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Genome Relationships in Wheat × *Agropyron Distichum* (Thunb.) Beauv. Hybrids[1])

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With 4 figures and 7 tables

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Abstract

Bread wheat and durum wheat were crossed with South African coastal wheat grass, *A. distichum*, 2n = 28, to study their genome relationships and to transfer genes for salt-tolerance and high protein content from the latter species to the wheats. Crosses were made with 20 bread wheat and 15 durum lines, but only those with the two bread wheat cultivars, 'Chinese Spring' and 'Inia 66' and the two durum cultivars, 'Calvin' and 'Nordum' yielded hybrids when the embryo culture technique was applied. The F_1-plants were vigorous, but completely sterile. Meiotic analyses were made on Feulgen stained squashes of PMC's from the F_1, their amphiploids and back-crosses. In the 'Inia 66' × *A. distichum* hybrid (2n = 35) 11.2 chromosomes associated into bivalents and multivalents. In the 'Nordum' × *A. distichum* hybrid (2n = 28) 13.88 chromosomes associated into bivalents and multivalents. The PMC's of the ('Inia 66' × *A. distichum*) × 'Inia 66' BC_1-plants with 2n = 56 had a mean of 50.66 chromosomes associated into bivalents and multivalents and the plants were very fertile. These results indicate that *A. distichum* is probably a segmental allopolyploid with two similar genomes which have little homology with the wheat genomes. The kernels of the 'Inia 66' and 'Calvin' amphiploids had 21.3 and 19.9 per cent protein respectively.

Key words: *Agropyron distichum* — *Triticum*—*Agrotricum* — perennial wheat — interspecific hybrids — amphiploids — genome analysis — protein content — salt-tolerance — Weizen × *Agropyron*-Bastarde

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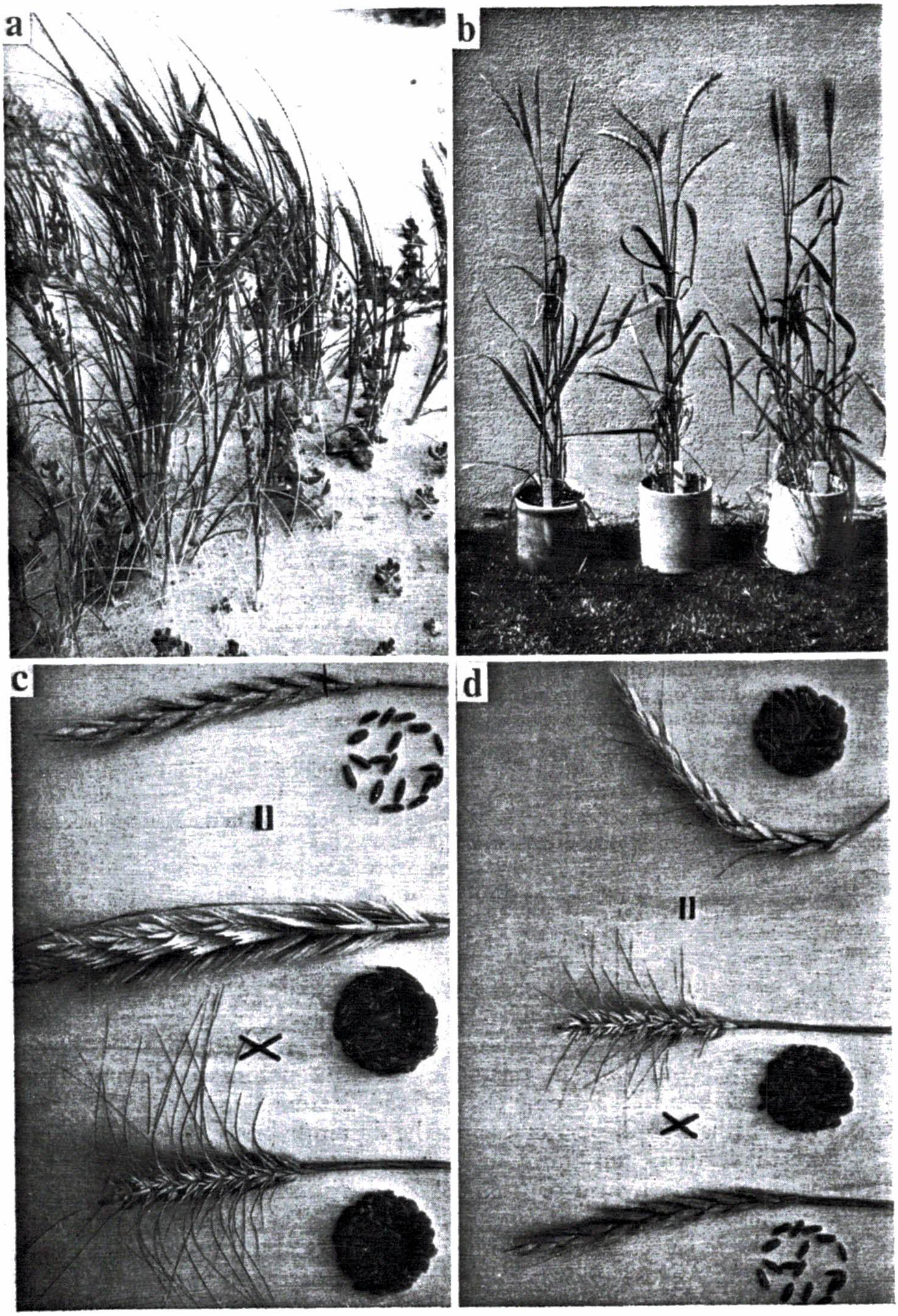
The first wheat × *Agropyron* hybrid was produced fifty years ago by N. V. TSITSIN in the U.S.S.R. (ARMSTRONG and MCLENNAN 1944, POPE and LOVE 1952). Since then many crosses between the different wheat and *Agropyron* species were made in various countries to produce perennial wheats and forage grasses, to incorporate genes for disease resistance, high protein content and other characteristics from *Agropyron* into commercial wheats, or for cytogenetic studies to determine chromosome homoeologies and genome and evolutionary relationships. Most of this work has been reviewed by AASE (1935, 1946), ARMSTRONG (1945), CAUDERON (1966 a, 1977, 1979), DEWEY (1977), DVOŘÁK and SOSULSKI (1974), ELLIOT (1957), KNOTT (1968), KNOTT and DVOŘÁK (1976), KNOTT et al. (1977), LACADENA (1977), LARSON and ATKINSON (1973), MORRIS and SEARS (1967), POPE and LOVE (1952), RILEY and KIMBER (1966), SCHULZ-SCHAEFFER and MCNEAL (1977), SEARS (1972, 1973, 1977), SINIGOVETS (1974), SMITH (1943), TSITSIN (1962), WANG and LIANG (1977), WHITE (1940), WIENHUES (1966, 1971, 1973), and ZELLER and FISCHBECK (1974). None of the crosses discussed included *Agropyron distichum* (Thunb.) Beauv.

A. distichum commonly known as coastal wheat grass or sea wheat, is indigenous to the Cape Province, South Africa, where it is limited to the south western, southern and eastern coast. It is a rhizomatous perennial which grows on sand dunes on the sea shore within the zone of constant salt spray and is occasionally inundated by spring high tides (*Fig. 1a*). It is a good stock grass, and a very efficient sand-binder. As such it is used in reclamation work. The spreading culms root from the lower nodes and then grow erect for 400—900 mm. It is juicy and contains a sweet sap. The glabrous, firm, blue-green leaves can be more than 400 mm long and are 5—7 mm wide. It flowers during November and early December and the 10 mm long spindly kernels ripen the end of January. The spikes are up to 250 mm long with the spikelets arranged singly, closely and alternately on either side of the thick, brittle axis with one surface facing the axis. The blue-green spikelets are 15—40 mm long, variously tinged with yellow and brown, and ellipsoid except at flowering time, when the florets open and the spikelets are more or less fan-shaped. They are strongly latterally compressed, hard, contain 5—12 closely packed florets and are almost entirely glabrous. The yellow-green anthers are 6—7.5 mm long (CHIPPINDALL and CROOK 1976—78). Its chromosome number is 2n=28 (PIENAAR 1955). The protein content of the kernels is 16 per cent (see *Table 5*).

Since the related species, *A. junceum* (L.) Beauv., has been successfully crossed with *T. turgidum* (ÖSTERGREN 1940) and *T. timopheevi* (WATANABE

Fig. 1 a. *Agropyron distichum* (Thunb.) Beauv. (2n = 28) growing on the beach just above the high tide level at the Strand, South Africa. b. From left to right: The amphiploid of *T. aestivum* var. *aestivum* cv 'Inia 66' × *A. distichum* (2n = 70); BC_1 ('Inia 66' × *A. distichum*) × 'Inia 66' (2n = 56); and 'Inia 66'. c. Spikes of 'Inia 66', *A. distichum* and their amphiploid (2n = 70). d. Spikes of the amphiploid from the cross 'Inia 66' × *A. distichum*; 'Inia 66'; and the back-cross ('Inia 66' × *A. distichum*) × 'Inia 66'. Note that the amphiploid is nearly awnless, but the spikes of the BC_1 plants have awns which are half as long as those of the wheat parent, 'Inia 66'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et al. 1960), the crosses between the tetraploid durum and hexaploid bread wheats with *A. distichum* were attempted to try and obtain salt-tolerant cereal and pasture plants with a high protein content.

All the initial wheat × *A. distichum* crosses failed, but in November 1976, the first successful cross was made with the hexaploid bread wheat cultivar, 'Chinese Spring' (PIENAAR et al. 1977).

Materials and Methods

'Chinese Spring' does not yield well in South Africa and a number of crosses were therefore made with 19 well adapted bread wheat (*T. aestivum* L. em. Thell. var. *aestivum*) and 15 durum (*T. turgidum* L. var. *durum* Desf. em. Bowden) cultivars and breeding lines using *A. distichum* from the Strand and the Gxulu river mouth, near East London, as pollen parents (*Table 1*). The kernels of the few successful crosses had underdeveloped endosperms 18 days after pollination and the embryos were therefore excised and cultured on sterile Difco Orchid Agar in McCartney bottles following the procedure of ROMMEL (1958). After the embryos had grown to the three leaf stage they were transplanted to pots in a growth chamber. The hybrid plants grew vigorously and were cloned. Some plants were saved for meiotic and fertility studies on the F_1-hybrids, the rest were amphiploidised with colchicine, using modifications of JENSEN's (1974) method.

The following colchicine treatment was the most successful: As soon as the cloned plants started to resprout at the basal nodes they were treated with 0.1 % colchicine in 2 % dimethyl sulphoxide (DMSO) for 24 hours in test tubes in a glasshouse at 20—25 °C. They were then rinsed with water and kept in water at 2 °C in a refrigerator for 24 hours, then transplanted into 2.5 liter pots, and placed in a dark room at 5 °C for 72 hours. These pots were then transferred to a growth chamber with a 10 hours light at 16 °C and 14 hours dark at 10 °C cycle for 2 months before placing them in a glasshouse.

The amphiploids obtained were back-crossed to their parents and allowed to self-pollinate.

Young spikes of the parents, the F_1-hybrids, the amphiploids and the BC_1-plants were fixed in 6 : 3 : 1 Carnoy's fixative for 24 hours and then stored in 70 per cent alcohol in the refrigerator. The pollen mother cells (PMC's) were stained according to the Feulgen procedure and squashed in 1 per cent Rosner aceto-carmine.

Results

The crossability of both the bread wheat and durum cultivars with *A. distichum* was very low (*Table 1*). Only 11 hybrid plants were obtained from pollinating 3 228 bread wheat florets with *A. distichum* — 10 from 'Chinese Spring' and 1 from 'Inia 66'. The 4 912 pollinated durum florets yielded only 5 hybrids, 3 from 'Calvin' and 2 from 'Nordum'. The bread wheat hybrids had 35 chromosomes and the durum hybrids 28.

Both the 'Calvin' and 'Nordum' F_1-hybrids with *A. distichum* were more vigorous than the F_1-hybrid of 'Inia 66' × *A. distichum*, and like the latter, had a perennial growth habit (*Figs. 1b* and *3a*). They produced numerous tillers with large errect leaves. The height of the 'Calvin' F_1-hybrid when it flowered during August 1979, was 970 mm, that of the 'Nordum' F_1-hybrid 1220 mm, compared to the 970 mm of the 'Inia 66' F_1-hybrid. Although 'Calvin', 'Nordum' and 'Inia 66' are awned cultivars, their hybrids with *A. disti-*

Tab. 1 Results of crossing (a) *T. aestivum* var. *aestivum* and (b) *T. turgidum* var. *durum* with *A. distichum*

Cultivar, line as ♀-parent	No. of florets pollinated	No. of kernels set		Kernel set (% pollinated florets)	Kernels with embryo	Successful embryo cultures	Mature plants obtained
		partly filled	shrivelled				
			(a) *T. aestivum* var. *aestivum* crosses				
'Chinese Spring'	272	14	0	5.1	14	10	10
'Inia 66'	92	1	0	1.1	1	1	1
18 add. lines	2864	0	0	0	0	0	0
Total	3228	15	0	0.5	15	11	11
			(b) *T. turgidum* var. *durum* crosses				
'Calvin'	698	3	13	2.3	3	3	3
'Cando'	770	2	0	0.3	2	0	0
'Nordum'	740	4	1	0.7	4	4	2
'D6654'	386	0	10	2.6	0	0	0
'D6962'	786	0	7	0.9	0	0	0
'7214-1-1-1-M'	118	0	2	1.7	0	0	0
9 add. lines	1414	0	0	0	0	0	0
Total	4912	9	33	0.9	9	7	5
Grand total	8140	24	33	0.7	24	18	16

chum differed in the expression of the awned trait; the spikes of the 'Calvin' and 'Nordum' F_1-hybrids had short awns on all spikelets, whereas those of the 'Inia 66' F_1-hybrid had tip awns only. The spikes of the 'Calvin'- and 'Nordum' F_1-hybrids were 180—190 mm long and contained 21 and 18 spikelets respectively; their respective spikelets possessed 8 and 6—7 florets. The 'Inia 66' F_1-hybrid had spikes which were 160—180 mm long and contained 17—20 spikelets, each of which possessed 5 florets. All the F_1-hybrids were completely selfsterile.

The chromosome associations in the PMC's at the first meiotic metaphase were determined in both the 'Inia 66'- and 'Nordum' F_1-hybrids. The data are given in *Table 2*. In the PMC's of the 'Inia 66' F_1-hybrid a mean of 11.2 of the 35 chromosomes associated in bivalents, trivalents and quadrivalents, and these associations had a mean chiasma frequency of 6.59 (*Fig. 2a*). As much as 31.6 per cent of the PMC's had 14 or more chromosomes associated in bivalents, trivalents and quadrivalents (Pienaar 1979). The 'Nordum' F_1-hybrid had a mean of 13.88 chromosomes per PMC associated in bivalents and multivalents by means of 9.17 chiasmata of which 9.08 were terminalised. As many as 55.5 per cent of the PMC's had 14 or more of the 28 chromosomes associated in bivalents and multivalents (*Fig. 3c*). This higher level of chromosome association in the 'Nordum' F_1-hybrid than in the 'Inia 66' F_1-hybrids was mainly due to the higher frequency of multivalents (Pienaar 1980b).

Tab. 2 Mean chromosome associations at first meiotic metaphase in the PMC's of (b) the F_1-hybrid of *T. aestivum* var. *aestivum* cv. 'Inia 66' × *A. distichum*, 2n = 35; and

No. of PMC's examined		Metaphase I chromosome associations			
		univalents	bivalents		
			rod	ring	total
(a)	200	14.12 (6—26)	3.55 (0—7)	1.26 (0—4)	4.81 (1—9)
(b)	300	23.78 (15—35)	4.05 (0—9)	0.06 (0—4)	4.65 (0—10)
(c)	100	5.34 (2—10)	6.77 (1—13)	17.88 (11—22)	24.76 (18—27)

The single 'Inia 66' × *A. distichum* F_1-plant obtained (*Table 1*), was cloned to produce 13 plants, 10 of which were treated with colchicine. Nine of the 10 plants had no fertile sectors, but one plant produced a spike with a few dehiscent anthers. It was decided to back-cross the spike to 'Inia 66', and 40 kernels were obtained which produced plants with chromosome numbers ranging from 52—56 (PIENAAR 1980 a); a plant with 69 chromosomes resulted from self-pollination. It is evident from the data in *Table 3 c* that the meiosis must have been irregular, since only 6 of the 38 back cross progeny had the expected chromosome number of 2n = 56. This was borne out by chromosome counts in the seedlings resulting from self-pollination, and a meiotic study of a few amphiploid PMC's — see below.

The C_1-tiller which produced the fertile spike was cut back after the spike was harvested, and repotted. It sprouted again and produced six partially fertile spikes, one of which was sacrificed for meiotic investigations. The other five spikes produced 26 kernels in 91 spikelets after self-pollination; 24 of these kernels germinated and the frequency distribution of the chromosome numbers of the C_2-seedlings is given in *Table 3 d*. The chromosome numbers ranged from 2n = 66—70; only one of the 24 seedlings had the complete amphiploid chromosome number of 2n = 70 (*Fig. 2 b*).

This new decaploid *Agrotricum* was 1 meter tall and produced spikes which were 150 mm long and contained up to 20 spikelets each (*Fig. 1 b* and *c*). Each spikelet had 5—6 florets. The spikes had a fairly strong rachis and except for very short tip awns, were awnless (*Fig. 1c*) — the awned spikes of 'Inia 66' is therefore recessive to the awnless spikes of *A. distichum*. The amphiploid had a perennial tendency and could be maintained by cloning. It had no vernalization or photoperiod requirement and flowered any time of the year, unlike *A. distichum* which flowers only during the latter part of November and early December.

The meiotic investigation of the partially fertile 'Inia 66' × *A. distichum* C_1-spike mentioned above, revealed that it was mixoploid — partly pentaploid and partly decaploid. Meiotic prophase in the decaploid PMC's appeared to be fairly normal, because the 7 PMC's observed at diakinesis had a mean bivalent frequency of 33.86 (range 33—35). Some bivalents, however, must have disjoined before metaphase I, since the mean univalent frequency per PMC at metaphase I, as deduced from the 20 scored cells at this stage, was

(a) the F_1-hybrid of *T. turgidum* var. *durum* cv. 'Nordum' × *A. distichum*, 2n = 28; *Tab. 2*
(c) the BC_1-hybrid (C_1: 'Inia 66' × *A. distichum*) × 'Inia 66', 2n = 56. Ranges in parentheses

Metaphase I chromosome associations multivalents				Chiasmata per PMC	
III	IV	V	VI	total	terminal
0.375 (0—2)	0.75 (0—2)	0.01 (0—1)	0.01 (0—1)	9.17 (1—14)	9.08 (1—14)
0.44 (0—2)	0.15 (0—1)	0	0	6.59 (0—12)	6.41 (0—12)
0.18 (0—2)	0.18 (0—2)	0	0	45.32 (37—51)	39.53 (27—49)

6.1 (range 2—10) (*Fig. 2 c*). In spite of this the anaphase I distribution appeared to be fairly regular — the mean distribution in 20 scored PMC's was 34.1—1—34.9. These findings do account for the chromosome numbers in the BC_1-progeny (*Table 3 c*) of which 35.13 per cent had 2n = 55 and 27.02 per cent 2n = 54, as well as in the C_2-progeny (*Table 3 d*) of which 41.67 per cent had 2n = 68. In order to produce a fully fertile amphiploid, selection for meiotic stability will have to be practiced in the subsequent generations as was done with triticale (ZILLINSKY and BORLAUG 1971).

The ('Inia 66' × *A. distichum*) × 'Inia 66' BC_1-plants with 2n = 56 were more vigorous than the amphiploid, grew 900—950 mm tall, had strong, erect culms, produced 5—6 primary spikes which were 150 mm long, and possessed 17—20 spikelets (*Figs. 1 b* and *d*). Each spikelet contained 5 florets which had 25—60 mm long awns; thus the awned trait was only very slightly suppressed in the BC_1-plants compared with the F_1-plants and amphiploids. The anthers were large and fully dehiscent. The plants were indeed very fertile and produced a mean of 229.8 kernels per plant; the thousand kernel mass was 55.2 g (*Table 4*). The kernels were well filled, vitreous, very much larger than those of 'Inia 66', and had a nice appearance. The biomass, grain

Tab. 3 **The frequency distribution of chromosome numbers in the progeny of (a) open-pollinated (with bread wheat) F_1-hybrids of 'Chinese Spring' × *A. distichum*, 2n = 35; (b) open-pollinated (with bread wheat) cloned F_1-hybrids of 'Inia 66' × *A. distichum*, 2n = 35; (c) C_1-spike of 'Inia 66' × *A. distichum*, 2n = 70, back-crossed to 'Inia 66'; and (d) C_1-plant of 'Inia 66' × *A. distichum* with 2n = 70 sectors, self-pollinated**

No. of (spikes) and spikelets pollinated			No. of kernels set	No. of kernels germinated	Number of progeny with chromosome number of													
					43	45	52	53	54	55	56	59	62	66	67	68	69	70
(a):	(14)	308	10	8	1	1	1	0	1	2	1	1	1	0	0	0	0	0
(b):	(82)	1432	2	2	0	0	0	0	0	0	1	0	0	0	0	1	0	0
(c)	(1)	17	40	38	0	0	3	5	10	13	6	0	0	0	0	0	1	0
(d)	(5)	91	26	24	0	0	0	0	0	0	0	0	0	1	7	10	5	1

Tab. 4 Seedset, yield, harvest index and thousand kernel mass grown in 2½ liter pots in a glasshouse (ranges

2n	No. of plants	Plants male-sterile	Biomass/pot	Grain yield/pot	Harvest index/pot (%)
52	3	2	23.8 (22.0—23.8)	6.07 (2.5—11.4)	26 (11—48)
53	5	4	25.4 (19.8—28.2)	2.32 (0—7.0)	9 (0—35)
54	10	4	25.5 (18.3—31.8)	6.95 (0.8—12.9)	27 (4—54)
54 + t	1	0	24.3	6.9	28
55	12	3	26.9 (24.5—30.9)	9.98 (0.9—15.2)	37 (3—50)
56	6	0	25.5 (23.5—26.9)	12.68 (10.6—13.5)	50 (45—53)
amphiploid 2n = 69	1	0	24.0	1.9	8
'Inia 66' 2n = 42	2	0	27.8 (27.0—28.5)	12.90 (12.7—13.1)	46 (44—46)

yield and harvest index of the BC_1-plants compared very well with those of 'Inia 66' (*Table 4*). The BC_1-plants flowered 10 days later than 'Inia 66'.

The aneuploid plants in the BC_1-generation were less fertile and yielded less than the euploid plants. This reduction in fertility and yield increased with the degree of aneuploidy. Many aneuploids were male sterile (*Table 4*).

The basis for the excellent fertility of the euploid BC_1-plants was sought in a meiotic analysis of their PMC's; the data are given in *Table 2c*. A mean of 50.66 of the 56 chromosomes associated into bivalents, trivalents and quadrivalents — 24.76 bivalents were produced, 0.18 trivalents and 0.18 quadrivalents (*Fig. 2d*). The PMC's had a mean of 5.34 univalents. In 47 per cent of the PMC's 4 univalents or less were observed; 17 per cent of the PMC's had only 2 univalents.

The cloned 'Calvin' and 'Nordum' F_1-hybrids with *A. distichum*, which were colchicine treated, yielded a number of C_1-plants, most of which had amphiploid sectors in one or more of the 17—19 spikes per plant that were produced during December, 1979. The spikes with the amphiploid sectors were partially or fully fertile and yielded up to 70 kernels per spike (*Fig. 3b*). The kernels were 10.5 mm long and had a 1000-kernel mass of 50.1 g. The height of the 'Calvin' and 'Nordum' derived C_1-plants were 1200 and 1260 mm respectively, and the spikes of both were up to 240 mm long (*Fig. 3b*). They contained 21 and 20 spikelets respectively. The spikelets of both had 9 florets. Unfortunately, none of the spikes sacrificed for meiotic investigations, had amphiploid sectors. A report on the meiosis of these octoploid amphiploids will have to stand over till a later date.

Some of the *durum* × *A. distichum* C_1-plants were irrigated with 50 per cent seawater and grew satisfactorily for three weeks, but then became chlorotic and had to be watered with fresh water for revival.

The kernels from the fertile sectors of the 'Calvin' × *A. distichum* C_1-plants, as well as those from the 'Inia 66' × *A. distichum* amphiploid, the ('Inia 66' × *A. distichum*) × 'Inia 66' BC_1-euploids, and all the parents were subjected to a micro-Kjeldahl analysis to determine their protein content.

of (C_1: 'Inia 66' × *A. distichum*) × 'Inia 66' BC_1-plants *Tab. 4*
in parentheses; mass is given in grams)

No. of spikes/pot	No. of spikelets/spike	No. of kernels/pot	No. of kernels/spike	1000 kernel mass
8 (7—10)	16.2 (15.6—16.5)	125 (36—263)	10.9 (3.6—37.6)	48.5 (43.3—69.4)
5.8 (5—7)	18.2 (16.3—19.7)	43.2 (1—131)	7.5 (0.2—26.2)	53.7 (23.5—65.4)
5.5 (4—9)	17.9 (15.8—19.0)	130 (12—273)	23.6 (2.0—54.6)	53.5 (44.3—66.7)
6	16.0	145	24.1	47.6
6.8 (5—9)	16.6 (13.1—18.8)	187.9 (13—308)	30.1 (2.6—42.2)	53.1 (44.6—71.4)
5.3 (5—6)	17.6 (16.7—18.6)	229.8 (188—254)	43.1 (37.6—50.8)	55.2 (50.6—59.5)
4	14.8	36	9	52.8
10.5 (9—12)	14.7 (14.1—15.6)	323.5 (294—353)	30.8 (29.4—32.7)	39.9 (35.9—44.6)

From the results given in *Table 5* it is evident that all the amphiploids as well as the BC_1-plants had excellent heterosis for protein content.

A number of new crosses, double crosses and back crosses were made during December 1979 with the 'Inia 66' × *A. distichum* amphiploid, its octoploid back-cross, the fertile amphiploid spikes on the C_1-plants derived from the 'Calvin' and 'Nordum' F_1-hybrids, and various cultivars of the parental species. The genomes of the parents, the amphiploids, and F_1- or BC-progeny, obtained from these crosses, are listed in *Table 6*. A very interesting set of genotypes are now available for breeding and cytogenic investigations.

Discussion

The chromosome associations in the PMC's at first meiotic metaphase of the F_1-hybrids given above are similar to those reported in other wheat × polyploid *Agropyron* hybrids by MATSUMURA and MURAMATSU (1956), ÖSTERGREN (1940), POPE and LOVE (1952), and WATANABE et al. (1960). It has been stated that *A. distichum* is closely related to the European species, *A. junceum* (CHIPPENDALL and CROOK 1975—1978), but they must differ cytogenetically,

Tab. 5 Protein analyses of *A. distichum*, *T. aestivum* cv. 'Inia 66', *T. durum* cv. 'Calvin' and their amphiploids with *A. distichum*.

Species, cultivar and hybrid	% N	% protein
1. *A. distichum* (2n = 28)	2.572	16.073
2. 'Inia 66' (2n = 42)	2.273	14.205
3. 'Inia 66' × *A. distichum* amphiploid (2n = 70)	3.430	21.349
4. BC_1: ('Inia 66' × *A. distichum*) × 'Inia 66' (2n = 56)	2.968	18.447
5. 'Calvin' (2n = 28)	2.197	13.415
6. 'Calvin' × *A. distichum* amphiploid (2n = 56)	3.194	19.965

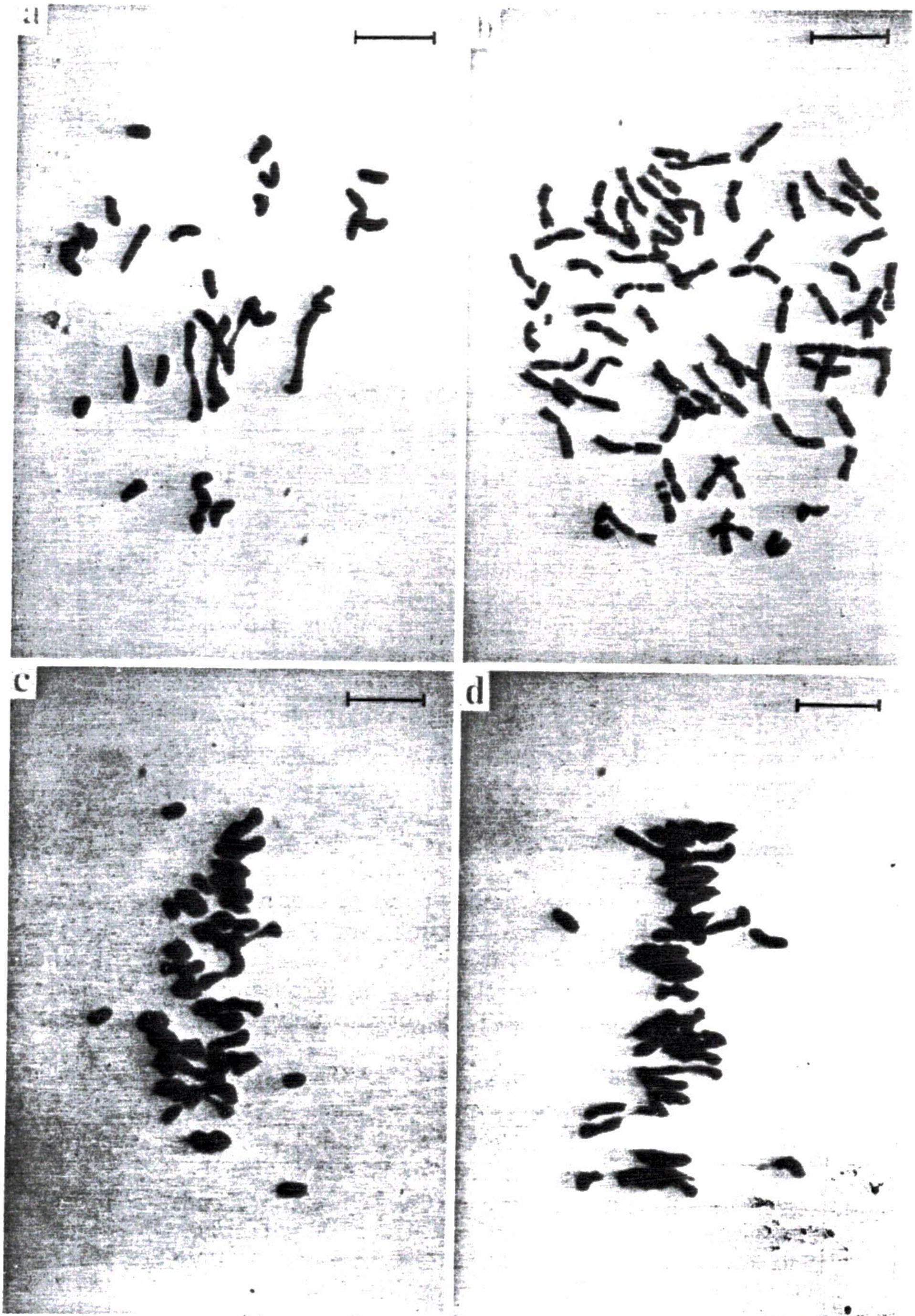

Fig. 2 a. A Feulgen squash preparation of a PMC at first meiotic metaphase from the F_1 of the cross *T. aestivum* var. *aestivum* cv. 'Inia 66' × *A. distichum* ($2n = 35$) showing 1 trivalent, 4 rod bivalents and 24 univalents. b. A Feulgen squash preparation of a root tip cell

Tab. 6 Successful wheat crosses which contain *A. distichum* germplasm, made to date

♀-parent, 2n, and genome formula	♂-parent, 2n, and genome formula	Progeny, 2n, and genome formula
1. *T. durum* (2n = 28) AABB	*A. distichum* (2n = 28) $X_1X_1X_2X_2$	Amphiploid-1 (2n = 56) $AABBX_1X_1X_2X_2$
2. *T. durum* (2n = 28) AABB	Amphiploid-1 (2n = 56) $AABBX_1X_1X_2X_2$	BC_1-I (2n = 42) $AABBX_1X_2$
3. Amphiploid-1 (2n = 56) $AABBX_1X_1X_2X_2$	*T. durum* (2n = 28) AABB	BC_1-II (2n = 42) $AABBX_1X_2$
4. *A. distichum* (2n = 28) $X_1X_1X_2X_2$	Amphiploid-1 (2n = 56) $AABBX_1X_1X_2X_2$	BC_1-III (2n = 42) $ABX_1X_1X_2X_2$
5. *T. aestivum* (2n = 42) AABBDD	*A. distichum* (2n = 28) $X_1X_1X_2X_2$	Amphiploid-2 (2n = 70) $AABBDDX_1X_1X_2X_2$
6. *T. aestivum* (2n = 42) AABBDD	Amphiploid-2 (2n = 70) $AABBDDX_1X_1X_2X_2$	BC_1-IV (2n = 56) $AABBDDX_1X_2$
7. Amphiploid-2 (2n = 70) $AABBDDX_1X_1X_2X_2$	*T. aestivum* (2n = 42) AABBDD	BC_1-V (2n = 56) $AABBDDX_1X_2$
8. *T. aestivum* (2n = 42) AABBDD	Amphiploid-1 (2n = 56) $AABBX_1X_1X_2X_2$	F_1-I (2n = 49) $AABBDX_1X_2$
9. Amphiploid-1 (2n = 56) $AABBX_1X_1X_2X_2$	Amphiploid-2 (2n = 70) $AABBDDX_1X_1X_2X_2$	F_1-II (2n = 63) $AABBDX_1X_1X_2X_2$
10. Amphiploid-2 (2n = 70) $AABBDDX_1X_1X_2X_2$	Amphiploid-1 (2n = 56) $AABBX_1X_1X_2X_2$	F_1-III (2n = 63) $AABBDX_1X_1X_2X_2$
11. BC_1-IV (2n = 56) $AABBDDX_1X_2$	*T. durum* (2n = 28) AABB	F_1-IV (2n = 42) $AABBDX_{1-2}$
12. *T. durum* (2n = 28) AABB	BC_1-IV (2n = 56) $AABBDDX_1X_2$	F_1-V (2n = 42) $AABBDX_{1-2}$
13. BC_1-IV (2n = 56) $AABBDDX_1X_2$	Amphiploid-1 (2n = 56) $AABBX_1X_1X_2X_2$	F_1-VI (2n = 56) $AABBDX_1X_2X_{1-2}$

because the hybrids of the latter species with *T. turgidum* and *T. timopheevi* had more univalents (18.4 and 20.28 respectively) and less multivalents (0 and 0.72 respectively) (Östergren 1940, Watanabe et al. 1960), than the *T. durum* × *A. distichum* F$_1$-hybrids which had 14.12 univalents and 1.15 multivalents. Further investigations are under way to determine the cyto-

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of the 'Inia 66' × *A. distichum* C_1-amphiploid (2n = 70) at mitotic metaphase after 30 hours in ice water (± 1 °C). c. A Feulgen squash preparation of a PMC at first meiotic metaphase from the 'Inia 66' × *A. distichum* C_1-amphiploid (2n = 70) showing 1 quadrivalent, 30 bivalents and 6 univalents. d. A Feulgen squash preparation of a PMC at first meiotic metaphase from a ('Inia 66' × *A. distichum*) × 'Inia 66' BC_1-plant (2n = 56) showing 1 quadrivalent, 25 bivalents and 2 univalents. (The bar in all photomicrographs is 10 μm long)

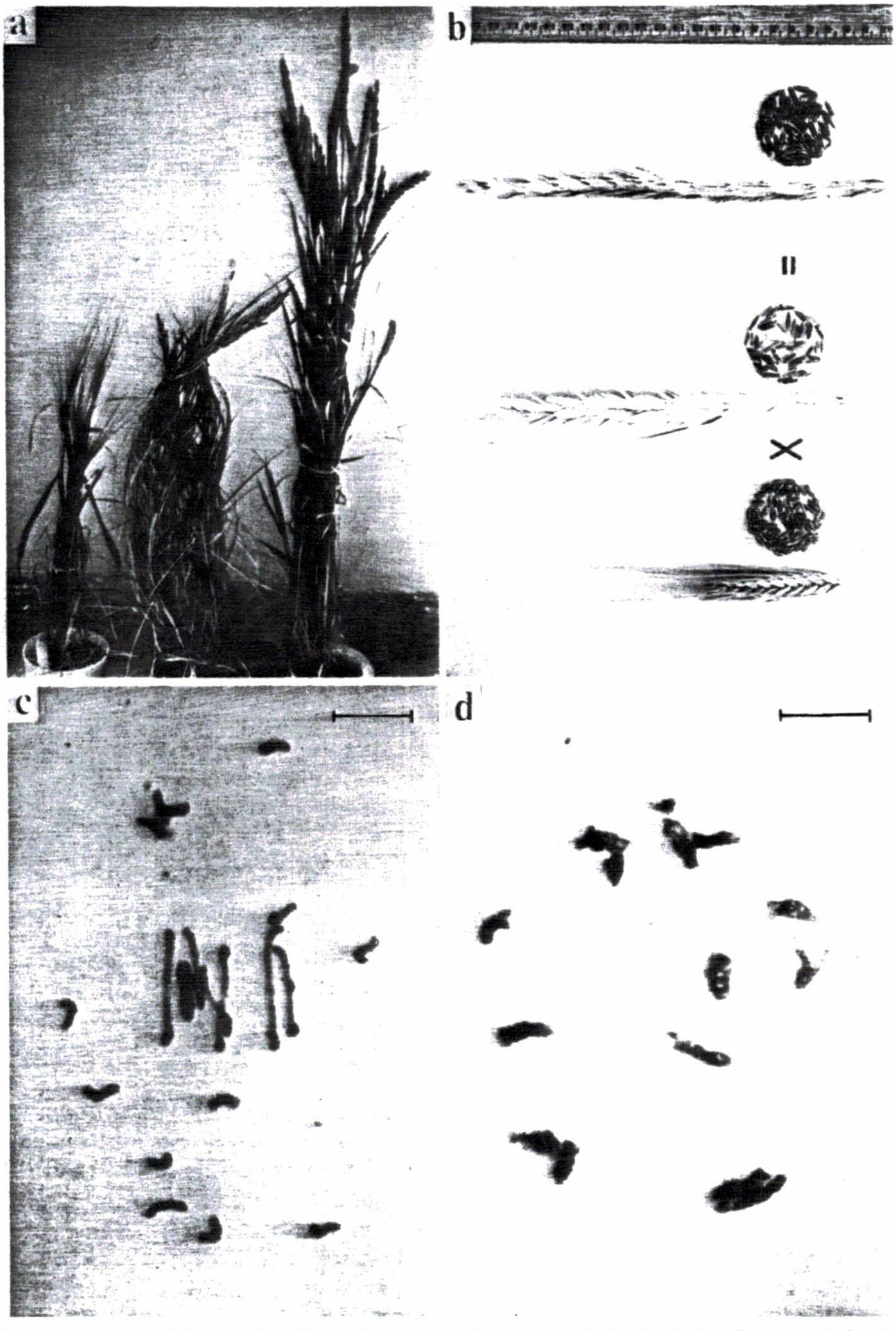


Fig. 3 a. From left to right: *T. turgidum* var. *durum* cv. 'Calvin', *A.distichum*, and the F$_1$-hybrid 'Calvin' × *A. distichum* (2n = 28). b. Spikes and kernels of *T. turgidum* var. *durum* cv. 'Calvin' (left), *A. distichum* (centre) and a fertile C$_1$- spike from their colchicine treated F$_1$-hybrid. c. A Feulgen squash preparation of a PMC at first meiotic metaphase from the 'Nordum' × *A. distichum* F$_1$-hybrid (2n = 28) showing 1 quadrivalent, 5 bivalents and 14 univalents. d. A Feulgen squash preparation of an *A. distichum* PMC at diakinesis with 14 bivalents, some of which show secondary pairing

genetic relationship between *A. distichum* and *A. junceum*. Plants of both diploid (2n = 14) and tetraploid (2n = 28) *A. junceum* lines grown from seed received from Dr. D. R. Dewey, Logan, Utah, are morphologically quite unlike the *A. distichum* plants grown under the same environmental conditions, and flowered later than the latter species.

Tab. 7 Chromosome pairing in *T. aestivum* cv. *aestivum* polyhaploids. Cultivar of polyhaploid (2n = 21) investigated: 'Chinese Spring'

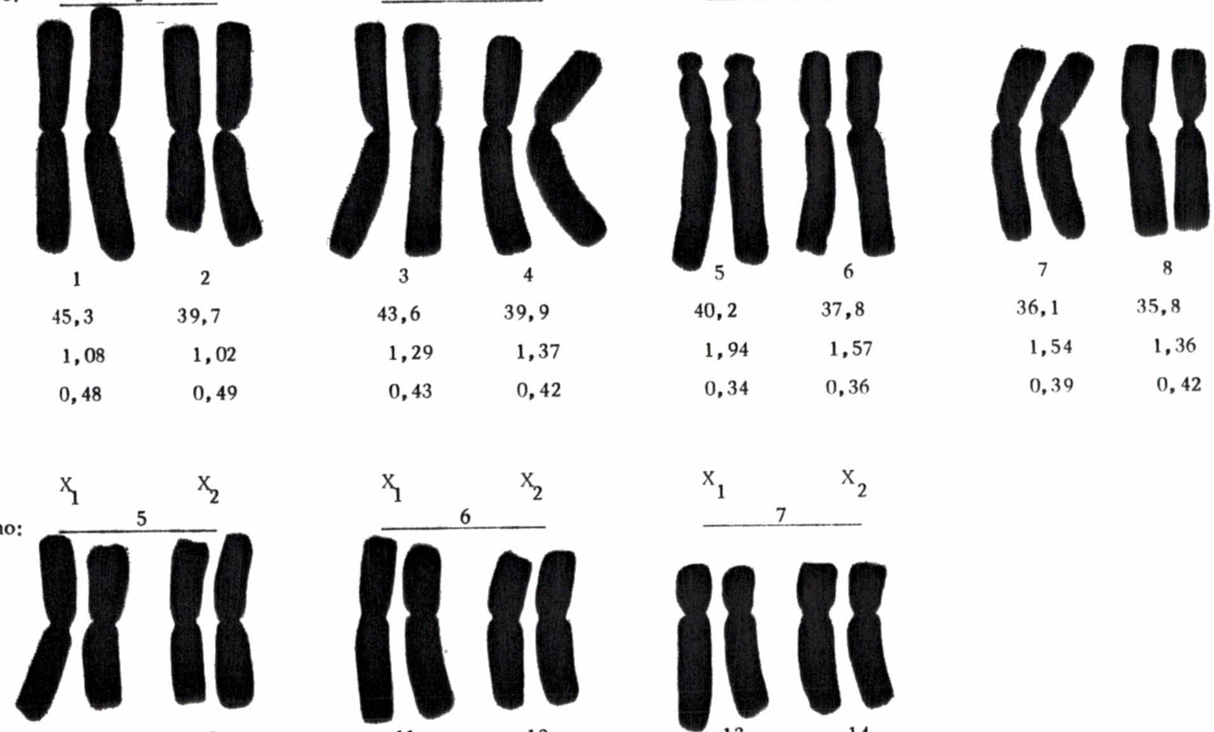
No. PMC's examined	Mean metaphase I chromosome associations (ranges in parentheses)					Author
	univalents	bivalents			III	
		rod	ring	total		
?	20.8 (19—21)	0.1 (0—1)	—	0.1 (0—1)	—	Miller and Riley (1972)
400	19.7	0.89	0.01	0.9	0.01	Kimber and Riley (1963)
240	20.52 (17—21)			0.24 (0—2)	—	Martin and Chapman (1977)

When the high levels of chromosome association in the 'Inia 66' × *A. distichum* and 'Nordum' × *A. distichum* F_1 are compared with the meiotic associations found in polyhaploid wheat (*Table 7*), it is evident that in the hybrids only one or two bivalents may result from the autosyndetic associations of the wheat chromosomes. The high incidence of associated chromosomes in the hybrids which leads to some kernel set on open pollination with wheat (*Table 3*) must therefore be due to one or more of the following:

a) The tetra- and hexaploid wheats have one genome in common with *A. distichum*, or the homoeology of many chromosomes of *A. distichum* and the two wheat species are so close that allosyndetic associations occur readily. McFadden and Sears (1946, 1947) considered one of the *Agropyron* species, viz. *A. triticeum*, as a candidate for the donor of the B-genome of wheat. Although they subsequently proved that this was not the case, it did not rule out the possibility that a polyploid *Agropyron* species may have a genome in common with wheat.

b) *A. distichum* is an autotetraploid or segmental-allopolyploid and as such its two genomes are able to produce autosyndetic associations in the hybrids. It is known from the investigations of Cauderon (1966b), Dewey (1977), and Schulz-Schaeffer and Allderdice (1966) that some *Agropyron* species are indeed auto-allopolyploids or segmental-allopolyploids.

c) The *A. distichum* genotype like those of *T. speltoides* (*Aegilops speltoides*), *T. tripsacoides* (*Ae. mutica*) and *Hordeum vulgare* suppresses the diploidising activity of the *Ph* gene in chromosome 5B of hexaploid wheat (Riley 1966, Riley and Kimber 1966, Fedak 1977), with the result that in its hybrids with wheat a number of allo- and autosyndetic associations can take place between the homoeologues of the four or five genomes.



Genome:	X_1	X_2	X_1	X_2	X_1	X_2	X_1	X_2
Homoeologous group no:	1		2		3		4	
Homologous pair no:	1	2	3	4	5	6	7	8
Relative length:	45,3	39,7	43,6	39,9	40,2	37,8	36,1	35,8
Arm ratio:	1,08	1,02	1,29	1,37	1,94	1,57	1,54	1,36
Centromere index:	0,48	0,49	0,43	0,42	0,34	0,36	0,39	0,42

Genome:	X_1	X_2	X_1	X_2	X_1	X_2
Homoeologous group no:	5		6		7	
Homologous pair no:	9	10	11	12	13	14
Relative length:	32,1	31,1	33,1	28,7	29,9	26,9
Arm ratio:	1,18	1,02	1,42	1,44	2,39	2,06
Centromere index:	0,46	0,49	0,41	0,41	0,29	0,33

Fig. 4 Karyotype and quantitative characteristics of the chromosomes of *Agropyron distichum* (Thunb.) Beauv. The two genomes are arbitrarily named X_1 and X_2

Investigations to determine which of the above alternatives is operative in the wheat × *A. distichum* hybrids, were therefore conducted.

Hybrids between *A. distichum* and the donors of the A- and B-genomes of wheat were as yet not possible, and the homology of the two *A. distichum* genomes with either the A- or B-genomes could not be determined. The chromosomes of the D-genome of wheat probably do not pair with those of *A. distichum* as less chromosomes were associated in the 'Inia 66' F_1-hybrid than in the 'Nordum' F_1-hybrid — a mean of 11.2 against 13.88 chromosomes.

It is also not yet possible to comment on the effect of the *Ph* gene or other "pairing" genes of wheat, on homoeologous pairing of the two *A. distichum* genomes; or vice versa, on the possible suppression of the diploidising genes in wheat by the genomes of *A. distichum*. Experiments are conducted to investigate this genetic system in the hybrids.

A conventional karyotype analysis of *A. distichum* revealed that the 28 somatic chromosomes can be arranged in 7 groups of 4 similar chromosomes (*Fig. 4*). However, the two pairs of chromosomes in each "homoeologous" group of 4 differ slightly in length, arm ratio, and centromere index. It is therefore unlikely that *A. distichum* is an autotetraploid. Karyotype analyses by means of the chromosome banding techniques are now under way to help solve this question. Meiotic investigations of *A. distichum*, however, revealed that 14 bivalents are regularly formed, with some secondary pairing (*Fig. 3 d*). This again is inconsistent with a hypothesis that *A. distichum* is an autopolyploid, but does not negate segmental-allopolyploidy.

Since dihaploid *A. distichum* plants with $2n = 14$ are not yet available to help solve the problem, a thorough meiotic comparison was made between the 'Inia 66' × *A. distichum* F_1-hybrid, its amphiploid and the back-cross of the amphiploid to 'Inia 66' (*Table 2 b* and *c*; *Figs. 1 b, c, d*). The few univalents (mean of 5.34) in the BC_1-plants with $2n = 56$, which contain 3 pairs of wheat genomes, and two *Agropyron* genomes, must be due to the fact that most of the homoeologues of the two *A. distichum* genomes are able to pair and form chiasmatic associations. The high frequency of chromosome associations in the PMC's of the 'Inia 66'- and 'Nordum' F_1-hybrids with *A. distichum* must likewise result from the autosyndetic pairing of the two *Agropyron* genomes. The large number of PMC's with multivalents in both the F_1-hybrids and the BC_1-plants, however, indicates that the two genomes of *A. distichum*, although very similar, differ from each other in certain chromosome segments due to at least two reciprocal translocations.

From the available evidence, it can only be deduced that *A. distichum* is a segmental allopolyploid. If the two genomes of *A. distichum* are arbitrarily named X_1 and X_2, then the genome constitution of this species is $X_1X_1X_2X_2$; that of its amphiploid with 'Inia 66', $AABBDDX_1X_1X_2X_2$; and that of the BC_1-plants, $AABBDDX_1X_2$. In the F_2 and later generations of these BC_1-plants, it should be possible to select true breeding, and fully fertile genotypes which have regular meioses with 28 bivalents and the genomic constitution $AABBDDX_1X_1$, $AABBDDX_2X_2$ or $AABBDDX_{1-2}X_{1-2}$ — the latter's genomes consisting partly of X_1 and partly of X_2 chromosomes, analogous to

'Armadillo' triticale in which the third genome consists partly of rye chromosomes and partly of D-genome chromosomes of wheat (GUSTAFSON and ZILLINSKY 1973). The plants with these genotypes may have agronomic potential in the sandy soils along the coast, as well as in saline soils, and may also be used in conventional wheat breeding programmes to improve certain traits, e.g. protein content (see below).

The meiotic investigations revealed that 16 or more chromosomes produced chiasmatic associations in 12.3 per cent of the PMC's of the 'Inia 66' F_1-hybrid and 31.5 per cent of the PMC's of the 'Nordum' F_1-hybrid. In the event that all 14 *A. distichum* chromosomes took part in these associations, the extra chromosomes involved were wheat chromosomes. These wheat chromosomes either associated autosyndetically to produce one or two bivalents as in wheat polyhaploids (see above) or allosyndetically with the *A. distichum* homoeologous to produce multivalents. If the latter alternative produced the extra associations observed, it will be possible to transfer genes from the *A. distichum* chromosomes to their wheat homoeologues by meiotic crossing-over.

The fewer chromosome associations in the 'Inia 66' F_1-hybrid than in the 'Nordum' F_1-hybrid must be due to the suppression of chromosome pairing by the D-genome. It has indeed been shown by MELLO-SAMPAYO and CANAS (1973), RILEY et al. (1973) and ATTIA et al. (1977) that chromosomes 3D and 5D also regulates chromosome pairing. They have shown that chromosome 3D suppresses homoeologous chromosome pairing.

The addition of the *A. distichum* genomes to those of bread- and durum wheat increased the protein content of the grain considerably (*Table 5*). Little is known about the nature of the increased protein content in wheat having *Agropyron* chromosomes. DVOŘÁK and SOSULSKI (1974) showed that five of the seven *A. elongatum* chromosomes individually added to the chromosome complement of the bread wheat 'Chinese Spring' significantly increased the grain protein content. Recently SOLIMAN et al. (1980) studying an *Agropyron* chromosome containing a gene causing blue colour in the aleurone layer of the grain endosperm, likewise found that the addition of this chromosome to the bread wheat complement produced a 15 per cent increase in total grain protein content. However, a substitution of part of this chromosome for a wheat chromosome had no effect on total protein content. In contrast LAW et al. (1977) found that the substitution of chromosome 2M from *T. comosum* for 2D in 'Chinese Spring' gave higher protein amounts than 'Chinese Spring'. They were able to rank the chromosomes of this homoeologous group in terms of their ability to produce protein as follows: $2A > 2M \geqslant 2B > 2C^u \geqslant 2D > 2R$. It may therefore be possible to obtain fertile hexaploid and octoploid derivatives from the durum-*A. distichum* and bread wheat-*A. distichum* back-crosses respectively which will have a high grain protein content. Furthermore, by crossing this material with wheat monosomics new substitution lines can be produced which may be useful in increasing the genetic variation for protein content and quality in wheat. Genes for other beneficial traits

such as salt-tolerance, the ability to grow in very sandy soils, large kernels, etc., can similarly be transferred from *A. distichum* to wheat.

Zusammenfassung

Genomanalyse bei Bastarden zwischen Weizen und *Agropyron distichum* (Thunb.) Beauv.

Zwei Brotweizensorten, 'Chinese Spring' und 'Inia 66', wie auch zwei Durum-Sorten, 'Calvin' und 'Nordum', wurden mit der südafrikanischen Küstenquecke *Agropyron distichum* ($2n = 28$) erfolgreich gekreuzt. Alle F_1-Bastarde waren völlig steril. Bei dem 'Inia 66' × *A. distichum*-Bastard ($2n=35$) vereinigten sich durchschnittlich 11,2 Chromosomen je PMZ zu Bivalenten, Trivalenten und Quadrivalenten mittels 6,59 Chiasmen. In den PMZ der 'Nordum' × *A. distichum*-Hybride ($2n = 28$) vereinigten sich 13,88 Chromosomen zu Bivalenten, Trivalenten und Quadrivalenten bei einer Chiasmenfrequenz von 9,17.

Der 'Inia 66'-Bastard wurde erfolgreich durch Colchicinbehandlung amphiploidisiert und an fünf C_1-Ähren wurden insgesamt 26 Samen erhalten. Die Rückkreuzung einer C_1-Ähre mit 'Inia 66' ergab 40 Samen, sechs davon lieferten Pflanzen mit $2n = 56$, die übrigen waren aneuploid. In den PMZ der R_1F_1-Pflanzen mit $2n = 56$-Chromosomen waren im Mittel 50,66 Chromosomen zu Bivalenten, Trivalenten und Quadrivalenten vereinigt. Alle diese Pflanzen waren voll fertil. Diese Ergebnisse deuten darauf hin, daß die zwei Genome von *A. distichum*, willkürlich X_1 und X_2 genannt, sich sehr ähnlich sind. *A. distichum* ist wahrscheinlich eine Segment-Allopolyploide.

Bei den Amphiploiden aus den Kreuzungen 'Inia 66' × *A. distichum* und 'Calvin' × *A. distichum* erreichte der Proteingehalt der Samen 21,3 % bzw. 19,9 %.

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