HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOLUME 21 MAY, 1952 NUMBER 15

COMPARATIVE CYTOLOGY OF COLCHICINE-INDUCED AMPHIDIPLOIDS OF INTERSPECIFIC HYBRIDS:

AGROPYRON TRICHOPHORUM x *TRITICUM DURUM*, *T. TIMOPHEEVI* and *T. MACHA*

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This paper presents a detailed comparison of meiotic chromosome behavior in sterile hybrids and in their relatively fertile, colchicine-induced amphidiploids. An analysis of the hybrid Agropyron trichophorum x Triticum is reported for the first time.

Results indicate that two factors are involved in these interspecific crosses: genic suppression of chromosome pairing in the hybrid and its amphidiploid; and disharmonious interaction of genes controlling the same cell processes in Triticum and Agropyron, resulting in failure of complete amphidiploid meiotic pairing.

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WARREN K. POPE[2] and R. MERTON LOVE[3]

THE *Triticum* x *Agropyron* combinations have attracted widespread attention since 1933, when N. V. Tzitzin in the U.S.S.R. reported success in the crossing of these two genera.

By contrast with the *Triticum* species, *Agropyron* species are usually perennial, often rhizomatous, and generally show greater resistance to disease. Each of these characters has potential practical value in the production of forage grasses with larger seeds and perennial wheats, and in the incorporation of disease resistance or other *Agropyron* characteristics into commercial wheats. McFadden and Sears (1947) postulated that the B genome of wheat originates in *Agropyron.* They therefore suggest the use of *Agropyron* species to improve the B genome.

The plants reported in this paper are descended from a group of *Triticum* x *Agropyron* hybrids made by W. J. Sando, Beltsville, Maryland, in 1937. Among the small progeny obtained from the F_1 hybrids, Love and Suneson (1945) found a few plants which had great vigor and partial fertility along with unexpected chromosome numbers and arrangements. Results of the earlier study prompted the present cytological study of colchicine-induced amphidiploids.

REVIEW OF LITERATURE

Hillman (1910) attempted hybridization of *Triticum vulgare* Vill. x *Agropyron repens* Beauv., but Percival (1921) considered the results doubtful. In 1914 and 1922 McFadden (1934) unsuccessfully attempted crosses of both *T. vulgare* and *T. durum* Desf. with *A. repens* and the North American species *A. tenerum, A. spicatum,* and *A. smithii.* In 1929, however, he succeeded in

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obtaining two plants which died as seedlings from the cross *T. vulgare* var. Buffum with an "off-type form" of *A. repens.*

The first apparently successful *Triticum* × *Agropyron* cross was made in 1930 in the North Caucasus, U.S.S.R., by N. V. Tzitzin (1933), who used *Triticum vulgare* var. Lutescens 062 × *Agropyron glaucum* Desf. (*A. intermedium* (Host) Beauv.). He reported success with many additional hybrids of *A. glaucum, A. elongatum* (Host) Beauv., *A. trichophorum* (Link) Richt., and *A. junceum* (L.) Beauv. There followed a series of technical and popular papers elaborating on these and other hybrids (Tzitzin 1935, 1936*a*, 1936*b*, 1937*a*, 1940*a*, 1940*b*), including a collection of papers edited by Tzitzin (1937*b*).

With this stimulus from the U.S.S.R., *Triticum* × *Agropyron* hybridization was undertaken in Canada (Armstrong, 1936); the United States (Vinall and Hein, 1937; Smith, 1942, 1943*a*); Australia (Raw, 1939); South Africa (Armstrong and Stevenson, 1947); Germany (Black and Driver, 1946); and Italy (Giovannelli, 1947; Rutti, 1948).

Peto (1936) and Vakar (1935) were, like most workers in the field, interested in the phylogenetic relationship of the *Agropyron* × *Triticum* combinations used.

Among the many attempted hybrids, only three or four *Agropyron* species—*A. elongatum, A. glaucum,* (*A. intermedium*), *A. trichophorum,* and possibly *A. junceum*—have been found to cross readily with the tetraploid and hexaploid *Triticum* species. These crossing relationships have been emphasized by Johnson (1938), White (1940), and Myers (1947). Other more generalized reviews have been made by Smith (1942, 1943*a*, 1943*b*), Armstrong (1945), and Aase (1946).

Hybrids with *Agropyron elongatum* and *A. glaucum* have been extensively reviewed, but only brief mention has been made in the Canadian and Russian literature of hybrids involving *A. trichophorum,* and in many cases the plants obtained were not carried beyond the sterile F_1 generation.

Tzitzin (1933) reported that in a cross of a spring type *Triticum vulgare* × *Agropyron trichophorum,* 148 seeds set on 574 florets pollinated. *T. durum* × *A. trichophorum* produced 2 seeds from 96 florets pollinated. No further mention was made of these plants. Veruschkine (1935*b*) noted that wheat backcrosses on *A. trichophorum* hybrids produced progressively fewer perennial forms. Nemlienko (1939) at the Rostov station found greater viability and more seeds set in crosses of *A. trichophorum* and *A. glaucum* with *T. durum* than with *T. vulgare.* The same observation had been made by Artemova (1935), who reported wide segregation in the second generation from *A. intermedium* and *A. trichophorum.* Fifty per cent of the F_2, but only 5 per cent of the F_3, were perennial.

White (1940) reported the first Canadian crosses with *Agropyron trichophorum.* "In crosses between *Triticum* spp. × *A. trichophorum,* 2.4 per cent of the 411 florets pollinated set seed." Armstrong (1945) and Armstrong and Stevenson (1947) mentioned that, although these initial crosses with *A. trichophorum* were successful, the F_1 plants were quite sterile and no advanced generation lines were continued.

Smith (1942) obtained 76 seeds, which produced 16 plants, from 1,128 common wheat florets pollinated with *Agropyron trichophorum.* In further crosses of *Triticum durum* × *A. trichophorum,* Smith (1943*a*) obtained 384 seeds from 937 florets pollinated. In additional common wheat crosses, 130 seeds were produced on 516 florets pollinated.

At Davis, California, F_1 hybrids and their derivatives from *Agropyron trichophorum* crosses with *Triticum durum, T. macha* Dek. and Men., *T. timopheevi* Zhuk., and *T. persicum* Vav. have been under observation since 1938 (Love and Suneson, 1945; Suneson and Pope, 1946). Agronomic characters of a few of these same derivatives have been reported by Reitz, Johnston, and Anderson (1945).

MATERIALS AND METHODS

The plants under investigation were the F_1 hybrids and their derivatives of the following three combinations: *Triticum durum* Desf. var. Mindum ($2n = 28$) × *Agropyron trichophorum* (Link) Richt. ($2n = 42$); *T. timopheevi* Zhuk. ($2n = 28$) × *A. trichophorum;* and *T. macha* Dek. and Men. ($2n = 42$) × *A. trichophorum.*

Amphidiploids of each F_1 hybrid were secured by immersing the entire roots and crowns of small slips in a 0.2 to 0.4 per cent aqueous solution of colchicine for 8 to 48 hours.

All chromosome examinations were made from acetocarmine smears by the method suggested by Love (1940). Photomicrographs were made at magnifications of × 580. Plate 1 shows them at × 440.

THE F_1 HYBRIDS

Fertility. For the period 1939 to 1944 Love and Suneson (1945) found a total of only 41 seeds on the F_1 hybrids. In 1945 a total of 85 seeds was found. The *Triticum durum, T. macha,* and *T. timopheevi* hybrids produced respectively 76 seeds on 1,770 spikes, 4 seeds on 925 spikes, and 5 seeds on 2,000 spikes. The seeds were all similar in having a conspicuous brush, a pointed, exposed germ, and wide, angular cheeks. They varied from shriveled to plump in size, and from 6 mm to 9 mm in length. All seeds were red except for 10 gray seeds found on the *T. durum* hybrids.

Chromosome Analysis. Love and Suneson (1945) made a complete cytological analysis of 50 PMC of each of the *Triticum durum* hybrids, 37306–1 and –2, and the *T. macha* hybrid 37308–2. These are included in table 1 for comparison with the amphidiploids. The *T. macha* hybrid, 37308–2, was unique in having only 41 instead of the expected 42 chromosomes. Its sib hybrid, 37308–3, did have the expected 42 chromosomes but did not otherwise differ in pairing behavior.

The hybrid of *Triticum timopheevi* × *Agropyron trichophorum,* 37307, was not previously reported. An analysis of 100 PMC (table 1) showed the expected 35 chromosomes, with an average of 4.9 bivalents (range 1 to 9), and an average of 10.8 chromosomes synapsed (range 2 to 21). There were no chains of 4, but 30 per cent of the PMC averaged one trivalent. In general, the pairing was intermediate between that of the hybrids involving *T. durum* and *T. macha.*

AMPHIDIPLOID F_1 PLANTS

The colchicine-induced amphidiploid sectors of the F_1 plants were isolated from the diploid tissue by two vegetative subdivisions. Plants developing from colchicine-treated slips were morphologically indistinguishable from untreated plants except for an occasional fertile or nearly fertile head, which was regarded as an indication of amphidiploidy.

Each undoubled F_1 hybrid was approximately intermediate between its parents in a total of 33 morphological characters in which the parents differed strikingly. The $4n$ plants of the *T. timopheevi* hybrid 37307 were virtually indistinguishable from the $2n$ form except for fertility. The *T. durum* amphidiploid 37306–2, however, was taller and coarser than the undoubled form. This plant remained a $2n$-$4n$ chimera through both subdivisions, a fact which would explain its erratic fertility. The *T. macha* hybrid, 37308–2, was distinctly different in the $4n$ form. The amphidiploid was taller and coarser, and failed to recover after cutting, even under irrigation.

No distinctly fertile heads were found on the *T. durum* hybrid 37306–2, 4 seeds being the maximum on any head. One sector isolated from this plant and presumed to be $4n$, later proved to be a $2n$-$4n$ chimera.

Fertility. Several hundred seeds were obtained; of these, all were red except for 11 gray seeds, the color of which was attributed to outcrossing. The fertile spikes were sometimes associated with shorter and heavier stems but were within the range of sizes found on a completely sterile plant. Heads with single seeds occurred in about the same frequency on treated as on untreated plants. The *Triticum timopheevi* hybrid, 37307, was an exception, having over five times as many single seeds on the treated plants as on the untreated ones.

Pollen Counts. From 1,000 to 2,000 pollen grains were examined in each $2n$ and $4n$ hybrid. All diploid hybrids had less than 1 per cent of pollen which appeared functional, while the amphidiploids varied from 56 per cent for the *T. macha* hybrid 37308–2 to 95 per cent for the *T. durum* hybrid 37306–2.

Sears, in 18 amphidiploids of the seven-chromosome Triticineae (1941*a*) and in hybrids of *Aegilops cylindrica* and *A. ventricosa* × *Triticum durum* (1944), also found the diploid hybrids to be intermediate between their parents and found a striking similarity of the $2n$ and $4n$ portions of the same colchicine-doubled F_1 plants.

Chromosome Analysis. Table 1 presents a comparison of the meiotic chromosome behavior of the F_1 diploid and colchicine-induced amphidiploid plants. The expected $4n$ chromosome number was obtained in each case. Only rarely, however, was the pairing complete in any of the amphidiploids. A similar failure of complete pairing was reported by Armstrong and McLennan (1944) in amphidiploids of hybrids of *Triticum* spp. with *Agropyron glaucum.*

In a comparison of the two *Triticum durum* hybrids, 37306–2 has the greater amount of pairing in both the $2n$ and $4n$ forms. The amphidiploid form of the *T. timopheevi* hybrid, 37307, showed almost regular pairing. The minimum number of bivalents observed was only 5 below the maximum possible,

TABLE 1

Meiotic chromosome behavior of diploid and amphidiploid F_1 hybrids of *Triticum durum* (37306–1 and –2), *T. timopheevi* (37307) and *T. macha* (37308–2), each with *Agropyron trichophorum*

	F_1 diploids				F_1 amphidiploids			
	37306-1	-2	37307	37308-2	37306-1	-2	37307	37308-2
PMC's examined	50*	50*	100	50*	67	65	50	50
2*n*	35	35	35	41	70	70	70	82
Univalents:								
Range	27–35	17–24	14–33	13–31	2–20	0–12	0–10	0–10
Average	31.8	20.2	24.2	22.6	11.5	5.6	3.6	3.2
Bivalents:								
Range	0–4	4–10	1–9	4–13	25–34	27–35	30–35	34–41
Average	1.6	6.1	4.9	7.7	29.2	31.7	33.1	37.4
Per cent	*9.1*	*34.9*	*28.0*	*37.6*	*83.4*	*90.6*	*94.6*	*91.2*
Closed bivalents:								
Range	0–1	0–2	0–2	0–3	10–25	16–33	21–31	20–36
Average	0.02	0.3	0.7	1.1	17.6	23.7	26.0	29.3
Open bivalents:								
Range	.....	.....	1–8	.....	5–18	2–14	1–12	3–15
Average	1.58	5.8	4.2	6.6	11.6	8.2	7.1	8.1
Trivalents:								
Range	0	0–3	0–2	0–3	0–1	0–2	0–1	0–3
Average	0	0.9	0.3	0.9	0.04	0.15	0.06	0.4
Number of rings	0	0	0	0	0	0	0	1
Quadrivalents:								
Range	0	0–2	0	0–1	Rare	0–2	0–1	0–2
Average	0	0.3	0	0.8	0	0.1	0.02	0.7
Number of rings	0	0	0	0	0	2	0	9
Chromosomes synapsed:								
Range	0–8	8–23	2–21	13–28	50–68	58–70	60–70	72–82
Average	3.2	14.8	10.8	18.4	58.5	64.4	66.4	78.8
Per cent	*9.1*	*42.3*	*30.9*	*44.9*	*83.6*	*92.0*	*94.9*	*96.1*
Chromosomes in multiple associations:								
Range	0	0–9	0–6	0–10	0–3	0–8	0–4	0–11
Average	0	3.9	0.96	5.8	0.13	0.85	0.26	4.0
Number of different pairing arrangements	5	20	16	27	12	18	9	26
Per cent irregular pollen quartets	*100*	*93*	*100*	*90*	.....	*90*†	*78.5*	.....
Micronuclei per quartet:								
Range	1–7	0–7	5–20	0–6	.....	0–11	0–11	.....
Average	3.4	2.3	11.5	2.1	.....	3.1	2.8	.....
Seeds per spike	0.03	0.01	0.003	0.005	30	15 †	25	20

* Data adapted from Love and Suneson (1945).
† Head was a $2n$-$4n$ chimera. Pollen may have been $2n$.

and there were 5 PMC, or 10 per cent of the total observed, with the maximum number of 35 bivalents. The *T. macha* hybrid 37308–2 also had a very high degree of pairing in the amphidiploid. Three PMC, or 6 per cent, had the maximum number of 41 bivalents.

In all four hybrids (table 1) the diploid pairing as measured by bivalents showed little relationship to the multivalent associations of the amphidiploids. By contrast, the multivalent associations of each $2n$ F_1 plant (except 37306–1, which had none) were matched by a corresponding, slightly lower average number of chromosomes in multiple associations in the $4n$ F_1 plants.

CHROMOSOME ANALYSIS OF D_2 PROGENY[4]

Derivatives of Triticum durum × Agropyron trichophorum 37306–1 and –2. The 8 amphidiploid progeny of 37306–1 analyzed cytologically are included in table 2. Plants –135, –134, –136 were from the same $4n$ F_1 head. The variations in pairing were well within the scope of possibilities from the variations found in the amphidiploid F_1 (table 1). The range of bivalents was lower, and the range of univalents higher than in the $4n$ F_1 plant. The only two plants with more than 70 chromosomes (–131 and –132) approximated the pairing of the $4n$ F_1 very closely. The coefficient of correlation of the number of seeds per spike to the number of chromosomes was only $+0.26 \pm 0.39$, while the correlation to the average per cent of synapsed chromosomes was $+0.72 \pm 0.28$.

Armstrong and McLennan (1944), in the comparable amphidiploid of *Triticum turgidum* ($n = 14$) × *Agropyron glaucum* ($n = 21$), found 39 F_3 plants to have a much higher correlation of chromosome number to fertility (0.55 ± 0.12). The pairing of their material, however, was much more regular, averaging 31.2 bivalents and only 2.2 univalents for all plants.

The chromosome behavior of six derivatives of open-pollinated plants of the F_1 hybrid 37306–1 not treated with colchicine is summarized in table 3. Plant 37306–1–15, with 64 chromosomes, had a pairing arrangement similar to some of the amphidiploid progeny (table 2). Two other plants, numbers –16 and –103, had more univalents and less pairing than amphidiploid derivatives with similar chromosome numbers. They are presumed to be outcrosses, since their chromosome numbers of 74 and 76 exceed the maximum theoretically possible from two unreduced 35-chromosome F_1 gametes.

The two plants 37306–1–10 and –11, with 54 and 56 chromosomes, strongly resembled *Triticum vulgare*. Megaspores with 33 and 35 chromosomes, each combined with 21-chromosome pollen from *T. vulgare*, would give the observed number of 54 and 56 chromosomes. The range of 8 to 13 bivalents approaches the expected number of 14 bivalents from a combination of the A and B genomes of the *T. durum* chromosomes in the unreduced F_1 gamete and the presumed *T. vulgare* pollen.

In contrast, the 56-chromosome plant –198c–2, found by Love and Suneson (1945), was morphologically intermediate between *Triticum vulgare* and the F_1 type, and quite fertile. The range of univalents (15 to 26), bivalents (14 to

[4] D_2 is used for all classes of progeny from F_1 plants. C_2 is used only for progeny from amphidiploid (colchicine-derived) F_1 plants.

TABLE 2

Meiotic chromosome behavior of amphidiploid derivatives of *Triticum durum* × *Agropyron trichophorum* 37306–1

	No. -131	No. -132	No. -133	No. -123	No. -135	No. -134	No. -136	No. -116
PMC's examined	10	10	10	10	20	10	9	10
2*n*	78	77	70	67	67	66	65	65
Univalents:								
Range	12–23	11–23	8–36	5–17	7–27	9–32	3–10	7–23
Average	16.4	15.5	18.7	9.6	16.1	21.2	7.1	14.8
Bivalents:								
Range	23–33	27–33	17–31	25–31	16–28	17–24	26–31	21–29
Average	28.7	28.9	25.2	28.5	23.5	22.1	28.8	25.1
Closed bivalents:								
Range	13–25	13–29	6–15	17–26	6–20	4–11	16–24	10–20
Average	18.5	19.9	11.1	21.6	13.2	9.2	20.3	14.1
Open bivalents:								
Range	6–13	4–14	11–19	4–12	4–16	9–18	7–13	7–15
Average	10.2	8.8	14.1	7.2	10.2	13.1	8.2	11.0
Trivalents:								
Range	0–3	0–3	0–1	0	0–4	0–1	0–1	0
Average	1.0	1.1	0.2	0	0.7	0.2	0.1	0
Number of rings	0	0	0	0	0	0	0	0
Quadrivalents:								
Range	0–2	0–1	0	0–1	0–2	0	0	0
Average	0.3	0.2	0	0.1	0.4	0	0	0
Number of rings	0	1	0	θ	1	0	0	0
Chromosomes synapsed:								
Range	55–66	54–66	34–62	50–62	40–60	34–57	55–60	42–58
Average	61.6	61.5	51.0	57.4	51.0	44.8	57.9	50.2
Chromosomes in multiple associations:								
Range	0–14	0–9	0–3	0–4	0–12	0–3	0–3	0
Average	4.2	4.1	0.6	0.4	4.1	0.6	0.33	0
Number of different pairing arrangements	9	10	10	6	20	9	5	7
Per cent irregular pollen quartets	.....	*100*	*99.4*	.....	*100*	*100*	.....	.....
Micronuclei per quartet:								
Range	.....	2–21	0–17	.....	3–14	4–20	.....	.....
Average	.....	11.6	8.2	.....	7.9	10.5	.....	.....
Seeds per spike	23.6	12.4	7.0	8.8	7.4	0	34.5	0.3
Growth score	20	20	25	20	30	10	30	20

TABLE 3

Meiotic chromosome behavior of unusual derivatives of the hybrid *Triticum durum* × *Agropyron trichophorum* 37306–1

	D₂ progeny types					
	Resembling maternal amphidiploid				Resembling *T. vulgare*	
	No. -8	No. -15	No. -16	No. -103	No. -10	No. -11
PMC's examined	20	10	10	10	10	15
$2n$	59	64	74	76	54	56
Univalents:						
Range	22–35	13–21	19–32	23–40	27–38	30–36
Average	22.9	16.8	24.6	32.6	32.6	33.7
Bivalents:						
Range	12–17	16–24	20–25	17–25	8–13	9–13
Average	13.9	20.3	22.8	19.9	9.8	10.9
Closed bivalents:						
Range	3–9	8–19	10–18	4–12	3–8	4–10
Average	6.0	12.2	15.4	8.0	4.8	6.0
Open bivalents:						
Range	4–12	4–12	4–12	8–15	3–6	1–8
Average	7.8	8.1	7.4	11.9	5.0	4.9
Trivalents:						
Range	0–1	0–3	0–3	0–2	0–1	0–1
Average	0.3	1.8	1.0	0.8	0.6	0.2
Number of rings	0	1	0	1	0	0
Quadrivalents:						
Range	0–1	0–1	0–1	0–1	0	0
Average	0.05	0.3	0.2	0.3	0	0
Number of rings	0	0	1	1	0	0
Chromosomes synapsed:						
Range	24–37	43–51	42–55	36–53	16–27	20–26
Average	29.1	47.2	49.4	43.4	21.4	22.3
Chromosomes in multiple associations:						
Range	0–4	3–13	0–9	0–7	0–3	0–3
Average	1.1	6.6	3.8	3.6	1.8	0.6
Number of different pairing arrangements	11	8	9	10	8	6
Seeds per spike	0	11.2	10.4	4.6	0	0.4
Growth score	40	40	30	30	20	50

TABLE 4

Meiotic chromosome behavior of derivatives of the F_1 hybrid of *Triticum macha* × *Agropyron trichophorum* 37308–2

	Open-pollinated	C_2 from colchicine F_1					
	No. -1	No. -45	No. -8	No. -53	No. -6	No. -44	No. -10
PMC's examined	40	10	15	10	10	10	10
2*n*	53	79	79	80	80	82	83
Univalents:							
Range	20–35	3–12	7–33	1–12	4–12	4–12	4–17
Average	28.5	8.4	15.3	5.5	8.6	7.5	10.0
Bivalents:							
Range	6–15	29–36	23–31	31–39	31–38	28–35	26–38
Average	11.0	32.3	27.9	35.7	33.6	31.4	32.8
Closed bivalents:							
Range	2–7	20–32	13–26	21–32	16–34	18–31	16–31
Average	4.7	25.1	18.9	26.0	25.2	24.1	25.3
Open bivalents:							
Range	3–10	4–9	5–11	7–13	4–14	4–13	4–11
Average	6.3	7.0	8.9	9.7	7.9	7.1	7.5
Trivalents:							
Range	0–2	0–2	0–4	0–2	0–2	0–2	0–3
Average	0.8	0.8	1.3	0.5	0.7	1.0	1.1
Number of rings	0	1	0	0	1	1	3
Quadrivalents:							
Range	0–1	0–2	0–3	0–1	0–2	0–3	0–2
Average	0.08	0.9	1.0	0.4	0.5	1.9	0.6
Number of rings	0	5	5	1	2	13	1
Association of 5 or more:							
Range	0	0	0	0	0	0–1	0–2
Average	0	0	0	0	0	0.2	0.3
Chromosomes synapsed:							
Range	18–33	67–76	46–72	68–79	66–76	70–78	66–79
Average	24.6	70.6	63.7	74.5	71.3	74.5	73.0
Chromosomes in muliple associations:							
Range	0–10	0–11	0–14	0–10	0–8	7–18	0–23
Average	2.6	6.0	8.0	3.1	4.1	11.7	7.4
Number of different pairing arrangements:	24	9	15	8	10	9	10
Per cent irregular pollen quartets	*100*	*100*	*98*	.....	*100*	*99.4*	*99.0*
Micronuclei per quartet:							
Range	1–12	1–14	0–16	.....	1–13	0–16	0–15
Average	4.9	5.7	9.6	.....	4.9	7.4	8.0
Seeds per spike	0	24.2	3.0	15	.....	1.8	19.2
Growth score	20	25	20	50	25	15	20

20), and chromosomes synapsed (30 to 41) found in –198c–2 did not even overlap the corresponding values for plants –10 and –11.

In the progeny of the second *T. durum* hybrid, 37306–2, a morphologically diverse group of six plants was examined and found to have almost identical chromosome arrangements. These plants ranged from very vigorous to very weak, with fertility varying from 0 to 65 seeds per spike. Fertility was not obviously related to plant vigor, chromosome number, or pairing arrangement. These plants were derived from seed obtained on colchicine-treated F_1 plants, but were probably not amphidiploids. The chromosome numbers were 63, 63, 64, 66, 71, and 71. For the entire group the univalents ranged from 7 to 22, bivalents 15 to 26, chains of three 0 to 5, chains of four 0 to 2, with occasional longer chains. The pairing behavior of the plant 198d–2, reported by Love and Suneson (1945) as being derived from this same F_1 hybrid, was very similar to that observed in these plants.

Derivatives of Triticum timopheevi × Agropyron trichophorum. Five C_2 amphidiploids were examined cytologically among the progeny of *Triticum timopheevi* × *Agropyron trichophorum* 37307. They were almost identical, having 66 to 68 chromosomes and 23 to 32 bivalents. Considering all five C_2 plants together, the number of bivalents decreased from the range of 30 to 35 in the $4n$ F_1 (table 1) to a range of 24 to 32 in the C_2 plants, with a corresponding increase in univalents. There was little other change from the amphidiploid F_1 except for uniformly low fertility and some fluctuation in plant vigor.

Derivatives of Triticum macha × Agropyron trichophorum 37308–2. A cytological analysis was made of only six amphidiploid and three unique non-amphidiploid progeny of the F_1 hybrid 37308–2 (table 4). Plant number 37308–2–1 had the rather unusual $2n$ chromosome number of 53, with an average of only 24.6 chromosomes synapsed. This 53-chromosome plant and a derivative of the *Triticum durum* hybrid 37306–1–8 (table 3) with 59 chromosomes, were the only plants examined cytologically whose chromosome numbers suggested they may have been derived from a highly reduced megaspore on the diploid hybrids.

The six amphidiploid progeny of 37308–2 (table 4) showed a general decrease in the number of bivalents and an increase in the number of univalents and multivalents over that found in the $4n$ F_1 parent (table 1). Chromosome arrangements in these plants were in no way similar to the 70-chromosome plant –198e, reported by Love and Suneson (1945) as being derived from the sib F_1 hybrid, 37308–1.

POSSIBLE CAUSES OF FAILURE OF AMPHIDIPLOID PAIRING

The unique feature of the foregoing data is the failure of the chromosomes of the somatically doubled F_1 hybrids to behave regularly at the first meiosis, with the resulting variation in chromosome number and fertility in the progeny.

The confusion from the conflicting results of the numerous experimentally induced auto- and allopolyploids has been partially clarified by Clausen, Keck, and Hiesey (1945). They explain the breakdown of many interspecific hybrids on the basis of "severe disturbances in the gene-determined physiological balances." Successful polyploids require that the genomes remain for the most part intact. This condition can be attained either through complete homology resulting in chromosome interchangeability (autoploidy), or—at the other extreme—the complete absence of homology, a state which will effectively prevent intergenome pairing.

The three hybrids of *Triticum durum, T. timopheevi,* and *T. macha,* each with *Agropyron trichophorum,* although vigorous, essentially intermediate F_1 plants, did not maintain their original genome balance. In each F_1 plant there was some regular pairing (table 1), and in each amphidiploid there was a failure of complete pairing.

At least four possible causes of this failure of amphidiploid pairing may be considered: (1) the mechanical obstacle to successful pairing of large numbers of chromosomes with their homologues (Armstrong and McLennan, 1944; Sears, 1944); (2) complications resulting from duplicate homologies, only part of which may have been expressed by diploid pairing (Jørgensen, 1928); (3) inhibition of pairing by a gene or gene complex; and (4) disharmonious gene interaction. The latter two are favored by the authors.

The mechanical-obstacle hypothesis does not seem to apply to this material, for the amphidiploid 37308–2 with the largest number of chromosomes ($2n$ = 82) has the maximum number and per cent synapsis (78.8; 96.1 per cent, table 1). Furthermore, high chromosome numbers in natural polyploids cause little interference with pairing. *Agropyron elongatum* with 70 chromosomes is essentially regular within the limits of its frequent multivalent associations (Peto, 1936). The natural amphidiploid, *Spartina townsendii* with the high diploid chromosome number of 126 has regular meiotic pairing (Huskins, 1930).

The failure of somatic doubling *per se* to establish meiotic chromosome stability in amphidiploids has been repeatedly observed (Clausen, Keck, and Hiesey, 1945). It is well illustrated by 18 amphidiploids produced by Sears (1941*b*) involving ten species in the seven-chromosome *Triticineae.* They ranged from an average of 5.48 to 13.82 bivalents and their fertility was occasionally, but not consistently, predictable from an inverse relationship with $2n$ pairing as suggested by Darlington (1929).

In the present *Triticum* × *Agropyron* hybrids, there seems to be no visible relationship between the diploid pairing and the multivalent associations of the amphidiploids. The actual number of chromosomes in multivalent associations in the corresponding $2n$ F_1 and $4n$ F_1 plants was numerically almost exactly the same (table 1).

Love and Suneson (1945) found that the two *Triticum durum* hybrids, 37306–1 and –2, showed an unexpected difference in pairing in the diploid form (3.2 versus 14.8 chromosomes synapsed; table 1). The amphidiploids kept the same relative pairing relationship (58.5 versus 64.4 chromosomes synapsed; table 1). These facts indicate a genetic suppression of pairing in 37306–1. There could not have been less chromosome homology in the diploid 37306–1 than in its sib hybrid 37306–2, or there would have been greater pairing in the amphidiploid 37306–1.

It seems to the authors that a simple and entirely logical explanation for the failure of complete pairing in these amphidiploids may be made. In any species there is, doubtless, genetic control of nuclear developments which accompany the meiotic process. These developments are regulated differently in *Triticum* and *Agropyron*. The meiotic disturbances in the hybrids and amphidiploids are the result of disharmonious interaction between parental genes that control the same processes. Love (1951) reported a similar situation in crosses of distantly related varieties of *T. vulgare*.

Whatever the explanation for failure of regular meiotic pairing in the amphidiploid F_1 plants, the meiotic irregularities of their progeny (tables 2, 4) were within the range of expectation, assuming random distribution of univalents and the possibilities from multiple configurations.

SUMMARY

1. The F_1 perennial hybrids and their progeny of *Triticum durum, T. timopheevi*, and *T. macha*, were obtained by crossing with *Agropyron trichophorum*. These were examined morphologically and cytologically.

2. The F_1 hybrid *Triticum timopheevi* × *Agropyron trichophorum* had the expected 35 chromosomes, with 1 to 9 bivalents and an occasional trivalent. This was similar to the other F_1 hybrids reported by Love and Suneson (1945).

3. The diploid F_1 hybrids were morphologically intermediate between their parents and were highly sterile. A total of 85 seeds were found on 4,700 spikes of 39 F_1 plants.

4. Fertile amphidiploids were produced in each F_1 hybrid by colchicine treatment. The somatically doubled tissue was isolated by vegetative subdivision. Each amphidiploid F_1 plant was markedly similar to its corresponding diploid hybrid, with the exception of the *T. macha* amphidiploid, which was taller, coarser, and more weakly perennial.

5. Cytologically each amphidiploid showed the expected $4n$ chromosome number. Only occasionally was pairing complete. There was no correlation between the frequencies of diploid bivalents and amphidiploid multivalents. The number of multivalents was almost the same in corresponding $2n$ F_1 and $4n$ F_1 plants. The failure of complete amphidiploid meiotic pairing is ascribed to disturbances in the meiotic process caused by disharmonious interaction of genes of *Triticum* and *Agropyron* which controlled the same cell processes.

6. Genetic suppression of synapsis in a *Triticum durum* hybrid was also effective in its amphidiploid.

7. The C_2 progeny from each amphidiploid showed a general decrease in vigor and fertility. They had variable chromosome numbers well within the range of possibilities present in the $4n$ F_1 pairing irregularities. Usually there was a decrease in the total number of chromosomes synapsed.

8. In the progeny of the amphidiploid *Triticum durum* hybrid, 37306–1, the fertility was positively correlated with the number of bivalents and total chromosomes synapsed, but showed only slight relation to the total number of chromosomes.

9. All amphidiploid lines appeared to be on the borderline between a cyto-

logical breakdown through genome interchange and segregation to some stable chromosome level.

10. Fourteen nonamphidiploid outcrossed progeny had chromosome numbers indicating that the F_1 megaspore was either unreduced or nearly unreduced. Only two plants were examined in which there was any possibility of much reduction in the chromosome number of the diploid F_1 megaspore.

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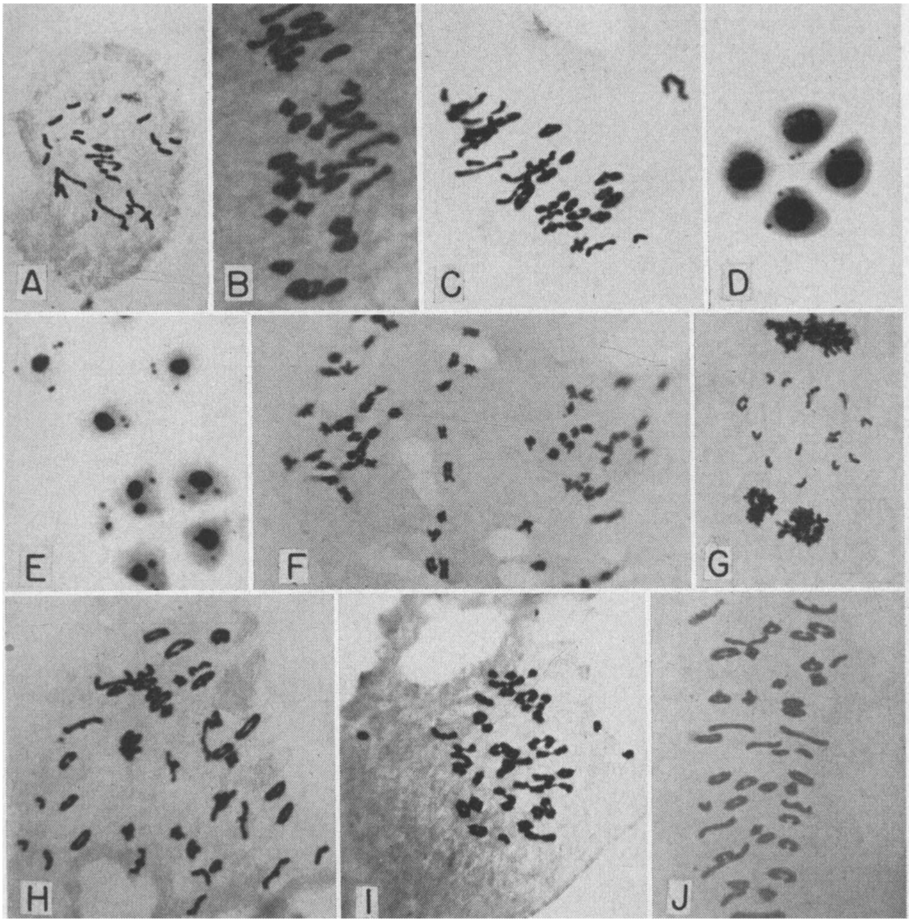

Plate 1, A–E. *Triticum timopheevi* × *Agropyron trichophorum*, 37307:

A, F_1 ($2n = 35$) $5_{II} + 25_I$

B, Amphidiploid F_1 ($2n = 70$) 35_{II}

C, Amphidiploid F_2 ($2n = 67$) $31_{II} + 5_I$

D, F_1 amphidiploid pollen quartet

E, F_1 pollen quartets

F–I. *Triticum durum* × *A. trichophorum* amphidiploid F_1 ($2n = 70$):

F, First anaphase, univalents on equatorial plate

G, First telophase, univalents lagging

H, First metaphase $27_{II} + 6_I$

I, First metaphase $1_{IV} + 31_{II} + 4_I$

J, *T. macha* × *A. trichophorum* amphidiploid F_1 ($2n = 82$) $1_{IV} + 38_{II} + 2_I$

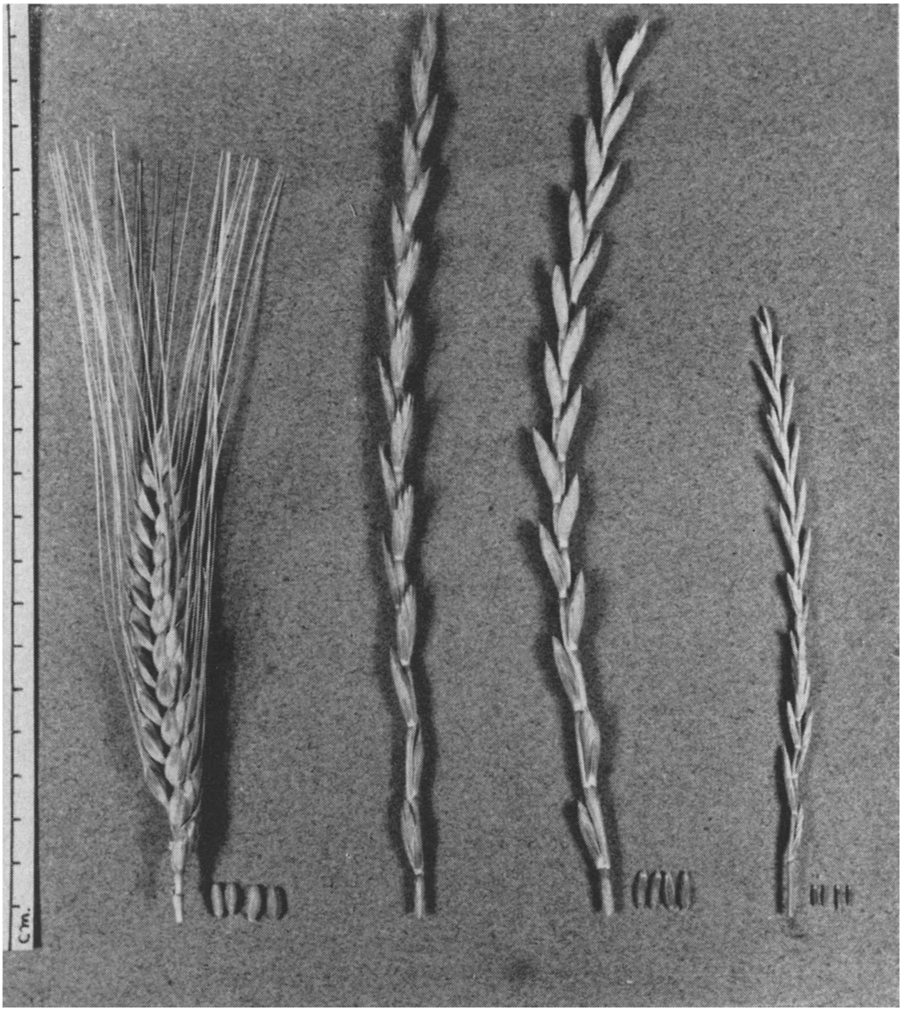

Plate 2. Left to right, *Triticum durum* var. Mindum, F_1 diploid 37306–1, F_1 amphidiploid, *Agropyron trichophorum*.

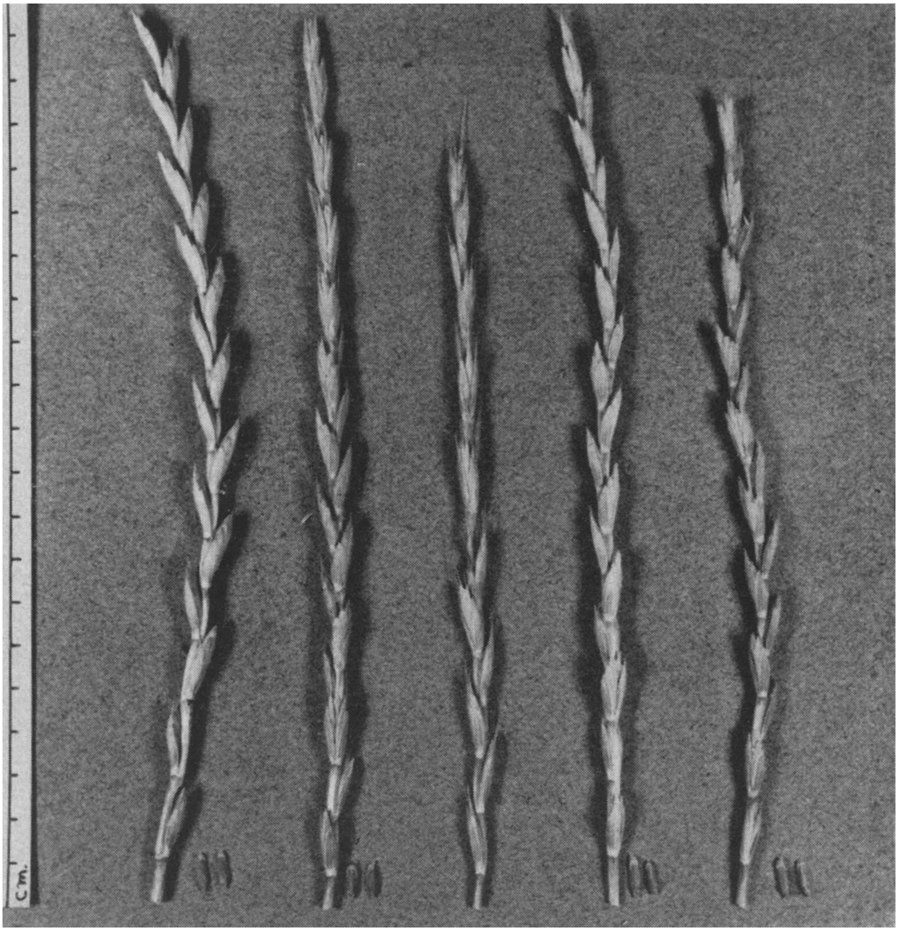

Plate 3. F_2 amphidiploid heads of *Triticum durum* × *Agropyron trichophorum*.

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