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GENOTYPIC AND CYTOLOGICAL INFLUENCES ON THE MEIOSIS OF HEXAPLOID TRITICALE

by

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ABSTRACT

Two groups of hexaploid triticale were synthesized from the crosses of two cultivars of diploid rye (*Secale cereale* L.) with (a): two varieties of tetraploid macaroni wheat (durum-group of *Triticum turgidum* L), and (b): extracted AABB tetraploids of three cultivars of hexaploid bread wheat (*T. aestivum* L. em. Thell.).

Statistical analyses of PMC meiotic data taken from the first generation after chromosome doubling showed the following:

i) The extracted triticales, as a group, showed the greater chromosome regularity in the division of their PMC's. This was attributed to the prior adaptation of their AABB component to the hexaploid meiosis of bread wheat.

ii) Much variation was found between triticales sharing the same wheat and rye varieties as parents. This genetic variability most likely came from the heterogeneity of gametes contributed by the two outbred cultivars of rye.

iii) There was an apparent decrease in the number of synapsed pairs of chromosome arms and a corresponding increase in the number of univalents in the course of MI. This was attributed to the premature disjunction of paired chromosome arms in the bivalents and occasional multivalents orientated on the metaphase plate.

iv) In PMC classified by the number of paired chromosome arms that they contained, the frequency of univalents for each cell class was higher than predicted by assuming that arm pairs were distributed at random among chromsomes of the complement. Premature disjunction of arm pairs would convert ring bivalents into rod bivalents and rod bivalents into univalents; therefore the

excess of univalents suggested that the paired arm of a rod bivalent was more likely to fail than either of the two paired arms of a ring bivalent.

v) The degree to which univalents were in excess was clearly influenced by the particular environment and the genotype of the triticale in question.

INTRODUCTION

Hexaploid wheat and hexaploid triticale are allopolyploids that combine the genomes of tetraploid wheat with the genomes of *Aegilops squarrosa* (McFadden and Sears, 1946) and rye (Larter *et al.*, 1970), respectively. Removal of the "squarrosa" component from hexaploid wheat by a backcrossing procedure, produced a tetraploid that was more like its hexaploid parent than any present or ancestral tetraploid (Kaltsikes *et al.*, 1969; Kerber, 1964). These "extracted" tetraploids were distinguished from normal tetraploids and hexaploids by their low vigour and fertility.

Physiological inadequacy of the extracted tetraploid genomes was most likely related to selection pressures, that were jointly exerted on the genomes over the many years since they were combined together in hexaploid wheat. This has meant that within one plant the genomes have become physiologically interdependent. Such co-selection to adjust the two parental genomes to each other has not yet taken place in most newly synthesised allopolyploids within the *Triticinae*, which were found to be either meiotically irregular and/or sterile (Bell and Sachs, 1953; Riley and Bell, 1959).

A feature of this meiotic irregularity is the presence of univalents at first meiotic metaphase (MI) (Riley and Bell, *loc. cit.*). Univalents seen in pollen mother cells (PMC's) of triticale have been tentatively identified by many observers as chromosomes of the rye genome in both hexaploid and octoploid types (Larter *et al.*, 1969; Müntzing, 1939; 1957; Riley and Bell, 1959; Riley and Miller, 1970; Sánchez-Monge, 1959). This suggestion was based on isolated cases where octoploid triticales had entirely reverted to wheat (Müntzing, 1957). Recently Pieritz (1970) also supported this idea when he found that in octoploid triticales, individual

chromosomes of rye were missing or in addition much more often than wheat chromosomes. However, Shigenaga et al. (1971) found no such difference between the two sets of parental chromosomes in hexaploid triticale. Moreover, Larter and Shigenaga (1972) showed that univalents found two by two in euploids had the same distribution of sizes as the 21 univalents that could often be found in PMC's of haploids of the same triticale strain. Because in triticale, chromosomes of wheat are consistently smaller than chromosomes of rye (Pieritz, 1970; Shigenaga and Larter, 1971), this shows that wheat chromosomes must have been present as univalents in the same proportion in the euploid as they were in the haploid.

Whatever the relative contribution of the genomes of wheat and rye to the numbers of univalents found in triticale, the physiological conditions that lead to this irregularity may be improved by manipulation of the wheat genomes. Thus, instead of merely adding the rye genome (RR) to the genomes of tetraploid wheat (AABB), the squarrosa (DD) component could be replaced by the rye genome (RR) and any adaptedness of the remaining wheat component (AABB) to hexaploid milieux would be expected to improve the functioning of meiosis in hexaploid triticale (AABBRR).

To test this hypothesis PMC meioses of triticales made with "durum" varieties ("durum triticales") were compared with PMC meioses of hexaploid triticales made with AABB tetraploids extracted out of hexaploid cultivars of bread wheat ("extracted triticales").

MATERIALS AND METHODS

Six wheat tetraploids (two durum cultivars and tetraploids extracted out of four cultivars of bread wheat) were crossed with two cultivars of rye (Table I). F_1 seed was readily set but because of endosperm breakdown in these crosses further development of the embryo was only possible in culture (Larter, 1968). Slants of 1.1% orchid agar were satisfactory when supplemented with 2 p.p.m. each of indoleacetic and gibberellic acids.

F_1 plants established were cloned to avoid chance loss. Fresh 0.1% colchicine solution was applied in soda straws (Bell, 1950) to the cut surface of older tillers (since these gave faster rates of uptake of the solution). Where no seed was set additional cycles of recloning and retreatment were carried out.

Seeds set by treated F_1 plants were sown individually in 5 inch pots and grown in three plantings, under glass. Entire spikes were fixed in Carnoys II fluid during a period from early April to early June. Two weeks or more after fixation spikes were transferred to 70% alcohol. Fixed material was refrigerated at all times. Macerated anthers were stained with 2% acetocarmine, heated, and then the slides were irrigated with acetic acid, before squashing. PMC's were scored at first metaphase (MI) for entire configurations, at first anaphase (AI) for univalent laggards and for micronuclei at the quartet stage.

Nested analysis of variance was made of four meiotic variables. These were: firstly the frequency of metaphase univalents per PMC, secondly the total number of synapsed pairs of chromosome arms per PMC (arm pairs), thirdly the frequency of univalent laggards at AI, and lastly the frequency of micronuclei per sporocyte. Four levels of nesting were investigated for univalents, arm pairs and micro-nuclei. These were within

anthers, within plants, within lines and within combinations. (A line is the family of a single intergeneric F_1 hybrid and a combination is a group of lines sharing both wheat and rye cultivars as parents.) Insufficient data were collected to measure plant to plant variation within lines for anaphase laggards.

To alleviate the marked correlation of means and variances of univalents, laggards and micronuclei these three variables were analysed as the square roots of 0.5 plus data. Denominator mean squares and their attached degrees of freedom were adjusted for unequal sample sizes by an approximate method (Sokal and Rohlf, 1969).

A factorial analysis of univalent frequencies was performed for two sets of data. The first set was an unpublished temperature study; data were kindly supplied by Dr. E. N. Larter. In this case different temperature treatments were used as one factor and the number of arm pairs as the second. The other set of data was taken from the present study. Here different parental tetraploid wheats supplanted temperature as the first factor. Sums of squares were adjusted for unequal sample sizes by use of harmonic means of the sample sizes (Snedecor and Cochran, 1967). All individuals in which multivalents were observed at MI were excluded from these analyses. Data were further reduced by eliminating levels of arm pairs containing cells in which sample size was less than five.

The relative frequencies with which cells with a particular number of paired arms contain 0, 2, 4, 6, etc., univalents was predicted on two assumptions. These were, firstly that only bivalents could be formed and secondly that arm pairs were distributed at random throughout the genome. In the following expression [B] and [C] are the relative frequencies of cells with x and (x + 2) univalents among cells with j arm-pairs. [A] is

the relative frequency of cells with (x +2) univalents among cells with (j - 1) arm pairs. Then:

$$[A] = [B]\left[1 - \frac{(2j - 42 + x)}{j}\right] + [C]\left[\frac{2j - 42 + (x + 2)}{j}\right].$$

Calculations can begin where j = 41. In this case $[B] = 1$ and $[C] = 0$ because there can be no cells with 41 arm pairs that contain any univalents. Mean frequencies of univalents expected for a given number of arm pairs are easily obtained from there relative frequencies of cell types.

In addition to scoring metaphases and anaphases for numbers of univalents and laggards, etc., that they contained counts were sometimes made of the frequencies of the various stages of meiosis shown by PMC's of the anther under study. PMC's in stages earlier than MI comprised one class, MI cells were the second class and all cells in stages later than MI accounted for the remainder. To obtain a numerical value related to the progress of the anther from the early stages of meiosis through MI and on to later stages, numerical scores were assigned to each class. These were arranged so that an early anther would score low and a late anther would score high. All cells still in prophase scored 0; cells in MI and later scored 0.5 and 1.0, respectively. Therefore, the more cells that had passed into metaphase and then onto anaphase, the higher each anther would score. Each anther score was then divided by the total number of cells whose stage had been recorded and this proportionate score was finally transformed into degrees. The correlation of this developmental stage of the anther with mean numbers of univalents and arm pairs was then determined.

Because many genetically different lines were involved, of which all were possibly different from each other in their means and variances,

there was no significant correlation. Differences in means were therefore accommodated by considering the deviation of the anther mean from the overall line mean. Differences in variability were accommodated by dividing the deviation of the anther mean from the overall line mean by the line standard deviation pooled over all cells. Line means were independent of these anther means in all but five cases. Correlation was then again determined, but with the number of degrees of freedom reduced by 5.

RESULTS AND DISCUSSION

Synthesis of the triticales

Viable wheat-rye hybrids were most difficult to isolate in crosses using tetra-Canthatch and tetra-Rescue. To succeed in this step it is necessary to find an optimum time for harvesting seed after pollination. This can be different for each wheat parent. For example, the optimum time for tetra-Prelude was around fifteen days whereas Stewart '63 was best harvested around twenty days or more.

In some cases it proved difficult to obtain seed from colchicine treated hybrid material. Apparent doubling of the chromosome number (as judged by pollen shedding and "gigas" appearance) was not always followed by seed set. Physiological and meiotic disorders must have reduced the seed setting of C_1 segments just as later generations of triticale have been partially or completely sterile under various conditions (Larter, 1968; Larter *et al.*, 1969; Müntzing, 1957; Sánchez-Monge, 1959).

Low vigour of the extracted tetraploids was largely compensated by the addition of the rye genome. Appearance and seed fertility of triticales involving extracted tetraploids were about the same as triticales out of the durum cultivars, though metrical characters other than of meiosis were not measured in C_2 as cytological collections left the plants considerably mutilated.

Meiosis

The mean meiotic characteristics of twenty-five of the lines isolated are given in Table I. Stewart '63 x OD289-6 was remarkable for the irregularity of its PMC divisions but because the only representative in C_2 was monosomic the line was discarded from further analysis. Another plant of interest was a double monosomic individual of Durum 60 x Prolific - 1

TABLE I

Meiotic characteristics (means and cell ranges) of 25 newly synthesised lines of triticale

Parentage*	Line	No. of plants** scored	No. of PMC's** scored	2n	Multi-valents	Ring Bi-valents	Rod Bi-valents	Uni-valents	Arm Pairs	Anaphase Laggards	Micro-nuclei
Triticum turgidum L. (durum group) x *Secale cereale* L.											
cv. 'Stewart '63' x cv. 'OD289'***	1	2	50	42		12.88 (7-17)	6.58 (2-11)	3.10 (0-10)	32.33 (25-38)	3.18 (0-8)	1.58 (0-6)
	2	3	65	42	0.04 (0-1)	13.15 (8-17)	5.66 (2-10)	4.27 (0-10)	32.03 (27-37)	4.41 (0-11)	1.13 (0-6)
	3	4	94	42		14.08 (7-20)	5.48 (1-11)	2.87 (0-10)	33.66 (23-41)	2.25 (0-8)	0.73 (0-5)
	4	1	71	42	0.10 (0-1)	13.54 (8-18)	5.61 (2-10)	3.29 (0-14)	33.01 (22-39)	2.59 (0-8)	0.59 (0-6)
	5	5	110	42	0.01 (0-1)	15.65 (7-20)	4.81 (1-9)	1.04 (0-12)	36.14 (22-41)	1.37 (0-4)	0.46 (0-5)
	6	1	51	41	0.03 (0-1)	9.29 (4-13)	5.90 (1-10)	10.67 (3-21)	24.59 (17-30)	10.55 (3-16)	1.44 (0-8)
cv. 'Stewart '63' x cv. 'Prolific'	1	3	52	42	0.10 (0-1)	13.68 (8-18)	6.04 (3-13)	2.23 (0-6)	33.62 (29-39)	3.75 (1-8)	1.29 (0-6)
	2	4	160	42		15.35 (8-20)	4.96 (1-11)	1.37 (0-6)	35.66 (27-41)	1.41 (0-6)	0.38 (0-4)

TABLE I - continued

Parentage*	Line	No. of plants scored**	No. of PMC's scored**	2n	Multi-valents	Ring Bi-valents	Rod Bi-valents	Uni-valents	Arm Pairs	Anaphase Laggards	Micro-nuclei
	3	5	113	42		13.93 (4-20)	5.99 (0-11)	2.15 (0-12)	33.86 (19-40)	2.03 (0-6)	0.63 (0-5)
	4	7	163	42	0.01 (0-1)	14.97 (10-21)	5.32 (0-9)	1.38 (0-6)	35.29 (28-42)	1.92 (0-6)	0.45 (0-4)
	5	4	102	42	0.07 (0-1)	13.87 (8-19)	5.89 (2-11)	2.22 (0-10)	33.78 (24-40)	1.08 (0-5)	0.61 (0-6)
cv. 'Durum 60' x cv. 'OD289'	1	1	34	42		13.29 (7-18)	5.76 (2-10)	3.89 (0-12)	32.34 (23-38)	2.03 (0-6)	0.42 (0-5)
cv. 'Durum 60' x cv. 'Prolific'	1	1	40	42		11.86 (7-16)	6.23 (2-11)	5.82 (2-10)	29.95 (24-34)	- -	2.00 (0-7)
	1a	1	56	40		15.01 (8-18)	3.64 (1-10)	2.70 (2-6)	33.66 (29-37)	2.0 (0-3)	0.71 (0-4)
	2	4	101	42	0.06 (0-1)	14.13 (8-20)	6.03 (1-13)	1.73 (0-8)	34.51 (28-41)	1.86 (0-8)	0.48 (0-4)
AABB tetraploids of *T. aestivum* L. em. Thell. x *S. cereale* L.											
'Tetra-Prelude' x cv. 'OD289'	1	1	30	42	0.26 (0-1)	12.13 (8-17)	6.30 (2-9)	4.10 (0-8)	31.43 (26-38)	2.75 (0-5)	0.29 (0-4)
	2	6	149	42	0.10 (0-1)	14.29 (7-20)	5.31 (0-12)	2.54 (0-14)	34.04 (22-41)	1.30 (0-9)	0.31 (0-4)

TABLE I - continued

Parentage*	Line	No. of plants scored**	No. of PMC's scored**	2n	Multi-valents	Ring Bi-valents	Rod Bi-valents	Uni-valents	Arm Pairs	Anaphase Laggards	Micro-nuclei
	3	2	54	42	0.03 (0-1)	14.73 (5-20)	5.87 (1-15)	0.69 (0-4)	35.43 (25-41)	0.67 (0-3)	0.31 (0-4)
'Tetra-Prelude' x cv. 'Prolific'	1	4	121	42	0.06 (0-1)	14.08 (2-19)	5.75 (1-13)	2.11 (0-14)	34.14 (16-39)	1.73 (0-5)	0.59 (0-5)
	2	3	70	42	0.03 (0-1)	15.07 (11-19)	4.95 (0-10)	1.86 (0-8)	35.08 (30-40)	0.44 (0-2)	0.30 (0-3)
	3	3	70	42	0.01 (0-1)	12.83 (6-17)	6.48 (3-13)	3.39 (0-10)	32.13 (15-36)	5.08 (0-16)	1.02 (0-5)
'Tetra-Thatcher' x cv. 'OD289'	1	3	164	42		16.15 (9-21)	4.38 (0-10)	0.94 (0-6)	36.68 (28-42)	0.47 (0-4)	0.38 (0-4)
	2	1	57	42	0.05 (0-1)	15.16 (11-18)	4.82 (1-10)	1.84 (0-8)	35.31 (29-39)	1.62 (0-10)	0.90 (0-7)
	3	4	89	42		15.09 (8-19)	5.14 (1-12)	1.53 (0-10)	35.32 (28-40)	1.97 (0-6)	0.60 (0-5)
'Tetra-Thatcher' x cv. 'Prolific'	1	6	141	42	0.01 (0-1)	16.44 (11-20)	4.29 (1-10)	0.51 (0-4)	37.19 (30-41)	0.69 (0-6)	0.23 (0-4)
'Tetra-Rescue' x cv. 'Prolific'	1	3	95	42	0.09 (0-1)	15.59 (9-20)	4.65 (1-10)	1.16 (0-6)	36.13 (31-41)	1.23 (0-6)	0.59 (0-4)

TABLE I - continued

* Two additional lines were isolated, one from the cross 'Tetra-Canthatch' x cv. 'Prolific', the other from the cross cv. 'Durum 60' x cv. 'OD289'.

** Represents sampling of metaphase variables only. Sampling of anaphase data was much more restrictive than this.

*** A spring type rye on the accession list of the Dept. of Plant Sci., Univ. of Manitoba, obtained from CIMMYT.

which was considerably more regular than its single disomic sister (Table I). This might indicate that interactions among a few chromosomes could be important in conditioning irregularity in triticale. No aneuploids contributed to any other of these means and none were considered in subsequent analysis.

Multiple associations occurred sporadically at MI in these triticales. Occasionally these were frequent enough to suggest heterozygosity for a translocation, but mostly quadrivalents and trivalents occurred with frequencies between 0 and 5%. These multivalents may represent pairing between the homoeologues of the two genomes of tetraploid wheat. However, Mello-Sampayo (1969) reported little such pairing between these two genomes in the pentaploid hybrids of tetraploid and hexaploid wheats; this result could mean that activity of the long arm of chromosome 5B that normally excludes pairing between the homoeologues of the A and B genomes (Riley, 1960; Riley _et al._, 1960) is relaxed in hexaploid triticale.

To avoid complications of the variable frequency of multivalents, only univalents and arm pairs were considered together with anaphase laggards and micronuclei. Nested analysis of variance of univalent frequencies and the number of arm pairs per cell showed that differences from anther to anther and from line to line were the most important sources of variation (Table II).

These significant differences among replicate triticale lines showed that there was much variability of rye gametes within a single variety of rye. Particular combinations of wheat and rye had no significant effect on the frequencies of univalents, arm pairs, anaphase laggards or micronuclei against this significant variability of the rye gametes (Table II). In 1939 Müntzing wrote that "the fate of a triticale strain will be largely

TABLE II

Percent variance components of four meiotic variables †

Source of variation	Univalents per PMC		Arm pairs per PMC		Anaphase laggards per PMC		Micronuclei per sporocyte	
Among combinations	-	n.s.	-	n.s.	-	n.s.	-	n.s.
Among lines within combinations	16.60	***	14.07	**	15.11	**	15.67	***
Among plants (or anthers) within lines	3.14	n.s.	7.75	*	8.72	***	3.25	***
Among anthers within plants	9.87	***	17.2	***	-	-	1.51	***
Within anthers	70.39	-	60.98	-	76.26	-	79.56	-

† This is a mixed-model anova and therefore no variance component was calculated among combinations. Denominator mean squares and their degrees of freedom were adjusted by approximation (Sokal and Rohlf, 1969).

Univalents, laggards and micronuclei analysed as $\sqrt{(0.5 + \text{data})}$.

n.s. Not significant.

* Significant at the 5% level.

** Significant at the 1% level.

*** Significant at the 0.1% level.

determined by the constitution of the rye pollen grain that happens to function in the primary cross". Nevertheless, the importance of this source of variability is still mostly undocumented. It seems to us that with the emphasis on inbred polyploids and "species building" the importance of outbred and diploid rye as a parent of triticale has been overlooked.

The meioses of durum triticales were then compared directly with the meioses of extracted triticales by a one-tailed "Mann-Whitney" test. As expected PMC's of the extracted triticales divided with fewer irregularities than PMC's of the durum triticales (Table III). Since more of the chromosome arms were paired in the extracted triticales there were fewer univalents in MI to lag and divide late in AI so that finally at the quartet stage fewer chromosomes were excluded in micronuclei.

The improvement of the meiosis of extracted triticales over the meiosis of durum triticales shows that the evolutionary success of hexaploid wheat has pre-adapted the AABB tetraploid component to its incorporation in hexaploid triticale. This means that to some extent adjustments of the genomes of tetraploid wheat to the presence of the squarrosa genome in hexaploid wheat is the same as the accommodations that have to be made for the rye genome in hexaploid triticale.

Chiasma Failure

In the course of this investigation two observations were made that seemed to explain how chromosomal irregularities could arise in the divisions of PMC's of triticale. Firstly, similar sized univalents were often found lying opposite one another, across the equator of the metaphase spindle. Secondly, where most PMC's within one anther had already passed from MI to AI cells still in MI contained more univalents than average. Conversely where most PMC's were still in prophase the few cells that had

TABLE III

One tailed Mann-Whitney tests of the meiotic superiority of extracted triticales over durum triticales

Variable	Extracted triticales		Durum triticales		Differences (Extracted-Durum)		Levels of significance
	Means	Medians	Means	Medians	Means	Medians	
Univalents per PMC	2.10	1.84	2.71	2.21	-0.62	-0.37	*
Arm pairs per PMC	34.86	35.22	33.54	33.67	+1.33	+1.55	*
Anaphase laggards per PMC	1.93	1.26	2.35	2.04	-0.42	-0.78	*
Micronuclei per sporocyte	0.50	0.38	0.81	0.58	-0.32	-0.20	*

* Significant at the 5% level.

entered MI already, often showed fewer univalents than average.

Further study showed that developmental stage of the anther was significantly correlated with both the relative frequency of univalents and the relative frequency of arm pairs. (For a discussion of the two statistics correlated the reader is asked to refer to the section on materials and methods.) Correlation of anther stage was negative with arm pairs ($r = -0.3495$, p 0.01) and positive with the number of univalents ($r = 0.3325$, p 0.01) indicating that there was a decline in the number of arm pairs during MI and that this decline allowed univalents to accumulate. Univalents have also been shown to increase in PMC's of triticale between diakinesis and metaphase (Tsuchiya, 1970). Premature disjunction of chromosomes could have occurred throughout MI if the chiasmata were not always able to support the continual pulling of opposing centromeres until general disjunction occurred. The failure of chiasmata in MI may therefore account for much of the chromosomal irregularity of triticale.

Univalents might also appear in PMC's of triticale because of difficulties in the synapsis of homologues or in the formation of chiasmata (Bennet _et al_., 1971; Riley and Bell, 1959; Riley and Miller, 1970). The relative importance of chiasma failure must therefore be assessed by following the progress of metaphase in several lines of triticale separately. This should indicate how many univalents are to be found in cells entering metaphase.

It is worth noting that these differences among anthers within individual plants that were so prominent at MI had largely disappeared by the quartet stage. This can be seen from the small size of the percent variance component of micronuclei among anthers (Table II). Differences among anthers at MI chiefly arose because they represented different stages of the metaphase which itself was changing. Once metaphase was over these dif-

ferences quite naturally disappeared.

The idea that chiasma failure could be a source of univalents in triticale suggests that the duration of MI could have some bearing on meiotic irregularity in this species. The longer MI is prolonged the greater would be the opportunity for chiasma failure. In octoploid triticales held at 20°C MI lasts 1.8 hours (Bennet et al., 1971). It is possible that selection for meiotic stability could produce genotypes that pass through MI rather more briskly than this.

The distribution of arm pairs

It is plain that the number of univalents found at MI will depend not only on the number of arm pairs but also on the way that arm pairs are arranged among all the chromosomes of triticale. Any factor that changed univalent frequencies independently of the number of arm pairs must, therefore, have changed the ways in which arm pairs were distributed.

Therefore, the number of univalents can be compared in two ways. Firstly, the absolute frequency of univalents may be influenced by experiment. Secondly, we can make comparisons of univalent frequencies of only those cells which have the same number of arm pairs. Treatments at three fixed temperatures (data were kindly supplied by Dr. E. N. Larter) showed that as temperatures rose there was a corresponding increase in the number of univalents that was independent of the number of arm pairs (Table IV). Furthermore, using data taken from the present study it was found that univalent frequencies could be changed from triticale to triticale also in a way that was not related to the number of arm pairs (Table IV). Since both genotypic and environmental factors can alter their distribution arm pairs cannot be distributed at random among the chromosomes of triticale. In fact there were usually more univalents

TABLE IV

The influence of (a) temperature and (b) genotype on numbers of univalents when the numbers of arm pairs was held constant

Source of Variation	Mean squares†	Degrees of freedom	"F"	Arithmetic mean	Transformed mean and standard error
(a)					
Fixed temperatures[1]	0.8056	2	10.69***		
15.6°C				2.08	1.18±0.023
21.1°C				2.47	1.24±0.029
26.6°C				2.68	1.28±0.032
Arm pairs‡	6.0376	11	80.11***		
Error	0.0754	960			
(b)					
Wheat parentage	0.4007	3	4.54**		
Stewart '63				1.82	1.12±0.015
Durum 60				2.15	1.18±0.042
Tetra-Thatcher				1.47	1.07±0.025
Tetra-Prelude				1.74	1.11±0.031
Arm pairs‡	8.8868	7	100.61***		
Error	0.0883	1162			

† Sums of squares were adjusted for unequal sample sizes by using harmonic means of N (Snedecor and Cochrane, 1967). Data analysed as $\sqrt{(0.5 + \text{datum}/2)}$.

‡ Temperature: arm pairs were 28, 30-40. Wheat parentage: arm pairs were 31-38.

** Significant at 1% level.

*** Significant at 0.1% level.

than were to be expected if arm pairs had been randomly distributed (Fig. I).

This excess of univalents may support suggestions of Müntzing and others (Larter et al., 1969; Müntzing, 1957; Riley and Bell, 1959; Riley and Miller, 1970; Pieritz, 1970) that univalents seen in triticale were mostly chromosomes of rye. Since this would have meant that only a few chromosomes were to be involved in the irregularity the number of chromosomes unpaired in both arms (univalents) would have been that much greater than if arm pairs were distributed at random among all the chromosomes of triticale.

The direct evidence that the rye genome alone is unstable is based mainly on observations of octoploid triticale (Müntzing, 1957; Pieritz, 1970). However, in one case at least hexaploids can behave differently. Larter and Shigenaga (1972) and Shigenaga et al. (1971) both found no difference in the behavious of the different parental genomes of hexaploid triticale. The relative contributions of each genome were the same to both univalent numbers and to the frequencies of aneuploid types. This makes it likely that arm pairs are distributed with equal probability to each chromosome in the complement of hexaploid triticale.

The observed excess of univalents may, therefore, come about in another way. It was suggested above that univalents were found in MI of triticale because several arm pairs were disjoined before AI began. Ring bivalents should have been quite resistant to the failure of arm pairing because the pull of each centromere against its partner was transmitted more or less evenly among two arm pairs. Rod bivalents by contrast might have been readily converted into univalents since the single arm pair that maintained each rod bivalent had to resist the pull of two opposed

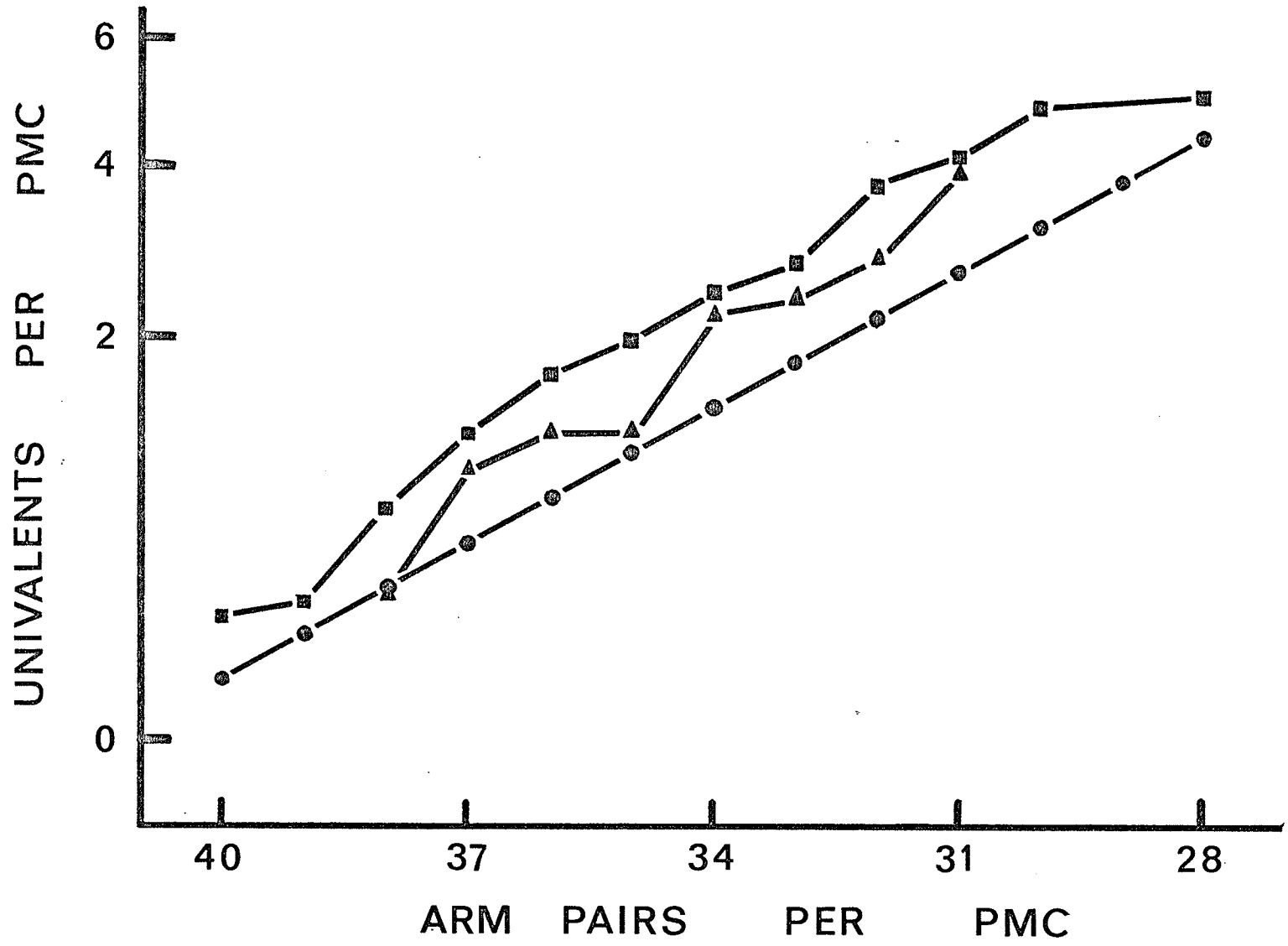
UNIVALENTS PER PMC
6
4
2
0
40
37
34
31
28
ARM PAIRS PER PMC

FIGURE 1

The relationship between numbers of univalents and arm pairs in hexaploid triticale. Circles, relationship predicted assuming arm pairs to be distributed at random; squares, means of three fixed temperature treatments; triangles, means of four groups of genotypes. Univalents scaled as square roots of arithmetic means.

centromeres unaided.

If this were true the excess of univalents is explained because relative to each bivalent type, rod bivalents would have changed into univalents at a rate that was faster than the rate at which ring bivalents were converted into rod bivalents.

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