS secondary constriction, while the secondary constrictions characteristic of 1RS are not detected (Merker 1982). Several sampling durations established somatic stability within each hybrid.

Our effort to diversify the genetic base of *T. aestivum* production of intergeneric hybrids reported in Table 2 is only the first step. For the introduction of desirable alien variation into *T. aestivum*, complicated cytogenetic manipulations may often be necessary. It is essential to have a clear understanding of the genomic relationships of the alien species and their influence or expression in the resulting hybrids. The recent development of numerical methods of assessing genomic affinity (Kimber and Hulse 1978; Kimber et al. 1981; Alonso and Kimber 1981; Kimber and Alonso 1981; Espinasse and Kimber 1981) has introduced some objectivity to genome analysis.

The tetraploid model was applicable to the *T. aestivum* – *A. junceum* hybrid ($n = 4x = 28$, ABDJu, Fig. 1). The pairing observed (1.004 chiasma/cell) did not provide any evidence of homologous or homoeologous associations. Alonso and Kimber (1980) and Sharma and Gill (1983b) made fairly similar conclusions when they observed 0.2 rod bivalents/cell and 0.93 chiasma/cell, respectively.

Hybrids of tetraploid *Agropyron* species with *T. aestivum* had variable mean meiotic associations with chiasmata ranging from 1.75 (*T. aestivum* – *A. curvifolium*) (Fig. 2) to 19.64/cell (*T. aestivum* – *A. stipaeifolium*) (Table 4). Breeding strategies for each hybrid combination have been formulated based on the chromosome pairing data analyses (G. Kimber, personal communication). The philosophy behind such categorization was associated with the earlier concepts as reported by Kimber (1984) relative to techniques of alien transfers. When the mean arm-pairing frequency and the relative affinity have values approaching one, the transfer can be made by recombination. At intermediate values of mean arm-pairing frequency, increased homoeologous pairing can be induced by changes in the systems regulating chromosome pairing. At very low values of the mean arm-pairing frequency, irrespective of the value of the relative

affinity, irradiation or centric break-and-fusion in derived aneuploids is the optimum method (Kimber 1984). It accordingly separates the hybrids into distinct categories and, judging the practicality of the alien species, the list is further condensed. The *c* values for the tetraploid and pentaploid hybrids are listed in Table 4 and aid in categorization of the pairing data.

The tetraploid *Agropyron* species may be considered either strict autotetraploids or partial allopolyploids. In the former case, autosyndetic genome associations would be maximized, whereas structural differences of the partial allopolyploids seemingly prevent such close alien genome associations. Maximum autosyndetic associations were expected in the F_1 but did not occur, presumably owing to the active *T. aestivum* 5B *Ph* locus, e.g., *T. aestivum* – *A. curvifolium*. Surprisingly, the level of pairing in *T. aestivum* hybrids with two partial allopolyploids (*A. junceum* and *A. scirpeum*) was considerably higher than that of the *T. aestivum* – *A. curvifolium* partial autopolyploid hybrid.

Of the 12 *Triticum*–*Agropyron* species hybrids reported here, 11 are classed under *Triticum*–*Thinopyrum* species when the genomically based nomenclature is used (Dewey 1984). The type species is *T. junceum* and the basic or core genome is JE, though other genomes may occur in certain complex polyploid species. Several species are autotetraploids (*A.* or *P. stipaeifolium*), segmental allotetraploids, or partial autopolyploids (*A.* or *T. curvifolium*, *A.* or *T. junceiforme*, *A.* or *T. scirpeum*), segmental allohexaploids (*A.* or *T. junceum*), or segmental autoallohexaploids (*A.* or *T. podperae*, *A.* or *T. varnense*) where there are two closely related genomes and the third genome is distinctly different from the other two. These relationships need to be observed to reach inferences about pairing in wheat–alien species hybrids, since advance of the F_1 hybrid for agricultural practicality is seemingly swifter where wheat–alien chromosome recombinations occur. Apart from F_1 wheat–alien species recombination events, there is a high probability that the alien genome composition may provide adequate options for unique genetic manipulation. In the segmental allotetraploid or partial autopolyploid, repeated selfings of the backcross I self-fertile derivatives may lead to the formation of a synthetic genome (Mujeeb-Kazi and Miranda 1984). In segmental autoallohexaploids there is the likelihood of the unrelated third genome to be eliminated and of fertile derivatives leading to the formation of stabilized synthetic genomes. Presumably the only hybrid where a dramatic recombinant inference may be reached is that for ‘Chinese Spring’ – *A. scythicum* with a mean meiotic chromosome association fre-

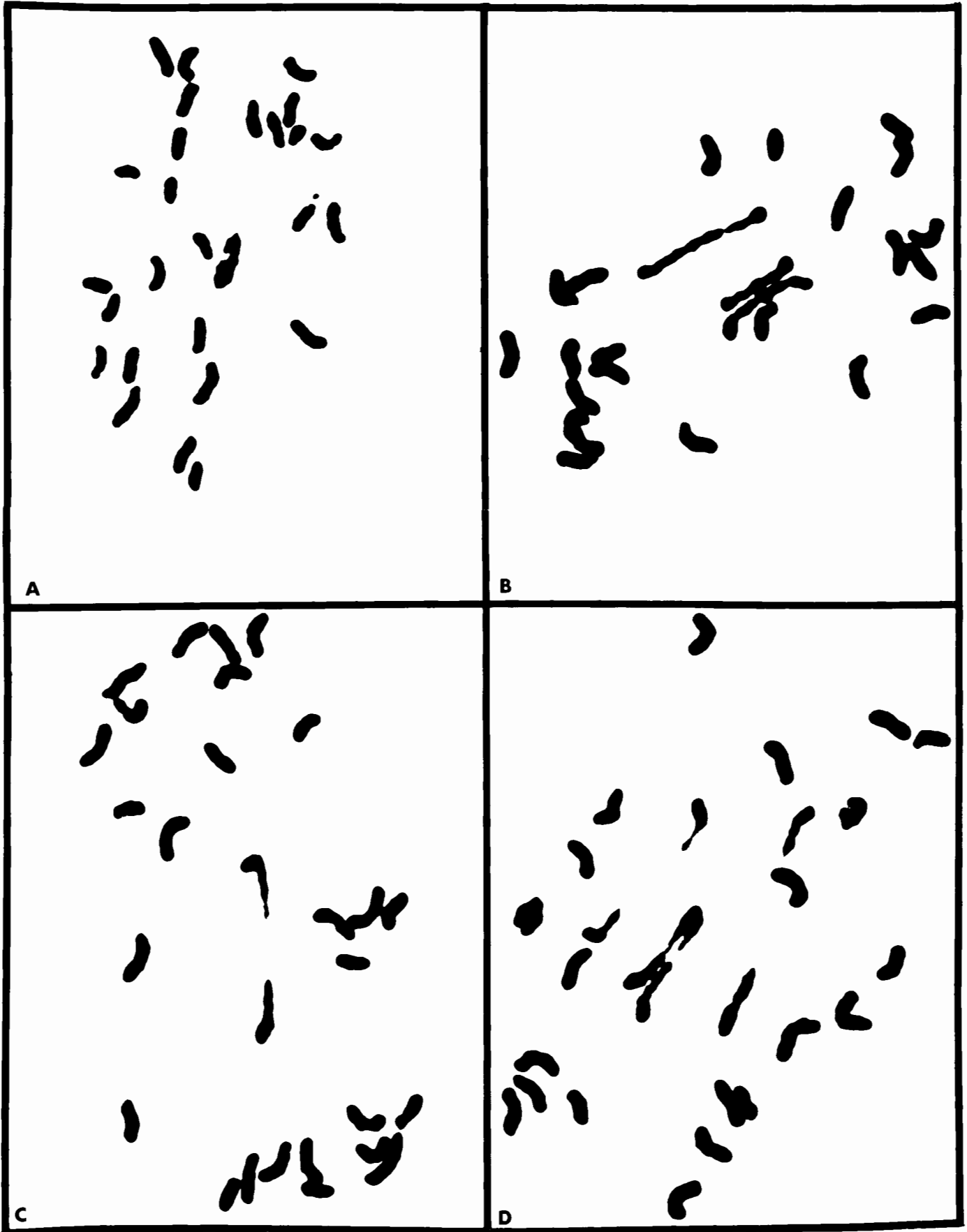


FIG. 1. Mean meiotic chromosome associations at metaphase I in a *Triticum aestivum* - *Agropyron junceum* (*Thinopyrum bessarabicum*) F_1 hybrid with $n = 4x = 28$ chromosomes showing in (A) 26 univalents + 1 ring bivalent, (B) 22 univalents + 3 rod bivalents, (C) 26 univalents + 1 rod bivalent, and (D) 21 univalents + 2 rod bivalents + 1 trivalent.

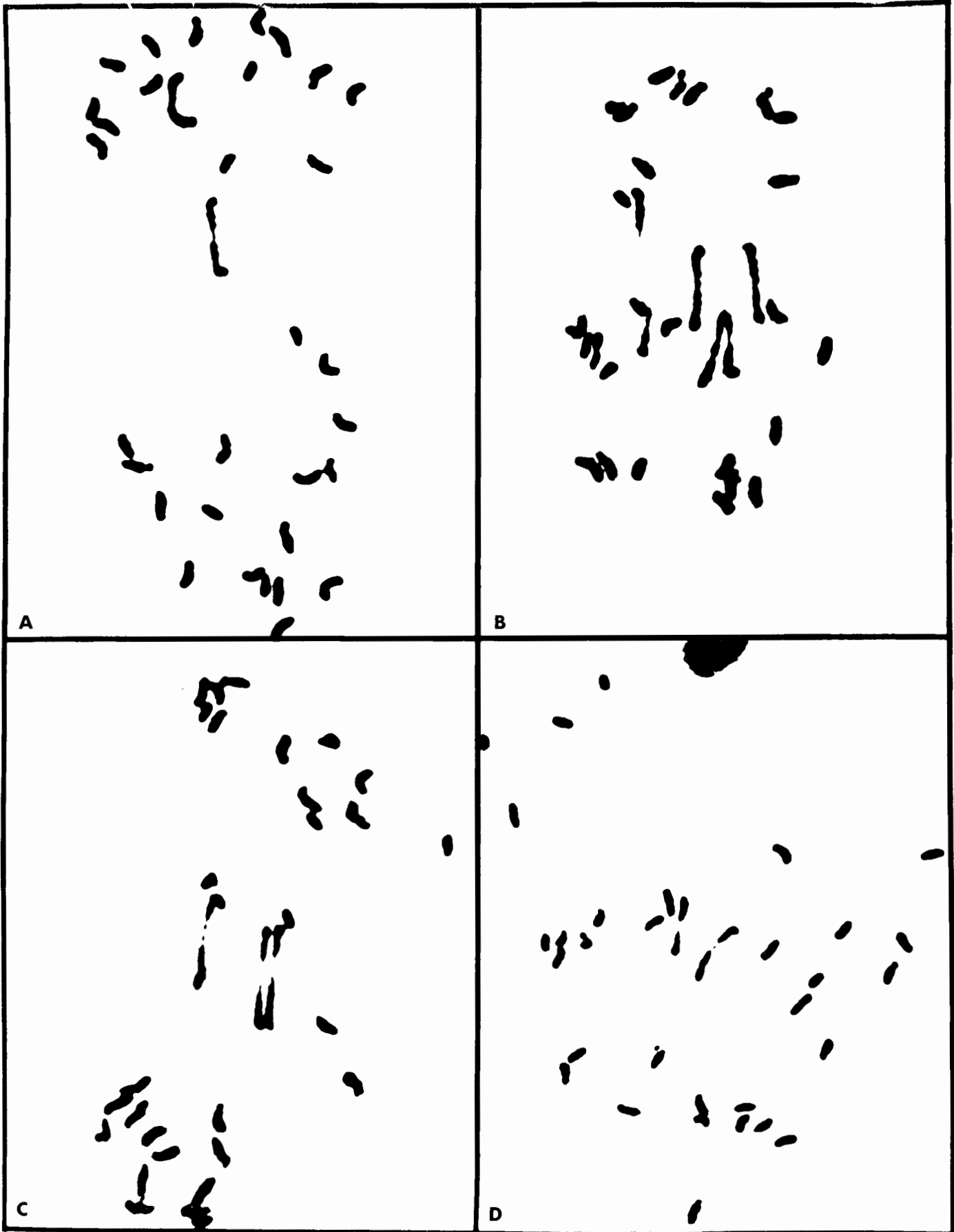


FIG. 2. Mean meiotic chromosome associations at metaphase I in a *Triticum aestivum* - *Agropyron curvifolium* (*Thinopyrum curvifolium*) F_1 hybrid with $n = 5x = 35$ chromosomes showing in (A) 33 univalents + 1 rod bivalent, (B) 26 univalents + 3 rod bivalents + 1 trivalent, (C) 29 univalents + 3 rod bivalents, and (D) 31 univalents + 2 rod bivalents.

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

Alien source involved in intergeneric hybrid combination	Mean meiotic chromosomal associations						Chiasmata/ cell	Mean arm pairing frequency* (c)	
	I	II (ring)	II (rod)	III	IV	V			VI
<i>A. caespitosum</i>	27.5	0.04	2.53	0.56	0.16		0.01	4.24	0.152
<i>A. curvifolium</i>	31.5	0.02	1.7	0.01				1.75	0.063
<i>A. gentryi</i>	15.8	4.81	5.9	1.48	0.07			18.68	—
<i>A. junceum</i> (2x)	24.8	0.08	1.51	0.02				1.00	0.058
<i>A. junceum</i> (4x)	16.4	0.92	7.53	0.53	0.04			10.54	0.377
<i>A. junceum</i> (6x)	28.97	0.57	4.95	0.70				7.48	—
<i>A. podperae</i>	16.59	2.0	7.23	2.12	0.01			15.91	—
<i>A. rechingeri</i>	32.73		1.13					1.13	0.040
<i>A. scirpeum</i>	25.66	1.36	3.31					6.03	0.215
<i>A. scythicum</i>	15.31	2.25	6.92	0.32				12.06	0.431
<i>A. stipaefolium</i>	10.6	7.08	4.41	0.54				19.64	0.702
<i>A. varnense</i>	26.26	0.64	6.37	0.65	0.05			9.10	—

*Analysis kindly performed by G. Kimber, University of Missouri, Columbia, MO, U.S.A.

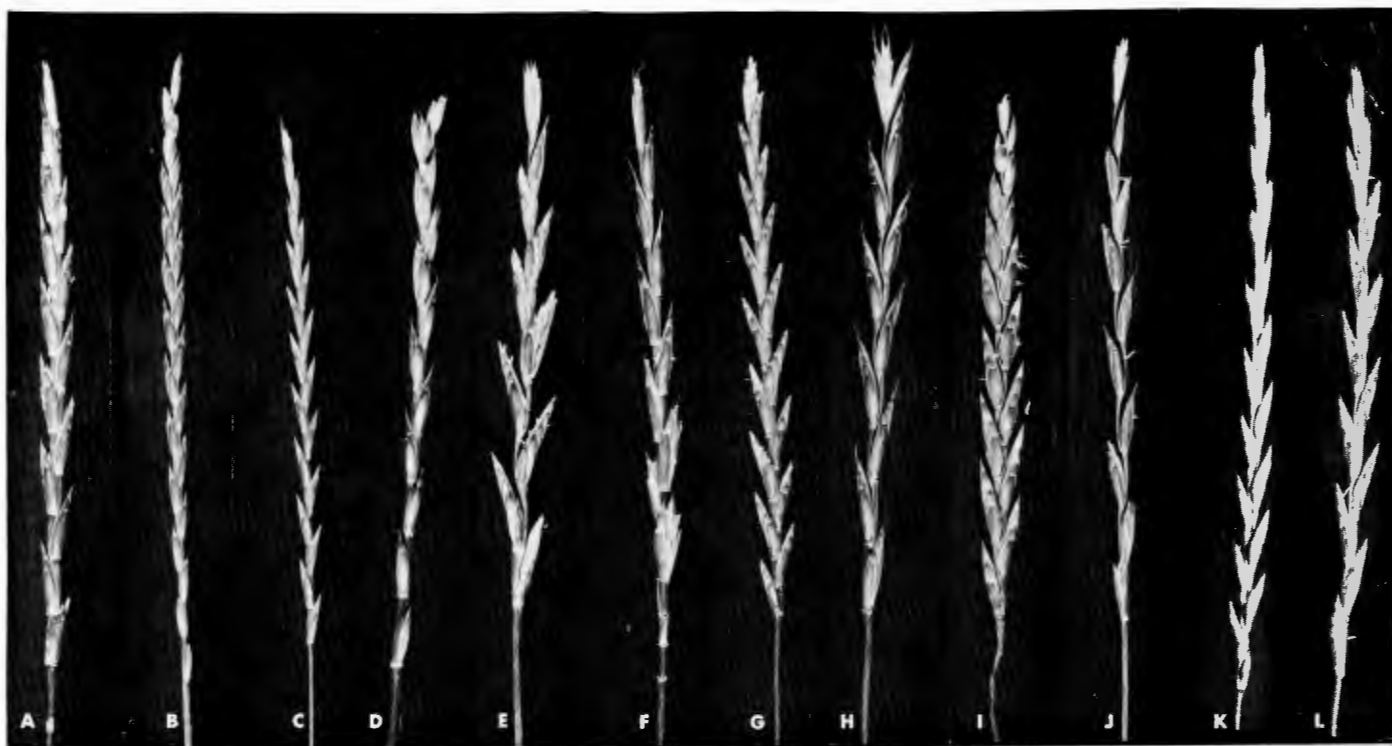


FIG. 3. F₁ spikes of intergeneric hybrid combinations involving *Triticum aestivum* L. cv. Chinese Spring and some caespitose *Agropyron* species. (A) *A. caespitosum* (*T. caespitosum*). (B) *A. curvifolium* (*T. curvifolium*). (C) *A. gentryi* (*T. gentryi*). (D) *A. junceum* (*T. bessarabicum*). (E) *A. junceum* (*T. junceiforme*). (F) *A. junceum* (*T. junceum*). (G) *A. podperae* (*T. podperae*). (H) *A. rechingeri* (*T. sartorii* = *rechingeri*). (I) *A. scirpeum* (*T. scirpeum*). (J) *A. scythicum* (*T. scythicum*). (K) *A. stipaefolium* (*T. stipaefolia*). (L) *A. varnense* (*T. varnense*).

quency of 15.31 I + 2.25 II rings + 6.92 II rods + 0.32 III (Table 4 and Fig. 4.).

Such interpretations can also be made for the *T. aestivum* – *A. stipaefolium* hybrid where a maximum of seven bivalents is expected due to the autotetraploid status of the pollen species. The mean meiotic data of 10.6 I + 7.08 II rings + 4.41 II rods + 0.54 III far exceed this anticipation. Interpretations, however, are kept flexible at this F₁ stage owing to variations that occur for pairing of the E₁E₁E₂E₂ autopolyploid species *A. curvifolium* and *A. scirpeum*. These genomes associate very infre-

quently in the *A. curvifolium* hybrid (Table 4), while in the *A. scirpeum* hybrid, the associations observed are well within the partial pairing trend with 1.36 II rings + 3.31 II rods (Table 4 and Fig. 5). The pairing seen in other hybrids does not provide evidence of enhanced associations between wheat and the alien species, hence associations of chromosomes in hybrids of wheat with *A. caespitosum* (Fig. 6), *A. junceum* (4x) (Figs. 7a and 7b), *A. rechingeri* (Fig. 8), and *A. varnense* (Figs. 7c and 7d) are within normal limits.

There is considerable theoretical merit in attempting to



FIG. 4. Mean meiotic chromosome associations at metaphase I in a *Triticum aestivum* - *Agropyron scythicum* (*Thinopyrum scythicum*) F_1 hybrid with $n = 5x = 35$ chromosomes showing in (A) 19 univalents + 2 ring bivalents + 6 rod bivalents, (B) 9 univalents + 3 ring bivalents + 7 rod bivalents + 2 trivalents, (C) 15 univalents + 3 ring bivalents + 7 rod bivalents, and (D) 17 univalents + 2 ring bivalents + 7 rod bivalents.



FIG. 5. Mean meiotic chromosome associations at metaphase I in a *Triticum aestivum* - *Agropyron scirpeum* (*Thinopyrum scirpeum*) F_1 hybrid with $n = 5x = 35$ chromosomes showing in (A) 27 univalents + 2 ring bivalents + 2 rod bivalents, (B) 23 univalents + 2 ring bivalents + 4 rod bivalents, (C) 25 univalents + 1 ring bivalent + 4 rod bivalents, and (D) 19 univalents + 1 ring bivalent + 7 rod bivalents.

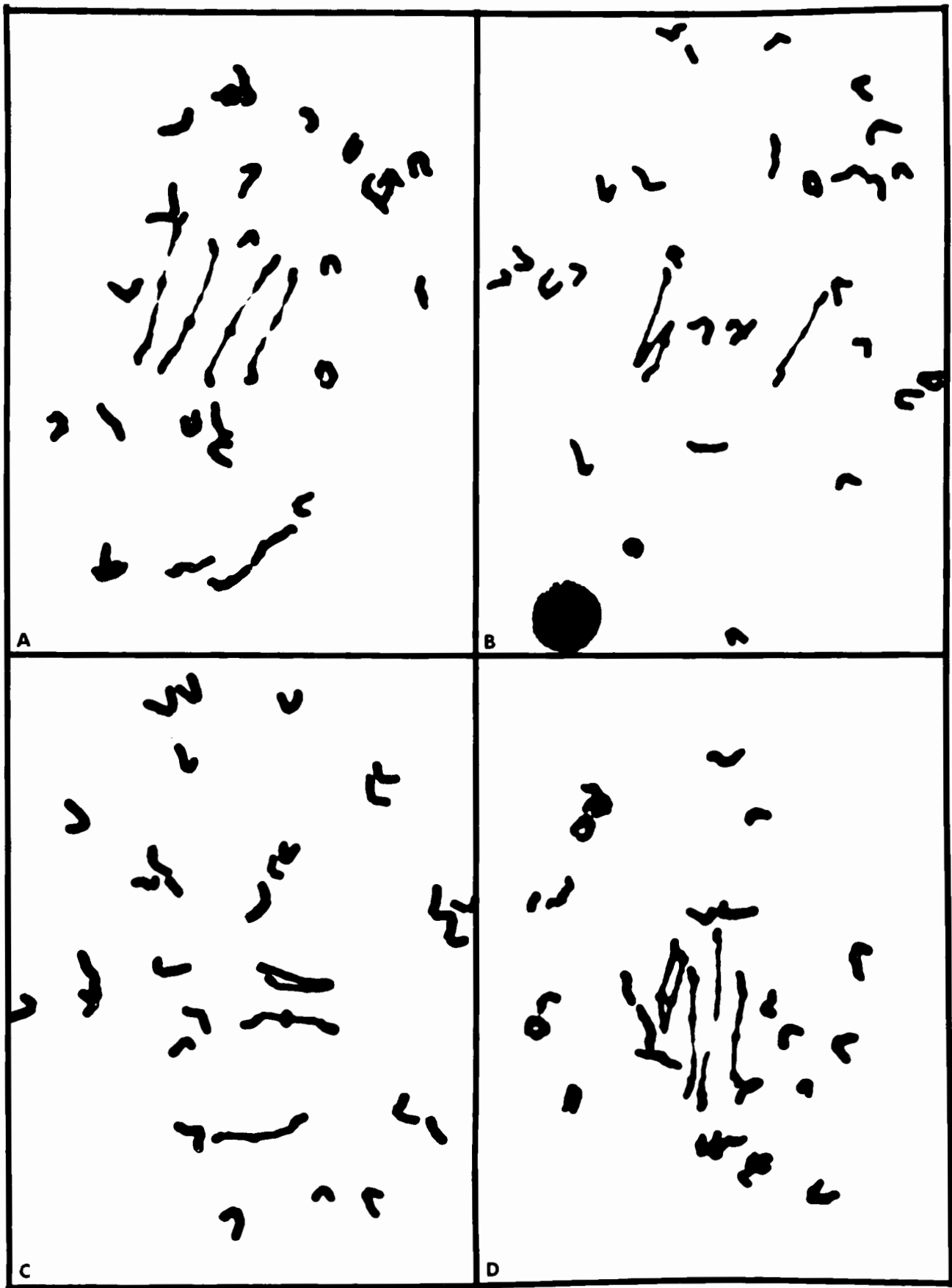


FIG. 6. Mean meiotic chromosome associations at metaphase I in a *Triticum aestivum* – *Agropyron caespitosum* (*T. caespitosum*) F₁ hybrid with $n = 5x = 35$ chromosomes showing in (A) 27 univalents + 4 rod bivalents, (B) 29 univalents + 1 rod bivalent + 1 quadrivalent, (C) 28 univalents + 2 rod bivalents + 1 trivalent, and (D) 26 univalents + 3 rod bivalents + 1 trivalent.

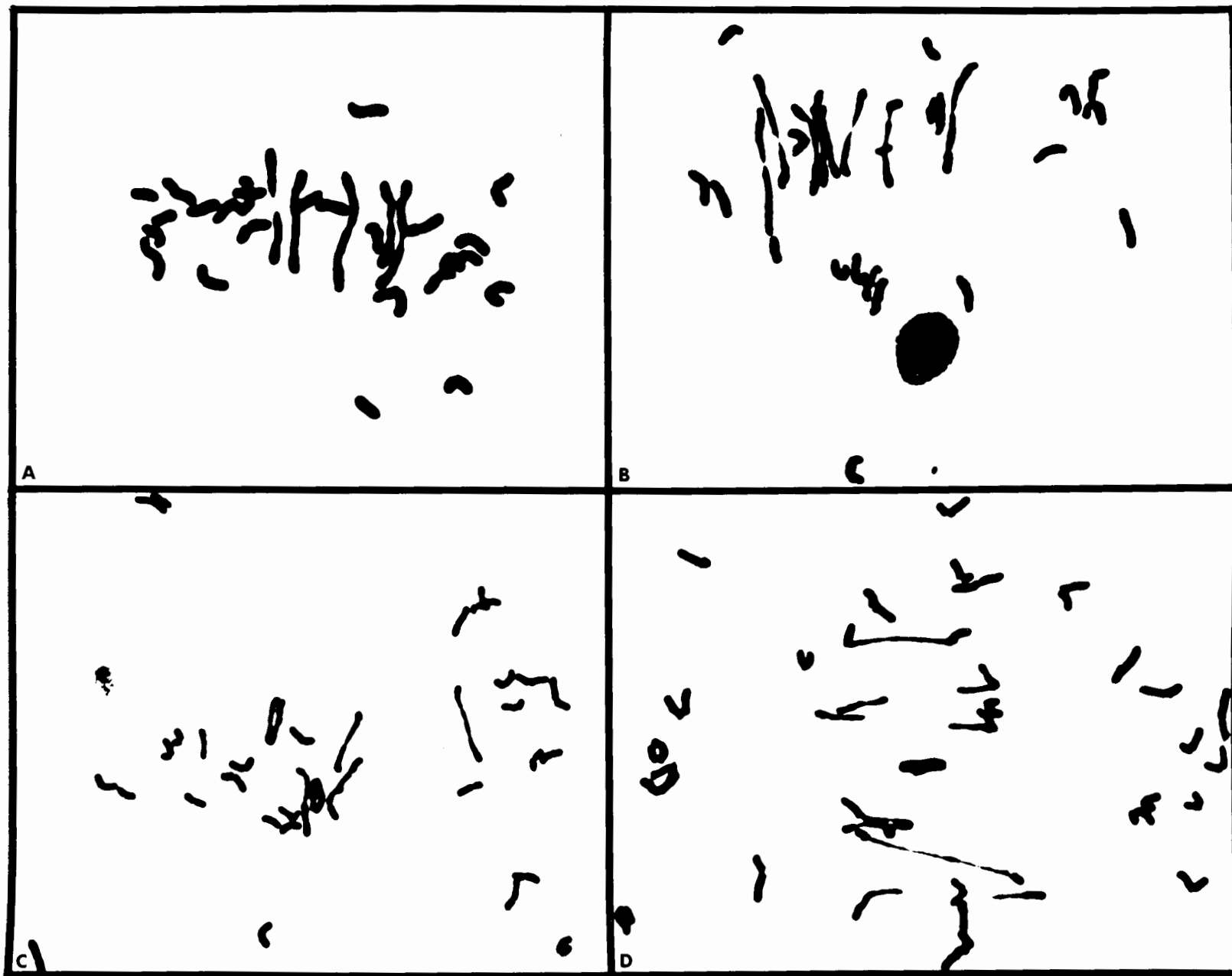


FIG. 7. Mean meiotic chromosome associations at metaphase I in a *Triticum aestivum* - *Agropyron junceum* (*Thinopyrum junceiforme*) F_1 in A and B with $n = 5x = 35$ chromosomes and in (C) and (D) for *T. aestivum* - *A. varnense* (*T. varnense*) with $n = 6x = 42$ chromosomes showing in (A) 25 univalents + 5 rod bivalents, (B) 19 univalents + 8 rod bivalents, (C) 29 univalents + 1 ring bivalent + 4 rod bivalents + 1 trivalent, and (D) 27 univalents + 1 ring bivalent + 5 rod bivalents + 1 trivalent.

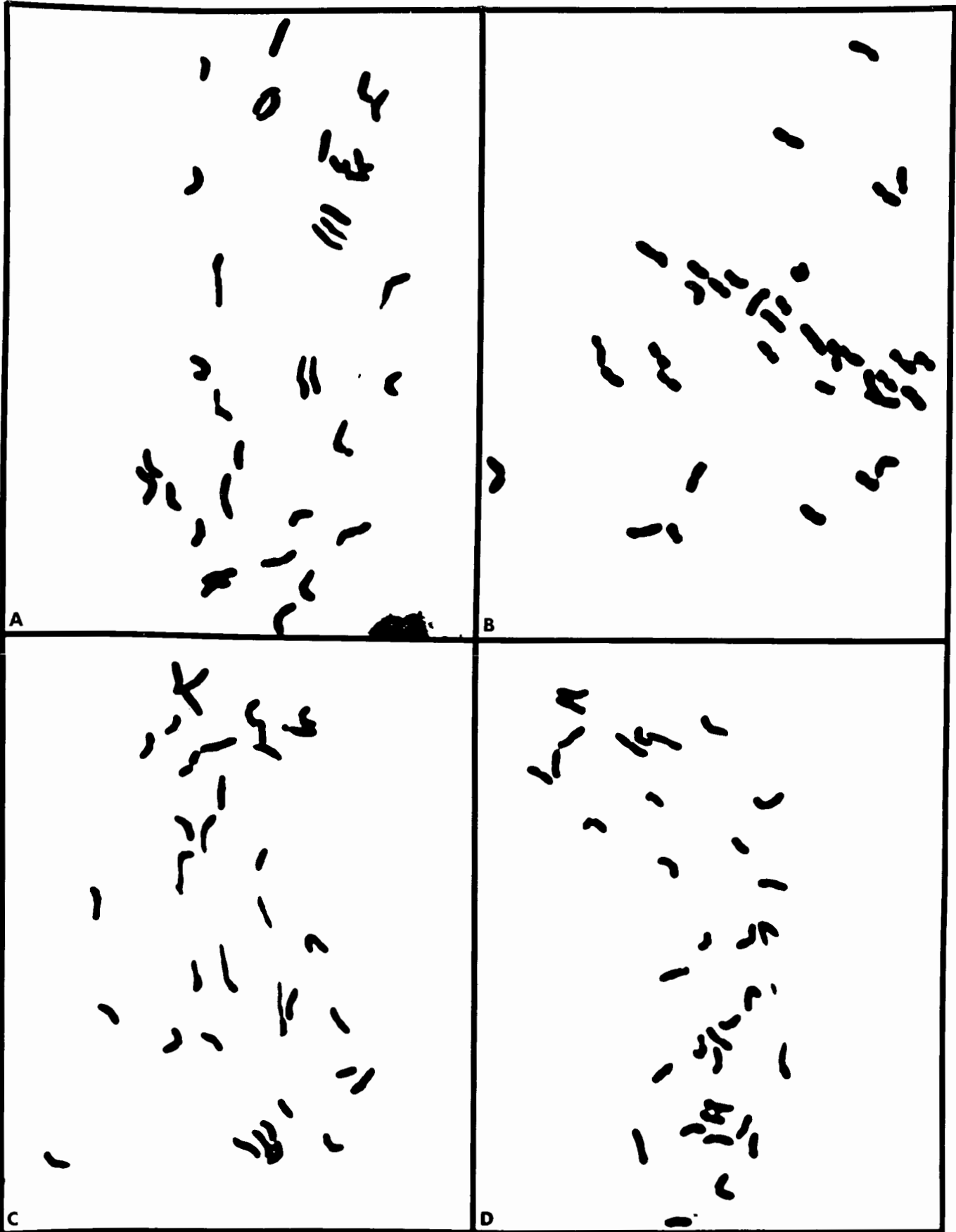


FIG. 8. Mean meiotic chromosome associations at metaphase I in a *Triticum aestivum* - *Agropyron rechingeri* (*Thinopyrum sartorii* = *rechingeri*) F₁ hybrid with $n = 5x = 35$ chromosomes showing in (A) 31 univalents + 2 rod bivalents, (B) 35 univalents, (C) 29 univalents + 3 rod bivalents, and (D) 33 univalents + 1 rod bivalent.

enhance recombinations in the F_1 hybrids that involve the *Ph* system (Darvey 1984; Forster and Miller 1985; Mujeeb-Kazi et al. 1984; Sharma and Gill 1983a, 1983b, 1983c). The procedures could involve as maternal parents the use of (i) nulli-5B wheat stocks, (ii) mono-5B, or (iii) *PhPh* mutant, etc. in the production of F_1 hybrids. Though such hybrids have exhibited a high meiotic chromosome pairing frequency, obtaining backcross derivatives from them has been problematic. Forster and Miller (1985) obtained normal and 5B-deficient hybrids of *T. aestivum* – *A. junceum* (*Thinopyrum bessarabicum*). The pairing in the normal hybrid was similar to that observed for this combination in Table 4, while that in one 5B-deficient hybrid was 8.46 I + 1.71 II rings + 2.39 II rods + 2.54 III + 0.58 IV + 0.07 V, with VI and VII chromosomal exchanges observed in the second 5B-deficient hybrid. From both the 5B-deficient hybrids, backcross derivatives have not been obtained, thus offsetting the demonstrated recombination advantages.

Darvey (1984) suggested use of the *Ph-1* mutant in wide crosses for enhancing the recombination frequencies in F_1 hybrids and to effect direct gene transfers. This received a variable response from Sharma and Gill (1986). They hybridized several *Aegilops* species with the 'Chinese Spring' *PhPh* mutant stock and indeed observed high pairing in the hybrids. Backcross derivatives, however, could not be obtained and inference was made that the unreduced egg formation may have been adversely influenced by the *Ph* stock. The authors suggested additional studies for wider applications.

In alien genetic transfers so far, only rather simply inherited traits have been introgressed (Dewey 1984; Knott and Dvořák 1976) and the major impact has been from species of the *Thinopyrum* group. Transferring polygenically controlled characters that are presumably recessive in nature, such as disease resistance (*Fusarium graminearum* *Helminthosporium sativum*) or stress tolerance (salt, drought, or heat tolerance), appears too difficult to achieve if short-term projections are made. Alien diploids would appear to have high priority in effecting gene transfers even if these would be for quantitative traits. The arsenal a researcher has ranges from inducing F_1 recombinations, if such do not occur normally, to developing alien addition lines, alien substitution lines, and translocations. Where genes are located on more than one alien chromosome, each gene can be introduced into a separate wheat background prior to pyramiding these independently transferred genes into a single line or variety. Such seems to be the choice for the *T. aestivum* – *A. junceum* ($2x$) combination that has superb potential for salt tolerance. In production of addition lines, there is definitely an advantage in first producing a fertile amphiploid. This amphiploid when crossed with wheat will result in BCI derivatives where the alien genome should be quite intact. We have used the alternative F_1 –wheat route to produce BCI seed. This gives us the option of maximizing aneuploidy and structural change effects that may permit beneficial reorganization of otherwise separated genetic factors (Jewell and Mujeeb-Kazi 1982; Mujeeb-Kazi and Bernard 1982). Numerous translocations have been reported in triticale–wheat crosses (Lukaszewski and Gustafson 1982) and a similar situation can be anticipated in the BCI derivatives reported here.

Spike characterization, cloning, and colchicine treatment

The spike characteristics of the F_1 hybrids were indicative of definite morphological differences (Fig. 3) when compared with 'Chinese Spring' wheat (Table 5). Predominant differences were for increased spike length and a lax internodal distance.

The modified F_1 phenotype has been an initial selection sieve for hybrid advance for practical traits in our program. We associate this with alien genetic penetrance and expressivity that does not become as evident in certain hybrids, e.g., *T. aestivum* – *H. vulgare*. We are aware that an unmodified F_1 hybrid phenotype may still possess subtle biochemical component variations but are not convinced about the ultimate expression of these effects. A major modification in our curtailing emphasis on F_1 phenotypic selection would occur when the Yd_2 gene expressivity occurs in *T. aestivum* – *H. vulgare* advanced derivatives or in the earlier backcross generations.

Cloning is a physical process where tillers of a perennial F_1 hybrid plant are separated, producing smaller groups. On an average a healthy F_1 plant under greenhouse conditions will produce at least five plants upon subdividing every 6 months. The colchicine application technique is via root treatment mediated by the penetrant dimethylsulfoxide and the successful doubling criterion is manifested by seed set on an otherwise self-sterile hybrid. There is the probability of doubled sectors on a treated plant not expressing or of being transmitted meiotically without imparting fertility. Such a phenomenon observed in *H. vulgare* – *T. aestivum* and *T. aestivum* – *Aegilops variabilis* hybrids (A. Mujeeb-Kazi, unpublished) led to our curtailing cytological identification of doubling events and instead using the seed set observation as an index of successful amphiploid induction.

So far, the only fertile amphiploid resulting from this study is that of *T. aestivum* – *A. rechingeri*, where the C-0 seed possessed 70 chromosomes. From the hybrid combinations included in this paper, it has been for the independently produced *T. aestivum* – *A. junceum* (*T. bessarabicum*) hybrid that fertile amphiploids have been obtained (Alonso and Kimber 1980; Forster and Miller 1985). Mujeeb-Kazi and Bernard (1985a) obtained doubled C-0 seeds from a *T. aestivum* – *A. junceum-mediterranean* hybrid that possessed 84 chromosomes; however, doubling leading to seed formation for the currently reproduced hybrid was not obtained. The untreated F_1 hybrids have since been cloned and will be treated with colchicine with concentration and treatment time modifications.

Undoubtedly, amphiploids have several advantages even if their production is not too simplistic. For intergeneric hybridization research, amphiploids form a critical step leading to backcross I seed in which the wheat and alien genome compositions are expected to be quite intact. The present failure in obtaining fertile amphiploids has not thwarted the program advance, since by pollinating the self-sterile F_1 hybrids with *T. aestivum* backcross I progeny can be obtained. This process of BCI seed production is rapid but does not guarantee that the BCI progeny contain normal wheat and alien species genomes owing to the probability of wheat–wheat, wheat–alien, and alien–alien chromosomal translocations. The merits and demerits of such an approach shall be presented in the practicality paper to be published later. It has been generally accepted that the amphiploids as a new crop concept are restricted to \times *Triticum secale* Wittmack and perennial wheat derived from wheat–*Agropyron* with derivatives of the former showing considerable promise as a crop species. It may be worthwhile to consider another amphiploid crop concept where a highly complex growth condition restricts wheat production. Salinity is one such stress factor that prohibits normal wheat cultivation. Presumably the genetics is quite complex and alien genetic transfers may not be able to overcome the constraint. It has been suggested (C. N. Law, personal communication) that an amphiploid of wheat–salt-tolerant alien species may be a reasonable crop on salt-

TABLE 5. Mean spike characteristics of intergeneric hybrids of *Triticum aestivum* L. cv. Chinese Spring with some caespitosum *Agropyron* species

Alien source involved in intergeneric hybrid combination and F ₁ chromosome no.	Spike length (cm)	Spike width (cm)	Nodes/spike	Internode length (cm)	Spikelet length (cm)	Spikelet width (cm)	Spikelets/spike	Florets/spikelet	Glume body length (cm)	Glume awn length (cm)	Lemma body length (cm)	Lemma awn length (cm)	Anther length (cm)
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
<i>A. caespitosum</i> (<i>T. caespitosum</i>)	11.3	0.5	14.5	0.7	1.2	0.8	14.5	4.8	0.8	0	1.0	0	0.3
<i>A. curvifolium</i> (<i>T. curvifolium</i>)	10.3	0.7	17.0	0.6	1.5	0.6	17.0	6.5	0.9	0	0.9	0	0.4
<i>A. gentryi</i> (<i>T. gentryi</i>)	17.2	0.6	22.0	0.7	1.6	0.7	22.0	6.0	0.9	0	1.0	0.1	0.4
<i>A. junceum</i> (2x) (<i>T. bessarabicum</i>)	8.3	0.7	6.0	1.0	1.6	0.8	6.0	5.8	1.1	0	1.3	0.1	0.4
<i>A. junceum</i> (4x) (<i>T. junceiforme</i>)	11.2	0.6	13.0	0.9	1.6	1.0	12.5	5.7	1.0	0	1.8	0.2	0.4
<i>A. junceum</i> (6x) (<i>T. junceum</i>)	13.7	0.6	15.0	0.9	1.5	1.1	14.0	3.8	1.0	0	1.2	0	0.4
<i>A. podperae</i> (<i>T. podperae</i>)	9.8	0.6	14.0	0.6	1.3	0.5	14.0	5.6	0.8	0	0.9	0	0.4
<i>A. rechingeri</i> (<i>T. sartorii</i>) (= <i>rechingeri</i>)	9.8	0.7	9.0	1.1	1.7	1.1	9.0	7.0	1.1	0	1.2	0.2	0.3
<i>A. scirpeum</i> (<i>T. scirpeum</i>)	13.0	0.6	15.3	0.8	1.1	0.5	15.3	4.0	0.8	0	0.9	0	0.4
<i>A. scythicum</i> (<i>T. scythicum</i>)	10.3	0.6	11.0	0.9	1.3	0.6	11.0	4.1	0.9	0	1.0	0	0.3
<i>A. varnense</i> (<i>T. varnense</i>)	13.6	0.6	12.7	1.1	1.5	0.6	12.7	5.6	0.9	0	1.1	0	0.5

- stressed lands that prohibit a wheat crop. The *T. aestivum* – *A. junceum* (*T. bessarabicum*) hybrid and its amphiploid produced by Forster and Miller (1985) have demonstrated its salt-tolerant potential under controlled laboratory tests. A field test in a saline site is forthcoming, and it is feasible to explore the concept despite the disease-susceptible wheat cultivar in the amphiploids pedigree.
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