

A CYTOGENETIC STUDY ON INTRASPECIFIC
RELATIONSHIPS IN TETRAPLOID WHEAT

by

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A Thesis

Submitted to the Committee on Graduate Studies
in Partial Fulfilment of the Requirements
for the Degree of Master of Science

THE UNIVERSITY OF MANITOBA

October 1958

ABSTRACT

Intraspecific relationships within some of the more important tetraploid wheat species were studied, chiefly on the basis of cytology, as a preliminary to interspecific crosses. Four to eleven varieties were selected to represent the range of types found within each of seven species considered to possess the A and B genomes. The varieties within each species were crossed in diallel, making a total of 175 intraspecific crosses.

The F_1 hybrids were grown in a growth cabinet under controlled environmental conditions. Cytological examination of the pollen mother cells showed that the numbers of univalents and open bivalents were only slightly greater in the hybrids than in the parent varieties. Multivalents, mostly in the form of rings, indicating translocations between the parent varieties, were found in 59.4% of the crosses, involving all seven species.

In a sample of the parent plants, cytological variation from floret to floret within the same head was found to exist. Therefore differences observed between crosses may be due partly to normal, non-genetic, variation.

No ratios were obtained for inheritance of morphological characters since the data was for the F_1 generation only. Some characters seemed to be completely dominant, and three were recessive, but in some cases the F_1 was phenotypically intermediate between the parents.

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ACKNOWLEDGEMENTS

Grateful acknowledgement is made to Dr. B. C. Jenkins for his help in planning this study, and for his advice and assistance during the course of the work and preparation of the manuscript.

Special thanks are extended to Professor L. H. J. Shebeski for his interest throughout the course of the work and for his helpful criticism and advice in the preparation of the manuscript.

The writer is indebted to Miss Hung-Shu Wang for help with the crossing and to Mr. Laurie Evans for help with crossing and cytology.

INTRODUCTION

Since the time of Linnaeus, who first placed all the cultivated wheats under the single genus Triticum, many taxonomists have worked on the classification of wheat. For the most part this has been done on the basis of morphology, without any reference to cytology. The 28-chromosome wheats have been divided into a number of different species, but their taxonomy is by no means clear-cut. Most authorities recognise about eight or nine tetraploid species, but there is no general agreement on this point.

This lack of agreement is indicative of the confusion that exists in wheat taxonomy generally. From a study of the available literature, it is often difficult to arrive at any clear distinction between one species and another, and, indeed, it is doubtful if there is any clear distinction between some of the species.

Each species is made up of a number of varieties, but a given variety may sometimes be allocated to different species, depending upon which classification is being followed.

In an attempt to clarify the situation, it was decided to make a cytological study of the more important species in the tetraploid group, to see if the cytological evidence would substantiate the morphological classification. In view of the confusion that exists, it seemed advisable to examine the intra-specific relationships first, so that representative varieties could be selected for interspecific crosses later.

Pairing at first meiotic metaphase in a hybrid is considered to be one index of degree of relationship between the two parents. Consequently, for this thesis, it was decided to make a series of intraspecific crosses and to examine the F_1 plants and their parents cytologically and morphologically.

REVIEW OF LITERATURE

The literature on the tetraploid species of Triticum can be divided into two sections, taxonomic and cytological. The former is quite extensive, but there is not very much of the latter. The term "tetraploid" was not used until after the chromosomes of wheat had been counted, but in the following review it will be used to designate the species now known to possess 28 chromosomes. It is surprising that the older taxonomists, lacking a knowledge of chromosome number, were able to separate the 28-chromosome wheats from the 14-chromosome and 42-chromosome species.

Taxonomy

As mentioned in the introduction, the taxonomy of the genus Triticum is in a very confused state. As a result of this, there is a lack of adequate, workable, keys to species and botanical varieties. Descriptions of varieties (except for some of the commercially-grown varieties) are not generally available. With the existing keys it is extremely difficult and sometimes impossible to classify species and varieties accurately.

Of the literature available, Percival's monograph (7) is one of the most useful publications. It is a standard work on taxonomy and morphology of the wheat plant. He reviewed the older literature on the classification of the genus Triticum and described some new species. The tetraploid

species, as outlined by Percival, will be considered briefly here. T. turgidum was described by Linnaeus in 1753, and T. polonicum in 1764. Desfontaines described T. durum in 1798. All the wheats which had a brittle rachis and were not free-threshing were for a time classified as T. spelta (a hexaploid species). Schrank, in 1789, thought that the emmers (with laterally-compressed heads) should be separated from the true speltas (with lax, non-compressed heads). This was done by Schubler in 1818 when he called the emmers T. dicoccum. Wild emmer, T. dicoccoides, was described by Kornicke in 1908. A number of other species were named by different taxonomists but most were subsequently referred to the above species. Percival described two new tetraploid species, T. orientale and T. pyramidale, but these are not recognised as species by all taxonomists, e.g. Flaksberger (4).

Contrary to many of the older taxonomists, who used floral characters, Percival considered the vegetative characters to be important in classification because he believed these characters had been relatively uninfluenced by selection. For example, he found the length, amount, and arrangement of hairs on young leaf blades to be more constant and characteristic of a species than the size, shape, and colour of grain. However, he continued to use Kornicke's scheme, i.e. characters of the ear, in his keys to varieties.

Percival recognised 195 varieties, of which 124 belonged to the seven tetraploid species. It is to be noted

that he did not give a key to the species of Triticum, merely a general description of each species. He pointed out that there are transitional types, particularly between durum, turgidum, and the European forms of dicoccum. Percival's T. dicoccum var. persicum has since been raised to specific rank by Vavilov (12).

Vavilov's geographical-ecological approach to taxonomy was somewhat different from Percival's. He separated the species into sub-species according to area of origin, e.g. T. durum was divided into ssp. abyssinicum and ssp. expansum (having a wide distribution); T. turgidum and T. polonicum were each divided into ssp. abyssinicum and ssp. mediterraneum; T. dicoccum had three sub-species, ssp. abyssinicum, ssp. europaeum, and ssp. asiaticum. Physiological characters, e.g. date of maturity, resistance to disease, reaction to temperature and moisture, were found to be reasonably constant within any one sub-species. By 1935, 650 varieties of wheat had been determined, many more than were known to Percival.

Clark and Bayles (3) state that the work of Flaksberger et al. (4) has been outstanding and that these authorities have given more attention to a study of the species and varieties of wheat than any other recent workers. Their classification gives keys to forms as well as to species and varieties. The only English translation available is a key to the species (Appendix I), published by Clark and Bayles (3).

Flaksberger's key is not satisfactory for separating the tetraploid species. This is chiefly due to the fact that no sharp distinction exists between some of the species and therefore it is impossible to construct a key to distinguish them.

Flaksberger does not recognise T. pyramidale or T. orientale and presumably includes them in T. durum. Since there are transitional types between T. pyramidale and T. durum and also between T. durum and T. orientale, it is probably an advantage to include all these types in T. durum. Distinctions made between T. durum and T. turgidum in the key do not correspond with the characteristics of the material used in this thesis. Clark and Bayles state that some varieties of T. turgidum and T. durum are so nearly alike that it is difficult to separate one species from the other. T. dicoccum in Flaksberger's key includes only forms which are laterally compressed and not free-threshing. The Abyssinian emmers, classified by Percival as T. dicoccum, are free-threshing and not compressed. These have been separated by Flaksberger as T. abyssinicum, and this appears to be a definite advantage. The distinction between T. abyssinicum and T. persicum is, however, not very great, and transitional types exist. On the whole, Flaksberger's classification seems more logical than that of Percival.

Cytology

Since 1918, when Sax and Sakamura, independently, first counted the chromosomes of wheat (Percival, 7) much

has been published on the cytology of T. vulgare and its hybrids, but the tetraploids have been almost entirely neglected.

Thompson and Robertson (11) published results of twelve crosses between six tetraploids, and only one of these crosses, that between Vernal and Khapli, both of which are varieties of T. dicoccum, was intraspecific. The number of univalents at metaphase and anaphase was recorded. "Percentage irregularity" was 0.5 - 3.4 in the parents, and 1.8 - 26.9 in the hybrids. The Vernal x Khapli cross was 24.5% irregular, i.e. although an intraspecific cross, it was one of the more irregular ones.

Love (6) studied meiosis in pentaploid F₁ hybrids. Vernal, Khapli, Iumillo, and Pentad were the tetraploid varieties used, and they had 0.02 to 0.36 univalents per cell. When these varieties were crossed with hexaploids, a few quadrivalents and higher associations were found. Hybrids with Pentad were exceptional in having 0.639 to 1.139 quadrivalents per cell.

Kostoff (5) reviewed a great deal of work concerning crosses with T. timopheevi. When T. timopheevi was crossed with T. turgidum, T. polonicum, T. persicum, and T. durum, 7-14 bivalents were recorded. However, there were three different varieties of T. durum, having 7-9, 9-10, and 8-13 bivalents respectively. This may indicate differences between the three durum varieties, but, as the number of cells examined is not stated, the results cannot be regarded as conclusive.

Bell and Sachs (2) examined T. dicoccoides vars. nudiglumis and kotschyanum, T. dicoccum var. farrum, T. turgidum var. iodurum, and T. durum var. coerulescens. The variety nudiglumis had 12.92 closed bivalents, 1.06 open bivalents, and 0.04 univalents per cell. All the others had approximately 13.50 closed bivalents and no univalents.

Sachs (8) crossed several tetraploid species (including the two dicoccoides varieties mentioned above) with T. timopheevi, and reported the following results:

		I	II	III	IV
<u>kotschyanum</u>	x <u>timopheevi</u>	5.62	10.00	0.74	0.04
<u>nudiglumis</u>	x "	0.20	13.90	0	0
"	x <u>kotschyanum</u>	10.16	8.02	0.60	0

Thus he found more cytological disturbance in an intra-specific hybrid than he found in interspecific hybrids. Despite normal meiosis, the nudiglumis x timopheevi hybrids had only 5% good pollen and no seeds were produced. In view of these results, the validity of the classification of these varieties may well be doubted.

Regarding translocations, there seem to be very few references. Possibly the quadrivalents mentioned by Love (6) indicate translocations between Pentad and the hexaploids with which it was crossed. Sakanaga (9) reported up to 37% quadrivalents in a hybrid (Carleton x S. cereale) x Iumillo, and stated that the progenies segregated into ring-forming and normal plants. Rings were also formed when (Carleton x S. cereale) was crossed with two other durums, i.e. Stewart and

F.P.I. 94587. Sakanaga thought this indicated translocations between the different durum varieties.

The Index Seminum of the Max-Planck-Institut (15) was found useful as an reference for names of botanical varieties and for the authorities for these names. Less comprehensive seed lists are published by the German Academy of Science (14) and by the All-Union Institute of Plant Industry, Leningrad (13).

MATERIALS AND METHODS

Forty-nine varieties belonging to seven tetraploid species, as follows, were used for the intraspecific crosses in this study.

<u>T. dicoccoides</u>	5	varieties
<u>T. dicoccum</u>	8	"
<u>T. persicum</u>	4	"
<u>T. orientale</u>	4	"
<u>T. pyramidale</u>	6	"
<u>T. durum</u>	11	"
<u>T. turgidum</u>	<u>11</u>	"
Total	<u>49</u>	

These varieties were selected because they differed in one or more characteristics, and represented as far as possible the range of types found within each species. Table I gives some general characteristics of the species with reference to the particular varieties used in this study. The only available descriptions of species are those to be found in Percival (7) and in Flaksberger (4). Percival regards T. persicum as a variety of T. dicoccum. Flaksberger does not recognise T. orientale or T. pyramidale (presumably these are incorporated in T. durum). Consequently, descriptions taken from these authors would not adequately describe the material used in this thesis. Table I was prepared from notes made on material grown in the field and in the growth cabinet. Descriptions are very brief but most characteristics are common

to several if not all the species and cannot be used to distinguish one species from another.

The characteristics of the varieties are listed in more detail in Table II. These characteristics are all to some extent quantitative, but in order to tabulate them, it has been necessary to describe each characteristic in two or three terms, e.g. leaves have been described as "pubescent", "intermediate", or "glabrous", whereas there are all degrees of pubescence, and it varies on different leaves of the same plant. The term "glabrous" has been used, but close inspection shows that most varieties have at least some short hairs on the leaf surfaces (Percival, 7).

The figures for head density (i.e. number of spikelets per 10 cm. of rachis) are only approximate. Only a few heads of each variety were available when the measurements were made, so each figure is based on two heads.

Glume shape, and shape of the keel tooth, cannot be adequately described in a table, but some fairly conspicuous differences were observed when the varieties were compared with each other. These characteristics were not particularly constant within species, however.

Since the authorities for varietal names are in some doubt, the authorities have not been used in the text, but are set out in Appendix II.

Table I: Some general characteristics of the species with reference to the particular varieties used in this study

<u>Species</u>	<u>Characteristics</u>
<u>T. dicoccoides</u>	Heads laterally compressed, rachis brittle, glumes hard and tightly enclosing the seed.
<u>T. dicoccum</u>	With the exception of Nero, heads laterally compressed, rachis rather brittle, glumes hard and tightly enclosing the seed. (Nero has free-threshing heads, not laterally compressed.)
<u>T. persicum</u>	Characterised by lax, free-threshing heads, with a long tooth or short awn on the outer glume.
<u>T. orientale</u>	Heads free-threshing, usually rather lax, with fairly long, pubescent glumes.
<u>T. pyramidale</u>	Heads free-threshing, fairly short and dense. Leaves usually rather wide.
<u>T. durum</u>	Heads free-threshing. It is impossible to pick out any particular character which distinguishes <u>T. durum</u> from all other species.
<u>T. turgidum</u>	Heads free-threshing. This species is equally indefinable. It is difficult to distinguish some varieties of <u>T. turgidum</u> from some varieties of <u>T. durum</u> .

Table II: Morphological characteristics of the parent varieties

Variety	Glumes		colour at maturity	Awns	Head density	Leaf pubescence	Cilia on auricles
	pubescent	glaucous		colour at maturity	Sp./10 cm. of rachis		
<u>T. dicoccoides</u>							
<u>aaronsohni</u> (1)*	no	yes	white	white	20	pubescent	yes
<u>aaronsohni</u> (2)	no	no	brown, shiny	brown	20	pubescent	no
<u>kotschyenum</u> **	yes	no	white	white	20	intermed.	no
<u>pseudo-rufo-villosum</u> ***	densely	yes	reddish	black	18	intermed.	yes
<u>tumanjani</u> ****	no	yes	white	white	21	pubescent	no

* Lower leaf sheaths are covered with conspicuous, erect hairs.

** This variety should not have pubescent glumes (Percival, 7).

*** Glume pubescence is variable. Some heads are less pubescent than others.

**** Head slightly branched.

Table II (cont'd.): Morphological characteristics of the parent varieties

Variety	Glumes		colour at maturity	Awns colour at maturity	Head density Sp./10 cm. of rachis	Leaf pubescence	Cilia on auricles
	pubescent	glaucous					
<u>T. dicoccum</u>							
<u>arras*</u>	no	yes	white	white	26	pubescent	yes
<u>nigro-ajar</u>	no	yes	white	white	26	pubescent	yes
<u>rufum</u>	no	yes	reddish	reddish	21	pubescent	yes
Khapli	no	no	white	white	20	pubescent	yes
Nero**	no	yes	purple-streaked	purple	17	intermed.	no
Yaroslav	no	yes	white	white	23	pubescent	yes
"pubescent"***	densely	yes	white	black	21	pubescent	yes
"compact"***	no	yes	white	white	42	pubescent	no

* Heads slightly branched. Looks very like T. dicoccoides var. tumanjani.

** Heads not laterally compressed, rachis tough, glumes free-threshing. Not a typical dicoccum. Seeds purple.

*** Unnamed varieties.

Table II (cont'd.): Morphological characteristics of the parent varieties

Variety	Glumes			Awns	Head density	Leaf pubescence	Cilia on auricles
	pubescent	glaucous	colour at maturity	colour at maturity	Sp./10 cm. of rachis		
<u>T. persicum</u>							
<u>fuliginosum</u> *	yes	slightly	black	black	13	intermed.	no
<u>rubiginosum</u> **	no	yes	black-streaked	black	18	glabrous	no
<u>stramineum</u> *	no	yes	white	white	17	intermed.	no
<u>T. persicum</u> (4)	no	yes	black-streaked	black	17	glabrous	no
<u>T. orientale</u>							
<u>insigne</u>	yes	yes	white	white	15	intermed.	no
<u>notabile</u> (1)	yes	yes	white	black	29	intermed.	no
<u>notabile</u> (2)	yes	yes	white	black	14	intermed.	no
Gigante ingles	yes	yes	white	black	22	intermed.	no

* Outer glumes bear awns about 3-5 cm. long.

** Some plants had black, pubescent glumes.

Table II (cont'd.): Morphological characteristics of the parent varieties

Variety	Glumes		colour at maturity	Awns colour at maturity	Head density Sp./10 cm. of rachis	Leaf pubescence	Cilia on auricles
	pubescent	glaucous					
<u>T. pyramidale</u>							
<u>albo-rubrum*</u>	no	yes	reddish	reddish	27	glabrous	no
<u>nigritans</u>	yes	no	black	black	24	glabrous	no
<u>pseudo-copticum</u>	no	no	white	white	34	glabrous	no
<u>recognitum</u>	no	no	white	white	32	glabrous	no
<u>thebaicum</u>	yes	no	white	black	27	glabrous	no
Beladi 164	no	yes	white	white	32	glabrous	no

* Glume shape and size were variable.

Table II (cont'd.): Morphological characteristics of the parent varieties

Variety	Glumes			Awns	Head density	Leaf pubescence	Cilia on auricles
	pubescent	glaucous	colour at maturity	colour at maturity	Sp./10 cm. of rachis		
<u>T. durum</u>							
Bald Medeah	no	yes	bluish-red	(awnless)	27	glabrous	no
<u>erethromelan</u>	no	yes	reddish	black	23	glabrous	no
Stewart	no	yes	reddish	reddish	22	glabrous	no
<u>leucurum</u>	no	yes	white	white	23	glabrous	no
Golden Ball ¹	yes	yes	white	black	28	glabrous	no
<u>murciense</u>	no	yes	reddish	reddish	23	glabrous	no
<u>provinciale</u>	no	yes	bluish-red	black	19	glabrous	no
<u>reichenbachii</u> ²	yes	yes	white	black	22	glabrous	no
Kahla ³	yes	yes	blue-black	black	24	glabrous	no
Camadi ⁴	no	yes	white	white	15	glabrous	no
"smooth-awn" ⁵	yes	no	white	black	31	glabrous	no

1 Head indistinguishable from T. turgidum var. melanatherum.

2 Glumes should not be pubescent (Percival, 7).

3 Pubescence, colour, tooth on glume, are all variable.

4 Purple seeds. Practically identical with T. dicoccum Nero.

5 Unnamed variety. Pubescence and size of glumes, and smoothness of awns, are variable.

Table II (cont'd.): Morphological characteristics of the parent varieties

Variety	Glumes			Awns	Head density	Leaf pubescence	Cilia on auricles
	pubescent	glaucous	colour at maturity	colour at maturity	Sp./10 cm. of rachis		
<u>T. turgidum</u>							
<u>buccale</u>	yes	yes	white	white	25	pubescent	yes
<u>dinurum</u> *	yes	yes	reddish	black	20	glabrous	yes
<u>dreischianum</u>	no	yes	reddish	reddish	20	intermed.	yes
<u>gentile</u> **	yes	yes	white	white	27	intermed.	yes
<u>megalopolitanum</u>	yes	slight	white	white	24	pubescent	yes
<u>melanatherum</u> ***	yes	yes	white	black	30	glabrous	no
<u>plinianum</u>	no	yes	white	black	(branched)	intermed.	yes
<u>ramoso-megalopolitanum</u>	yes	slight	white	white	(branched)	intermed.	yes
<u>rubrialbum</u>	slight	yes	reddish	black	19	intermed.	no
<u>salomonis</u>	yes	no	white	black	23	glabrous	no
<u>speciosum</u>	no	yes	reddish	reddish	20	intermed.	yes

* Awns should be red (Percival, 7).

** Glumes should not be pubescent (Percival, 7).

*** Glumes should not be pubescent (Percival, 7).

All parental varieties were grown in the field at Winnipeg during the summer of 1957. Morphological notes were taken and crosses were made between the different varieties within each species. Crosses were made in reciprocal, except in the case of the branched-headed varieties of T. turgidum. For the most part, these were used as male parents only, due to the difficulty of emasculating them. In all, 175 crosses were made, involving nearly 350 heads.

Six F₁ plants of each cross were grown in pots in a growth cabinet. In the case of T. durum, T. dicoccoides, T. persicum, T. orientale, and T. pyramidale, six-inch pots were used, with three plants to a pot. The F₁ plants of T. dicoccum and T. turgidum were grown in 3½-inch pots, one plant per pot. Plants of the parent varieties were grown at the same time as the hybrids.

Since the growth cabinet was not large enough to hold all the hybrids at once, four successive plantings were made. To eliminate as far as possible any cytological variation due to changes in environment, conditions of light and temperature were kept the same for each planting. Lights (fluorescent and incandescent) were on for 18 hours per day. The temperature was maintained at approximately 55°F. for the first three weeks after germination, then gradually increased to approximately 68°F. at the time of P.M.C. formation.

The first head from each plant was collected for cytological examination. The fixative used was Carnoy's

fluid "A", and anthers were stained with acetocarmine according to the technique of Smith (10).

At first, three plants from each cross were examined, but no great differences between plants were found. Thereafter only two plants per cross were examined, a third one being included only if the first two gave widely divergent results.

As far as possible, 50 cells at first metaphase were checked in each plant. The 50 cells usually came from one anther but sometimes this was impossible. The number of univalents, open bivalents, closed bivalents and higher associations were recorded. It became apparent that different florets within one head could give somewhat different results, so it was decided to examine this variation in some of the parent varieties. To do this, 50 cells from two different florets were checked, the florets being from different parts of the same head.

As soon as the first head had been collected for cytological examination, each plant was removed from the growth cabinet and grown to maturity in the greenhouse. The morphological characteristics were recorded at all stages of growth, and each plant was carefully compared with the parent varieties to make sure none was the result of self-pollination.

RESULTS AND DISCUSSION

Four hundred and sixty-nine plants were examined cytologically (102 plants of the parent varieties and 367 hybrids). The numbers of univalents, open bivalents, closed bivalents, rings or chains of four, and rings or chains of six, per cell, have been recorded and this information is set out in Tables III to IX and XII to XXV. The last column in these tables shows the number of cells (usually 50) examined in each plant. Whenever possible these cells were all from one anther.

Results for the parent varieties are set out in Tables III to IX. Each table represents the data for the varieties within one species. Table X shows that some non-genetic variation exists from floret to floret within heads in a sample of the parent varieties. It was thought that this variation might be correlated with position on the head, so in Table XI the closed bivalents were listed according to position of the spikelet on the head. A paired "t" test showed the difference between upper and lower spikelets to be not significant.

Tables XII to XXV contain the data for the hybrids. For each intraspecific group of crosses there is a general table of cytological results followed by a summary table of translocations. These summary tables have been set up to demonstrate the relationship between the varieties of each species with respect to translocations. An interpretation of the translocations follows.

Finally Table XXVI is a brief comparison of numbers of univalents and open bivalents in both parents and hybrids.

Table III: Metaphase I of meiosis in the parent varieties - T. dicoccoides

Variety	Univalents per cell		Open II per cell		Closed II per cell		Total II per cell	No. of cells
	Range	Mean	Range	Mean	Range	Mean		
aaronsohni (1)			0-2	0.34	12-14	13.66	14.00	50
			0-3	0.92	11-14	13.08	14.00	50
aaronsohni (2)	0-2	0.04	0-3	0.48	10-14	13.50	13.98	50)
			0-3	0.64	11-14	13.36	14.00	50) same head
			0-4	0.70	10-14	13.30	14.00	50
			0-2	0.64	12-14	13.36	14.00	50
kotschyanum			0-2	0.28	12-14	13.72	14.00	50
			0-2	0.14	13-14	13.86	14.00	50
pseudo-rufovillosum	0-2	0.12	0-3	0.50	11-14	13.44	13.94	50)
			0-2	0.04	13-14	13.78	13.98	50) same head
	0-2	0.04	0-3	0.40	11-14	13.60	14.00	50)
			0-3	0.94	11-14	13.04	13.98	50) same head
tumanjani	0-2	0.04	0-5	1.22	9-14	12.76	13.98	50)
			0-3	0.86	11-14	13.14	14.00	50) same head
			0-4	1.32	10-14	12.68	14.00	50
			0-5	1.73	9-14	12.27	14.00	37

Table IV: Metaphase I of meiosis in the parent varieties - T. dicoccum

Variety	Univalents per cell		Open II per cell		Closed II per cell		Total II per cell	No. of cells
	Range	Mean	Range	Mean	Range	Mean		
arras			0-2	0.28	12-14	13.72	14.00	50
			0-2	0.48	12-14	13.52	14.00	50
Yaroslav			0-3	0.58	11-14	13.42	14.00	50
			0-3	0.48	11-14	13.52	14.00	50
"compact"	0-2	0.04	0-3	0.50	11-14	13.48	13.98	50
			0-2	0.50	12-14	13.50	14.00	50
rufum	0-2	0.04	0-4	0.58	10-14	13.40	13.98	50
			0-3	0.74	11-14	13.26	14.00	50
nigro-ajar	0-2	0.08	0-6	1.76	8-14	12.20	13.96	50
			0-4	0.92	10-14	13.08	14.00	50
Nero	0-4	0.80	0-8	3.70	6-14	9.90	13.60	50
	0-2	0.22	0-6	1.64	8-14	12.25	13.89	55
Khapli	0-4	1.28	0-9	4.48	5-14	8.88	13.36	50
	0-2	0.12	0-5	2.10	9-14	11.84	13.94	50
"pubescent"	0-2	0.08	0-6	1.50	7-14	12.46	13.96	50

Table V: Metaphase I of meiosis in the parent varieties - T. persicum

Variety	Univalents per cell		Open II per cell		Closed II per cell		Total II per cell	No. of cells
	Range	Mean	Range	Mean	Range	Mean		
fuliginosum	0-2	0.04	0-3	0.48	11-14	13.50	13.98	50
			0-4	1.04	10-14	12.96	14.00	50
stramineum	0-2	0.04	0-3	0.76	11-14	13.22	13.98	50
			0-4	1.13	10-14	12.87	14.00	61
rubiginosum	0-2	0.16	0-5	2.08	9-14	11.84	13.92	50
	0-2	0.04	0-4	1.71	10-14	12.27	13.98	51
T. persicum (4)	0-4	0.16	0-5	1.82	9-14	12.10	13.92	50
	0-2	0.08	0-5	2.15	9-14	11.81	13.96	48

Table VI: Metaphase I of meiosis in the parent varieties - T. orientale

Variety	Univalents per cell		Open II per cell		Closed II per cell		Total II per cell	No. of cells	
	Range	Mean	Range	Mean	Range	Mean			
insigne			0-4	1.02	10-14	12.98	14.00	50	
	0-4	0.12	0-4	1.44	10-14	12.50	13.94	50)	same head
	0-4	0.52	0-5	1.76	9-14	11.98	13.74	50)	
	0-2	0.12	0-4	1.18	10-14	12.76	13.94	50)	same head
0-2	0.08	0-4	1.12	10-14	12.84	13.96	50)		
notabile (1)			0-2	0.28	10-14	13.72	14.00	50	
			0-4	1.16	10-14	12.84	14.00	50)	same head
	0-2	0.04	0-4	0.44	10-14	13.54	13.98	50)	
notabile (2)			0-3	0.50	11-14	13.50	14.00	50	
			0-2	0.42	12-14	13.58	14.00	50	
			0-2	0.34	12-14	13.66	14.00	29)	same head
			0-2	0.50	12-14	13.50	14.00	50)	
Gigante ingles			0-4	0.98	10-14	13.02	14.00	50	
			0-4	1.02	10-14	12.98	14.00	50	

Table VII: Metaphase I of meiosis in the parent varieties - T. pyramidale

Variety	Univalents per cell		Open II per cell		Closed II per cell		Total II per cell	No. of cells
	Range	Mean	Range	Mean	Range	Mean		
pseudo-copticum	0-2	0.04	0-3	0.52	11-14	13.48	14.00	50
			0-4	0.84	10-14	13.14	13.98	50
albo-rubrum	0-2	0.04	0-3	1.14	11-14	12.86	14.00	50
			0-4	1.54	10-14	12.44	13.98	50
nigritans	0-2	0.08	0-5	2.22	9-14	11.74	13.96	50
	0-2	0.12	0-5	2.22	9-14	11.72	13.94	50
thebaicum	0-2	0.24	0-4	1.88	10-14	12.00	13.88	50
	0-2	0.20	1-7	2.40	7-13	11.50	13.90	50
Beladi	0-4	0.40	0-6	2.26	8-14	11.54	13.80	50
	0-4	0.52	0-9	2.64	4-14	11.10	13.74	50
	0-4	0.12	0-4	1.36	10-14	12.58	13.94	50
recognitum	0-4	0.72	1-10	3.70	4-13	9.94	13.64	50

Table VIII: Metaphase I of meiosis in the parent varieties - T. durum

Variety	Univalents per cell		Open II per cell		Closed II per cell		Total II per cell	No. of cells
	Range	Mean	Range	Mean	Range	Mean		
Bald Medeah			0-2	0.42	12-14	13.58	14.00	50
			0-2	0.44	12-14	13.56	14.00	50
Golden Ball			0-3	0.72	11-14	13.28	14.00	50
			0-4	1.00	10-14	13.00	14.00	50
leucurum			0-3	0.44	11-14	13.56	14.00	50)
			0-4	1.42	10-14	12.58	14.00	50) same head
provinciale			0-2	0.54	12-14	13.46	14.00	50
			0-2	0.40	12-14	13.60	14.00	50
"smooth-awn"			0-2	0.30	12-14	13.70	14.00	50)
			0-3	0.32	11-14	13.68	14.00	50) same head
			0-2	0.30	12-14	13.70	14.00	50
Kahla			0-3	0.62	11-14	13.38	14.00	50
			0-3	0.34	11-14	13.66	14.00	50
			0-3	0.40	11-14	13.60	14.00	50)
			0-3	0.38	11-14	13.60	13.98	50) same head
	0-2	0.04						

Table VIII (cont'd.): Metaphase I of meiosis in the parent varieties - T. durum

Variety	Univalents per cell		Open II per cell		Closed II per cell		Total II per cell	No. of cells	
	Range	Mean	Range	Mean	Range	Mean			
murciense			0-4	1.24	10-14	12.76	14.00	50)	same head
	0-2	0.04	0-6	1.84	8-14	12.14	13.98	50)	
	0-2	0.12	0-7	0.90	7-14	13.04	13.94	50	
	0-2	0.04	0-6	1.18	8-14	12.80	13.98	50)	
	0-2	0.08	0-4	1.82	10-14	12.14	13.96	50)	
erethromelan	0-2	0.12	0-6	1.90	8-14	12.04	13.94	50)	same head
	0-2	0.16	0-6	2.56	8-14	11.36	13.92	50)	
	0-2	0.12	0-6	2.42	8-14	11.52	13.94	50	
reichenbachii			0-6	1.40	8-14	12.60	14.00	30)	same head
	0-2	0.32	1-8	4.38	6-13	9.46	13.84	50)	
	0-2	0.12	0-7	2.38	7-14	11.56	13.94	50	
	0-2	0.16	1-6	3.38	8-13	10.54	13.92	50)	
	0-2	0.16	0-6	1.90	8-14	12.02	13.92	50)	
Stewart			0-4	0.78	10-14	13.22	14.00	40	same head
	0-2	0.20	0-5	1.58	9-14	12.32	13.90	50)	
	0-2	0.32	0-5	1.84	9-14	12.00	13.84	50)	
Camadi	0-2	0.12	0-6	2.44	8-14	11.50	13.94	50	

Table IX: Metaphase I of meiosis in the parent varieties - T. turgidum

Variety	Univalents per cell		Open II per cell		Closed II per cell		Total II per cell	No. of cells
	Range	Mean	Range	Mean	Range	Mean		
buccale			0-2	0.34	12-14	13.66	14.00	50
			0-2	0.48	12-14	13.54	14.00	50
gentile			0-4	0.68	10-14	13.32	14.00	50
			0-2	0.48	12-14	13.52	14.00	50
megalopolitanum			0-2	0.58	12-14	13.42	14.00	50
salomonis			0-2	0.44	12-14	13.56	14.00	50
			0-2	0.26	12-14	13.74	14.00	50
rubrialbum			0-2	0.64	12-14	13.36	14.00	50
			0-2	0.40	12-14	13.60	14.00	50
dinurum			0-4	0.82	10-14	13.18	14.00	50
			0-2	0.48	12-14	13.52	14.00	50
plinianum	0-2	0.04	0-4	0.82	10-14	13.16	13.98	50
	0-2	0.04	0-5	0.76	9-14	13.22	13.98	50
ramoso- megalopolitanum			0-3	0.50	11-14	13.50	14.00	50
	0-2	0.04	0-3	0.34	11-14	13.64	13.98	50
speciosum	0-2	0.04	0-2	0.90	12-14	13.08	13.98	50
	0-2	0.08	0-2	0.50	12-14	13.46	13.96	50
melanatherum			0-3	0.66	11-14	13.34	14.00	50
	0-2	0.04	0-5	1.50	9-14	12.48	13.98	50
dreischianum			0-4	1.10	10-14	12.90	14.00	50
	0-2	0.08	0-4	1.23	10-14	12.73	13.96	47

Table X: Differences in numbers of univalents and open bivalents within plants of T. dicoccoides, T. orientale, and T. durum

Variety	Univalents			Open Bivalents		
	Floret (a)	Floret (b)	Difference	Floret (a)	Floret (b)	Difference
<u>T. dicoccoides</u>						
<u>aaronsohni</u> (2)	0	0.04	-0.04*	0.64	0.48	0.16
<u>pseudo-rufovillosum</u>	0.12	0.04	0.08	0.50	0.20	0.30
"	0.04	0	0.04	0.94	0.40	0.54
<u>tumanjani</u>	0.04	0	0.04	1.22	0.86	0.36
<u>T. orientale</u>						
<u>insigne</u>	0.52	0.12	0.40	1.76	1.44	0.32
"	0.12	0.08	0.04	1.18	1.12	0.06
<u>notabile</u> (1)	0	0.04	-0.04*	1.16	0.44	0.72
<u>notabile</u> (2)	0	0	0	0.50	0.34	0.16
<u>T. durum</u>						
<u>leucurum</u>	0	0	0	1.42	0.44	0.98
"smooth-awn"	0	0	0	0.32	0.30	0.02
Kahla	0	0.04	-0.04*	0.40	0.38	0.02
<u>murciense</u>	0.04	0	0.04	1.84	1.24	0.60
"	0.08	0.04	0.04	1.82	1.18	0.64
<u>erethromelan</u>	0.16	0.12	0.04	2.56	1.90	0.66
<u>reichenbachii</u>	0.32	0	0.32	4.38	1.40	2.98
"	0.16	0.16	0	3.38	1.90	1.48
Stewart	0.32	0.20	0.12	1.84	1.58	0.26
Mean			0.06			0.60

* Except for these three cases, the floret with the higher number of open bivalents also had the higher number of univalents.

Cytological differences between two florets of the same head

It was found that different florets of the same head could give somewhat different results. These differences must have been physiological, i.e. non-genetic and not due to the external environment. It seemed desirable to try to evaluate this variation so that it could be taken into account when assessing differences between parents and hybrids and/or between different hybrids.

It was decided to use some of the parent varieties (in T. dicoccoides, T. orientale, and T. durum) for this purpose. In many heads there was only one floret at the stage of first metaphase but in 17 plants two florets were found. As far as possible, two first florets, or two second florets were used so that the results would be more comparable.

Table X shows the numbers of univalents and open bivalents for two florets in each of 17 plants. The two florets have been called (a) and (b), and (a) is the one with the higher number of open bivalents.

In all but three cases, the floret with the higher number of open bivalents also had the higher number of univalents. This correlation suggests that univalents and open bivalents are both part of the same phenomenon. The mean difference between the (a) florets and the (b) florets proved to be 0.06 univalents and 0.60 open bivalents. As this is only a small sample it is not suggested that these values are an accurate measure of the non-genetic variation, but at least they indicate that

variation exists. This should be borne in mind when comparing cytological results of different plants, since the observed differences may fall within the range of normal non-genetic variation.

Table XI: A comparison of numbers of closed bivalents in upper and lower spikelets within plants of T. dicoccoides, T. orientale and T. durum

	<u>No. of closed bivalents</u>		<u>Position on head</u>		No. of spikelets in head	
	lower spikelet	upper spikelet	fl. sp.	fl. sp.		
<u>T. dicoccoides</u>						
<u>aaronsohni</u> (2)	13.50	13.36	1	6	1 16	25
<u>pseudo-rufovillosum</u>	13.44	13.78*	2	9	2 12	20
"	13.60	13.04	1	7	1 13	17
<u>tumanjani</u>	12.76	13.14*	**1	5	2 21	25
<u>T. orientale</u>						
<u>insigne</u>	12.50	11.98	**2	4	1 14	16
"	12.76	12.84*	1	5	1 11	15
<u>notabile</u> (1)	13.54	12.84	2	4	2 12	17
" (2)	13.66	13.50	2	4	2 11	13
<u>T. durum</u>						
<u>leucurum</u>	13.56	12.58	3	7	3 16	17
"smooth-awn"	13.70	13.68	1	6	1 8	-
Kahla	13.60	13.60	2	4	2 10	-
<u>murciense</u>	12.76	12.14	2	4	2 12	16
"	12.80	12.14	**2	4	1 14	16
<u>erethromelan</u>	12.04	11.36	1	4	1 14	-
<u>reichenbachii</u>	12.60	9.46	**1	4	2 8	16
"	10.54	12.02*	2	4	2 14	16
Stewart	12.32	12.00	1	8	1 11	-
Mean	12.92	12.56				

fl. = floret. The first floret is the most mature floret in each spikelet.

sp. = spikelet. Spikelets are numbered from bottom of head.

* In these four cases there were more closed bivalents in the upper spikelets.

** In these four cases a first floret was being compared with a second floret.

Correlation between cytological variation and position of the spikelet on the head

In the 17 plants previously discussed, the usual method of sampling was first to search for a suitable floret in the lower part of the head and then to find a comparable one in the upper part. It seemed that spikelets towards the top of the head were more irregular, i.e. had more univalents and open bivalents than those near the bottom.

In an attempt to find out if this were really the case, the numbers of closed bivalents in the two florets were listed in Table XI according to position on the head, i.e. those from lower spikelets were placed in one column and those from upper spikelets in another. There is a flaw in the data - in four cases a first floret is being compared with a second floret. (These four items were omitted when a paired "t" test was carried out.)

In all but four cases the lower spikelet had more closed bivalents than the upper one. However a paired "t" test showed the difference to be not significant.

t = 1.00 at 12 D.F. P.05 = 2.18
 P.01 = 3.06

Table XII: Metaphase I of meiosis in the hybrids - T. dicoccoides

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		Ring or ch. VI per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
aaron.(1) x aaron.(2)	0-2	0.04	0-5	1.10	7-12	10.66	0-1	0.72	0-1	0.26	50
aaron.(2) x aaron.(1)	0-2	0.04	0-3	0.84	8-12	10.84	0-1	0.70	0-1	0.30	50
aaron.(1) x tumanjani	0-2	0.16	0-5	1.42	7-10	8.82	0-2	1.84			50
tumanjani x aaron.(1)	0-2	0.32	0-7	1.26	4-10	8.66	0-2	1.96			50
aaron.(1) x pseudo-ruf.	0-2	0.12	0-2	0.60	10-12	11.38	0-1	0.98			50
pseudo-ruf. x aaron.(1)			0-3	0.67	9-12	11.33	1	1.00			54
aaron.(1) x kotschyanum	0-2	0.12	0-5	1.88	7-12	10.06	1	1.00			50
tumanjani x aaron.(2)	0-2	0.20	0-5	1.62	8-12	10.84	0-2	0.72			50
aaron.(2) x tumanjani	0-4	0.56	0-7	2.48	5-12	9.92	0-1	0.66			50
aaron.(2) x pseudo-ruf.	0-2	0.16	0-4	1.58	9-14	11.26	0-1	0.54			50
pseudo-ruf. x aaron.(2)	0-4	0.44	0-6	2.72	5-14	10.10	0-1	0.48			50
aaron.(2) x kotschyanum			0-4	0.86	10-12	11.54	0-1	0.80			50
kotschyanum x aaron.(2)	0-2	0.04	0-5	2.06	7-12	10.44	0-1	0.74			50
tumanjani x pseudo-ruf.	0-2	0.08	0-4	1.28	8-12	10.68	1	1.00			50
pseudo-ruf. x tumanjani			0-5	1.14	7-12	10.86	1	1.00			50
tumanjani x kotschyanum	0-2	0.28	0-6	2.34	6-12	9.68	0-2	0.92			50
kotschyanum x tumanjani	0-2	0.52	0-6	2.76	6-12	9.42	0-2	0.78			50
pseudo-ruf. x kotschy.	0-2	0.12	0-5	1.90	7-14	11.92	0-1	0.06			50
kotschy. x pseudo-ruf.	0-4	0.08	0-5	1.82	9-14	11.98	0-1	0.08			50

Table XIII: Translocations - T. dicoccoides

	aaronsohni (1) a-b	aaronsohni (2) b'-c	tumanjani d-e	pseudo- rufovill. -	kotsch- yanum -?
aaronsohni (1) a-b	-	IV 0.71 VI 0.28	2IV 1.90	IV 0.99	IV 1.00
aaronsohni (2) b'-c		-	IV 0.69	IV 0.51	IV 0.77
tumanjani d-e			-	IV 1.00	2IV 0.85
pseudo-rufovillosum -				-	IV 0.07
kotschyanum -?					-

Roman numerals indicate bivalents, quadrivalents, etc. Arabic numerals indicate the mean number of quadrivalents, etc. per cell for two plants.

T. dicoccoides translocations (Table XIII)

This is perhaps the most difficult group to interpret in terms of translocations. The other groups (the turgidum group in particular) give a much clearer picture, but it is customary to treat the wild species, T. dicoccoides, first, so that procedure is being followed in this thesis.

Before an interpretation of the translocations can be attempted, the data in the table need some explanation. In the cross aaronsohni (1) x aaronsohni (2), there were IV's and VI's but they never occurred in the same cell. Rings and chains were formed in approximately equal numbers. A chain of four might be part of a potential ring of six, but a ring of four is not so easily explained. In the cross kotschyannum x tumanjani only 6% of the cells had two IV's while 73% had one IV per cell. In tumanjani x aaronsohni (2) there were two IV's in only 2% of the cells.

When a plant carrying one translocation is crossed with a normal plant, the hybrid has one quadrivalent per cell. Two translocations with one chromosome in common give rise to one ring of six per cell. Bearing this in mind, a series of translocations is postulated to explain the results in Table XIII. The letters used to designate the translocation have no special significance. The same letters will be used for the other species, though it is not known whether the translocations are the same or not. It would be necessary to make a series of interspecific crosses to determine this.

The variety aaronsohni (1) has the translocation a-b, and aaronsohni (2) has b'-c, b and b' being sufficiently alike to give VI's in 28% of the cells in the hybrid. Suppose the chromosome designated b'-c is almost a normal c chromosome, with only a very small b' segment, and therefore it does not readily form IV's. As a result, the IV's in 71% of the cells are chiefly due to a-b. Assume that tumanjani has the translocation d-e. Then tumanjani x aaronsohni (1) gives two IV's in most of the cells. Now tumanjani x aaronsohni (2) might also be expected to give IV's per cell, but IV's were seen in only two of the cells. Again let us assume that b'-c does not readily give rise to IV's.

The variety pseudo-rufovillosum can be regarded as lacking translocations. The translocations already postulated for the other varieties would account for the IV's in the hybrids with pseudo-rufovillosum, though here b'-c gives rise to IV's in 51% of the cells, a higher percentage than expected for this particular translocation.

The variety kotschyanum differs a little from pseudo-rufovillosum since the cross between these two has 0.07 IV's per cell. The hybrids with kotschyanum give somewhat different results from those with pseudo-rufovillosum but it is difficult to interpret these small variations in terms of translocations.

Table XIV: Metaphase I of meiosis in the hybrids - T. dicoccum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
nigro-ajar x Khapli	0-2	0.44	0-7	3.38	7-13	10.40			50
Khapli x nigro-ajar	0-2	0.16	0-7	2.04	7-14	11.88			50
rufum x Khapli	0-6	2.48	0-8	3.98	6-14	8.78			50
Khapli x rufum	0-6	0.80	0-8	3.70	6-13	9.90			50
"pubescent" x Khapli	0-2	0.12	0-6	1.54	8-14	12.40			50
Khapli x "pubescent"	0-2	0.16	0-7	2.20	7-14	11.72			50
rufum x nigro-ajar	0-4	0.76	1-5	2.60	9-13	11.02			50
nigro-ajar x rufum	0-4	0.40	0-5	1.96	7-14	11.84			50
nigro-ajar x "pubescent"	0-2	0.08	0-6	1.50	8-14	12.46			50
" " "	0-2	0.38	0-6	2.91	8-14	10.90			32
rufum x "pubescent"			0-5	1.10	9-14	12.90			50
"pubescent" x rufum			0-4	0.76	10-14	13.24			50
Khapli x arras	0-2	0.16	0-5	1.34	7-12	10.74	0-1	0.92	50
" " "	0-4	0.77	0-4	1.26	8-12	10.67	0-1	0.84	31
Khapli x Yaroslav	0-4	0.72	0-8	3.16	5-12	9.20	0-1	0.64	50
Yaroslav x Khapli	0-2	0.12	0-5	1.68	8-12	10.62	0-1	0.82	50
Khapli x Nero	0-2	0.12	0-5	2.12	6-12	9.86	0-1	0.98	50
Nero x Khapli	0-6	0.52	0-6	2.42	5-12	9.52	0-1	0.90	50

Table XIV (cont'd.): Metaphase I of meiosis in the hybrids - T. dicoccum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
nigro-ajar x arras	0-2	0.04	0-5	1.62	6-12	10.64	0-1	0.86	50
arras x nigro-ajar	0-4	0.08	0-5	1.18	8-12	10.98	0-1	0.90	50
nigro-ajar x Yaroslav	0-2	0.04	0-6	1.54	7-12	10.84	0-1	0.80	50
Yaroslav x nigro-ajar	0-2	0.04	0-4	0.84	8-14	11.58	0-1	0.78	50
nigro-ajar x Nero	0-2	0.08	0-3	0.88	8-11	10.08	1	1.00	VI 50
" "	0-2	0.20	0-5	1.86	7-12	10.16	0-1	0.94	IV 50
" "	0-4	0.69	0-6	3.26	5-13	8.56	0-1	0.57	IV) 50
							0-1	0.23	VI) 50
rufum x arras			0-3	0.54	9-12	11.46	1	1.00	50
arras x rufum			0-5	1.04	7-12	11.04	0-1	0.96	50
rufum x Yaroslav	0-2	0.12	0-4	1.10	8-12	11.20	0-1	0.82	50
Yaroslav x rufum	0-2	0.08	0-5	0.68	9-12	11.48	0-1	0.90	50
rufum x Nero	0-2	0.04	0-4	1.38	8-12	10.86	0-1	0.96	50
" "			0-3	0.92	9-12	11.08	1	1.00	50
"pubescent" x arras	0-2	0.08	0-3	0.94	9-12	11.10	0-1	0.96	50
arras x "pubescent"			0-3	0.76	9-12	11.24	1	1.00	50
"pubescent" x Yaroslav			0-3	0.44	9-12	11.56	1	1.00	50
Yaroslav x "pubescent"	0-2	0.08	0-3	0.76	8-12	11.24	0-1	0.98	50

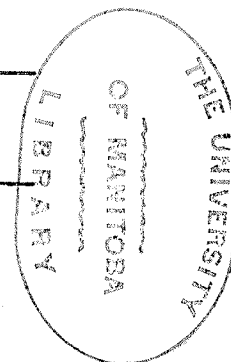


Table XIV (cont'd.): Metaphase I of meiosis in the hybrids - T. dicoccum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
"pubescent" x Nero	0-4	0.73	0-7	3.30	6-12	8.73	0-1	0.80	30
Nero x "pubescent"	0-4	0.28	0-7	2.22	7-12	9.88	0-1	0.88	50
"compact" x Khapli	0-2	0.08	0-5	1.32	7-12	10.60	1-2	1.02	50
" " " "	0-2	0.12	0-7	2.30	5-12	9.56	1-2	1.04	50
nigro-ajar x "compact"			0-3	0.88	9-12	11.12	0-2	1.00	50
" " " "	0-4	0.24	0-6	1.36	8-12	10.58	0-2	0.97	33
"compact" x rufum			0-4	1.08	8-10	9.92	1-2	1.50	50
rufum x "compact"	0-2	0.08	0-5	0.92	5-10	9.88	1-2	1.58	50
"compact" x "pubescent"			0-3	0.60	9-12	10.74	1-2	1.33	45
"pubescent" x "compact"			0-2	0.32	10-12	11.32	1-2	1.18	50
Yaroslav x arras	0-2	0.08	0-2	0.34	8-12	9.90	1-2	1.86	50
arras x Yaroslav	0-2	0.04	0-3	0.78	7-12	9.44	1-2	1.88	50
Nero x arras			0-2	0.64	10-12	9.72	1-2	1.82	50
" " " "			0-2	0.72	9-10	9.40	1-2	1.94	50
"compact" x arras	0-2	0.32	0-7	1.06	6-14	12.30	0-1	0.24	50
" " " "			0-1	0.20	12-14	13.68	0-1	0.06	50
Nero x Yaroslav			0-3	0.76	8-10	9.36	1-2	1.94	34
Yaroslav x Nero			0-3	0.33	9-10	9.75	1-2	1.96	45

Table XIV (cont'd.): Metaphase I of meiosis in the hybrids - T. dicoccum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
"compact" x Yaroslav			0-2	0.68	8-12	10.08	0-2	1.62	50
Yaroslav x "compact"			0-3	0.62	8-12	9.74	1-2	1.82	45
"compact" x Nero			0-3	0.38	9-10	9.70	1-2	1.96	50
Nero x "compact"			0-3	0.74	7-10	9.38	1-2	1.94	50

Table XV: Translocations - T. dicoccum

	Khapli -	nigro-ajar -	rufum -	"pubescent" -	arras a-b	Yaroslav c-d	Nero e-f	"compact" a-b,g-h
Khapli -	-	II	II	II	IV 0.89	IV 0.73	IV 0.94	2IV 1.03
nigro-ajar -		-	II	II	IV 0.88	IV 0.79	*	2IV 0.99
rufum -			-	II	IV 0.98	IV 0.86	IV 0.98	2IV 1.54
"pubescent" -				-	IV 0.98	IV 0.99	IV 0.85	2IV 1.25
arras a-b					-	2IV 1.87	2IV 1.88	IV 0.15
Yaroslav c-d						-	2IV 1.95	2IV 1.70
Nero e-f							-	2IV 1.95
"compact" a-b,g-h								-

Roman numerals indicate bivalents, quadrivalents. Arabic numerals indicate the mean number of quadrivalents per cell for two plants.

* In the cross nigro-ajar x Nero, there were rings of six, as well as rings of four.

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T. dicoccum translocations (Table XV)

The first four varieties, Khapli, nigro-ajar, rufum, and "pubescent", will be referred to as group 1. The next three, arras, Yaroslav, and Nero, form group 2. The varieties in group 1, when crossed with each other, do not form multivalents. Therefore, they have no translocations with respect to each other, though they may have translocations with respect to other species. The members of group 2, when crossed with group 1, give rise to one IV per cell. When crossed with each other, two IV's per cell result. Therefore, each has one translocation and these translocations are different from each other, i.e. a-b, c-d, and e-f. "Compact", the eighth variety, forms only 0.15 IV's per cell with arras. Therefore, these two differ by a translocation g-h which has only a very small effect. The variety arras has been designated a-b, so "compact" is a-b, g-h. "Compact" when crossed with the varieties of group 1 gives two IV's in some of the cells, but the mean is only 0.99 to 1.54 IV's per cell, i.e. g-h has only a small effect as expected.

"Compact" x Yaroslav is a-b, g-h x e-f, i.e. three translocations. Three IV's were not found in any of the cells, so g-h may not exist with respect to e-f. Similar reasoning applies to the "compact" x Nero cross.

There is one anomalous cross, nigro-ajar x Nero. One plant had VI's, another had IV's and a third had some of each. Quadrivalents were expected. The reason for the VI's is unknown.

Table XVI: Metaphase I of meiosis in the hybrids - T. persicum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
fuliginosum x rubiginosum	0-2	0.08	0-4	1.60	8-12	10.68	0-1	0.84	50
" " "	0-2	0.44	0-4	2.36	8-12	10.14	0-1	0.64	50
" " "	0-2	0.16	0-4	1.52	8-12	10.56	0-1	0.92	50
fuliginosum x T. pers.(4)	0-4	0.54	0-4	1.54	8-12	10.35	0-1	0.92	37
" " "	0-2	0.12	0-4	1.20	8-12	10.86	0-1	0.94	50
T. pers.(4) x fuliginosum	0-2	0.08	0-4	1.52	8-12	10.44	1	1.00	50
stramineum x T. pers.(4)	0-2	0.16	0-5	1.62	7-12	10.46	0-1	0.92	50
T. pers.(4) x stramineum	0-4	0.31	0-6	2.27	6-12	10.03	0-1	0.77	26
rubiginosum x T. pers.(4)	0-2	0.04	0-4	2.16	10-14	11.82			50
" " "	0-4	0.40	0-4	2.00	10-13	11.80			50
T. pers.(4) x rubiginosum	0-2	0.14	1-5	2.47	9-13	11.46			55
stramineum x rubiginosum	0-4	0.72	1-7	3.00	7-13	10.64			50
" " "	0-2	0.04	0-5	1.90	9-14	12.08			50
fuliginosum x stramineum	0-2	0.04	0-4	1.56	10-14	12.42			50
stramineum x fuliginosum	0-2	0.04	0-3	1.36	11-14	12.62			50
" " "			0-3	0.84	11-14	13.16			50

Table XVII: Translocations - T. persicum

	fuliginosum -	rubiginosum a-b or -	T. persicum (4) a-b	stramineum -
fuliginosum -	-	IV 0.80	IV 0.95	II
rubiginosum a-b or -		-	II	II
T. persicum (4) a-b			-	IV 0.87
stramineum -				-

Roman numerals indicate bivalents, quadrivalents. Arabic numerals indicate the mean number of quadrivalents per cell for two (or three) plants.

T. persicum translocations (Table XVII)

These results are hard to explain. The most likely explanation is that some plants of rubiginosum carried a translocation while others did not. This variety was variable morphologically. There is cytological data for fuliginosum x rubiginosum and stramineum x rubiginosum but unfortunately none for the reciprocal crosses. Assume that rubiginosum is either a-b or normal, and that T. persicum (4) is a-b. These translocations would explain the cytological data.

Table XVIII: Metaphase I of meiosis in the hybrids - T. orientale

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		Ring or ch. VI per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
insigne x notab.(2)	0-2	0.08	0-3	0.46	9-11	10.56	0-1	0.06	0-1	0.94	50
notab.(2) x insigne			0-3	0.66	8-12	10.38	0-1	0.10	0-1	0.92	50
insigne x Gi. ingles	0-4	0.72	0-7	1.50	4-12	9.72	0-1	0.42	0-1	0.56	50
Gi. ingles x insigne	0-2	0.32	0-7	1.80	7-12	9.28	0-1	0.18	0-1	0.80	50
insigne x notab.(1)	0-4	0.40	0-5	1.58	6-12	9.26	0-1	0.10	0-1	0.92	50
notab.(1) x insigne	0-2	0.12	0-5	1.42	5-11	9.58	0-1	0.12	0-1	0.90	50
notab.(2) x Gi. ingles	0-2	0.28	0-6	2.08	8-14	11.66	0-1	0.06			50
Gi. ingles x notab.(2)	0-4	1.24	0-5	2.00	9-14	11.06	0-1	0.16			50
notab.(2) x notab.(1)	0-2	0.24	0-5	1.72	9-14	12.16					50
notab.(1) x notab.(2)	0-2	0.16	0-6	2.14	8-14	11.30	0-1	0.24			50
notab.(1) x Gi.ingles	0-2	0.08	0-4	1.64	10-14	12.32					50
Gi. ingles x notab.(1)			0-4	1.14	10-14	12.86					50

Table XIX: Translocations - T. orientale

	insigne a-b	notabile (2) b'-c		Gigante ingles b'-c		notabile (1) b'-c	
insigne a-b	-	IV 0.08	VI 0.93	IV 0.30	VI 0.68	IV 0.11	VI 0.91
notabile (2) b'-c		-		IV 0.11		IV 0.12	
Gigante ingles b'-c				-		II	
notabile (1) b'-c						-	

Roman numerals indicate bivalents, quadrivalents, etc. Arabic numerals indicate the mean number of quadrivalents, etc., per cell for two plants.

T. orientale translocations (Table XIX)

All crosses with the variety insigne gave rise to IV's and VI's but these were rarely both in the same cell. There were far more VI's than IV's and the IV's were mostly chains. It is assumed that some potential VI's remained as chains of four. The following translocations are postulated: The variety insigne has the translocation a-b and the other varieties have b'-c, and b' differs from b just enough to prevent regular VI's in all cells. Gigante ingles x notabile (1) does not give rise to multivalents, so these varieties are similar to each other. When crossed with notabile (2) they give rise to a few IV's, so probably the translocation in notabile (2) is slightly different. Alternatively, there may be another very small translocation involved, since just a few of the cells in notabile (1) x insigne had two multivalents.

Table XX: Metaphase I of meiosis in the hybrids - T. pyramidale

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell	No. of cells
	Range	Mean	Range	Mean	Range	Mean		
pseudo-copt. x alborubrum	0-2	0.04	0-5	2.36	9-14	11.62		50
" " "	0-4	1.20	1-8	3.08	6-13	10.32		50
alborubrum x pseudo-copt.	0-2	0.20	0-6	2.64	8-14	11.26		50
pseudo-copt. x Beladi	0-6	1.40	0-10	3.70	4-14	9.60		50
" " "	0-4	1.20	0-7	3.60	7-14	9.80		50
Beladi x pseudo-copt.	0-4	1.08	0-10	3.34	4-14	10.12		50
pseudo-copt. x nigritans	0-2	0.08	0-4	1.16	10-14	12.80		50
" " "	0-2	0.04	0-5	1.34	9-14	12.64		50
nigritans x pseudo-copt.	0-4	0.20	0-5	1.62	9-14	12.28		50
pseudo-copt. x recognitum	0-2	0.08	0-7	1.92	7-14	12.04		50
" " "	0-4	0.64	0-9	2.84	5-14	10.84		50
recognitum x pseudo-copt.			0-5	2.10	9-14	11.90		50
Beladi x alborubrum	0-2	0.36	0-6	1.92	8-14	11.90		50
" " "	0-4	0.32	0-8	2.66	6-14	11.26		50
nigritans x alborubrum	0-2	0.12	0-5	1.60	9-14	12.34		50
" " "	0-2	0.16	0-4	1.38	10-14	12.54		50
recognitum x alborubrum	0-2	0.16	0-5	2.26	8-14	11.66		50
alborubrum x recognitum	0-2	0.04	0-4	1.50	10-14	12.48		50
Beladi x nigritans	0-2	0.32	0-8	2.04	6-14	11.80		50
" " "	0-4	0.56	0-10	2.76	4-14	10.96		50
nigritans x Beladi	0-6	0.84	0-8	2.92	6-14	10.66		50

Table XX (cont'd.): Metaphase I of meiosis in the hybrids - T. pyramidale

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
nigritans x recognitum	0-2	0.44	1-8	3.56	6-13	10.22			50
" "	0-2	0.12	0-5	1.80	9-14	12.14			50
thebaicum x pseudo-copt.	0-2	0.04	0-6	1.68	8-12	10.28	0-1	0.84	50
" "			0-6	1.28	8-12	10.92	0-1	0.90	50
pseudo-copt. x thebaicum	0-2	0.08	0-4	1.36	10-12	10.84	0-1	0.88	50
thebaicum x alborubrum	0-4	0.20	0-7	1.38	7-14	11.00	0-1	0.76	50
" "	0-4	0.40	0-7	1.86	7-12	10.46	0-1	0.74	50
alborubrum x thebaicum	0-2	0.08	0-5	1.10	7-13	11.14	0-1	0.86	50
thebaicum x Beladi	0-6	1.28	0-8	3.46	6-13	8.78	0-1	0.56	50
" "	0-8	1.45	1-9	4.33	5-11	7.75	0-1	0.60	40
Beladi x thebaicum	0-2	0.20	0-6	1.50	8-12	10.75	0-1	0.83	40
thebaicum x nigritans	0-2	0.08	0-5	1.38	9-13	11.38	0-1	0.60	50
nigritans x thebaicum	0-2	0.28	0-5	2.30	9-13	10.32	0-1	0.62	50
" "	0-2	0.16	0-4	1.28	10-14	11.24	0-1	0.70	50
thebaicum x recognitum	0-2	0.08	0-6	2.64	8-13	10.36	0-1	0.48	50
recognitum x thebaicum	0-4	0.20	0-8	2.74	6-13	10.04	0-1	0.56	50
" "	0-4	0.20	0-7	2.34	7-12	10.28	0-1	0.64	50
Beladi x recognitum	0-8	2.12	2-11	5.04	3-12	7.74	0-1	0.08	50
" "	0-2	0.60	1-6	3.24	8-13	10.30	0-1	0.08	50
recognitum x Beladi	0-12	3.64	2-10	5.12	4-11	6.78	0-1	0.14	50

Table XXI: Translocations - T. pyramidale

	thebaicum a-b	pseudo- copticum	alborubrum	Beladi	nigritans	recognitum
thebaicum a-b	-	IV 0.87	IV 0.79	IV 0.66	IV 0.64	IV 0.56
pseudo-copticum		-	II	II	II	II
alborubrum			-	II	II	II
Beladi				-	II	IV 0.10
nigritans					-	II
recognitum						-

Roman numerals indicate bivalents, quadrivalents. Arabic numerals indicate the mean number of quadrivalents per cell for two (or three) plants.

T. pyramidale translocations (Table XXI)

The variety thebaicum has one translocation with respect to the other five varieties, or from another point of view it might be said that the other varieties have a translocation in common, and thebaicum has none. Quadrivalents varied in the different crosses from 0.87 per cell to 0.56 per cell. This may indicate slight differences between the varieties. However, when they were crossed with each other, there were no multivalents formed except in the case of Beladi x recognitum. Here 10% of the cells had IV's. Perhaps the translocation in either Beladi or recognitum is slightly different from the others.

Table XXIII: Metaphase I of meiosis in the hybrids - T. durum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell	No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range Mean	
"smooth-awn" x Bald Medeah			0-2	0.36	12-14	13.64		50
Bald Medeah x "smooth-awn"			0-3	0.48	11-14	13.52		50
"smooth-awn" x Golden Ball			0-3	0.56	11-14	13.44		50
Golden Ball x "smooth-awn"			0-3	0.54	11-14	13.46		50
"smooth-awn" x provinciale			0-3	0.78	11-14	13.22		50
provinciale x "smooth-awn"			0-3	0.60	11-14	13.40		50
"smooth-awn" x leucurum	0-2	0.08	0-4	1.02	10-14	12.94		50
leucurum x "smooth-awn"	0-2	0.08	0-4	0.90	10-14	13.06		50
"smooth-awn" x murciense			0-2	0.72	12-14	13.28		50
murciense x "smooth-awn"	0-2	0.04	0-5	1.08	9-14	12.90		50
"smooth-awn" x erethromelan	0-2	0.24	0-5	1.64	9-14	12.24		50
erethromelan x "smooth-awn"	0-2	0.12	0-4	1.28	10-14	12.66		50
"smooth-awn" x reichenbachii			0-4	0.56	10-14	13.44		50
reichenbachii x "smooth-awn"	0-2	0.08	0-4	0.80	10-14	13.16		50
"smooth-awn" x Stewart			0-4	1.08	10-14	12.92		50
" " " "	0-2	0.44	0-3	0.66	11-14	13.12		50
"smooth-awn" x Kahla			0-2	0.34	12-14	13.66		50
Kahla x "smooth-awn"			0-2	0.54	12-14	13.46		50
Golden Ball x Bald Medeah	0-4	0.60	0-7	3.20	7-13	10.50		50
" " " "	0-4	0.44	0-6	2.68	8-14	11.10		50

Table XXII (cont'd.): Metaphase I of meiosis in the hybrids - T. durum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell	No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range Mean	
Bald Medeah x provinciale	0-4	0.44	0-7	3.28	7-14	10.50		64
provinciale x Bald Medeah			0-4	0.98	10-14	13.02		50
Bald Medeah x leucurum	0-4	0.12	0-6	2.26	8-14	11.68		50
leucurum x Bald Medeah			0-5	1.92	9-14	12.08		50
Bald Medeah x murciense	0-4	0.56	0-6	2.56	8-14	11.16		50
murciense x Bald Medeah	0-4	0.44	0-6	2.26	8-14	11.52		50
Bald Medeah x erethromelan	0-4	0.60	0-7	3.24	6-14	10.46		50
erethromelan x Bald Medeah	0-4	0.80	0-6	2.82	8-14	10.78		50
Bald Medeah x reichenbachii	0-2	0.68	0-5	2.36	9-14	11.30		50
" " "	0-4	1.24	0-5	2.70	9-14	10.68		50
Bald Medeah x Stewart	0-4	0.12	0-4	1.44	10-14	12.50		50
Stewart x Bald Medeah			0-3	0.72	11-14	13.28		50
Bald Medeah x Kahla	0-2	0.04	0-4	1.26	10-14	12.72		43
Kahla x Bald Medeah			0-3	0.74	11-14	13.26		50
Golden Ball x provinciale	0-2	0.28	1-7	2.94	7-13	10.92		50
provinciale x Golden Ball	0-4	0.20	0-7	2.28	7-14	11.62		50
Golden Ball x leucurum			0-3	0.40	11-14	13.60		50
leucurum x Golden Ball	0-2	0.08	0-4	0.76	10-14	13.20		50
Golden Ball x murciense			0-2	0.52	12-14	13.48		50
murciense x Golden Ball	0-2	0.20	0-5	2.04	9-14	11.86		50

Table XXII (cont'd.): Metaphase I of meiosis in the hybrids - T. durum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
Golden Ball x erethromelan	0-4	1.80	1-8	4.06	6-13	9.04			50
" " "	0-2	0.12	0-6	1.64	8-14	12.30			
erethromelan x Golden Ball	0-2	0.36	1-7	2.32	7-13	11.50			50
Golden Ball x reichenbachii	0-2	0.36	1-8	3.84	6-13	9.98			50
" " "	0-2	0.24	0-7	2.54	7-14	11.34			
Golden Ball x Stewart	0-4	0.76	0-7	2.70	7-13	10.92			50
Stewart x Golden Ball	0-2	0.16	0-6	1.84	8-14	12.08			
provinciale x leucurum	0-4	0.36	0-6	2.89	8-14	10.93			45
leucurum x provinciale	0-4	0.84	2-7	4.14	7-12	9.44			
provinciale x murciense	0-2	0.12	0-6	1.80	8-14	12.14			50
murciense x provinciale	0-2	0.28	0-6	2.32	8-14	11.54			
provinciale x erethromelan	0-4	0.52	0-7	3.12	6-14	10.62			50
erethromelan x provinciale	0-4	0.52	0-6	2.12	7-14	11.62			
provinciale x reichenbachii	0-2	0.24	0-4	1.08	10-14	12.80			25
reichenbachii x provinciale			0-4	0.96	10-14	13.04			
provinciale x Stewart	0-4	0.12	0-5	1.46	9-14	12.48			50
Stewart x provinciale	0-2	0.12	0-7	1.98	6-14	11.96			
leucurum x murciense	0-4	0.20	0-6	1.86	8-14	12.04			50
murciense x leucurum	0-2	0.12	0-6	2.10	8-14	11.84			

Table XXII (cont'd.): Metaphase I of meiosis in the hybrids - T. durum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell	No. of cells
	Range	Mean	Range	Mean	Range	Mean		
erethromelan x leucurum	0-2	0.04	0-4	1.48	10-14	12.50		50
" " "	0-2	0.08	0-4	1.26	10-14	12.70		50
leucurum x reichenbachii	0-2	0.12	0-6	1.12	8-14	12.82		50
reichenbachii x leucurum	0-2	0.08	0-6	1.86	8-14	12.10		50
Kahla x leucurum	0-4	0.20	0-4	1.24	10-14	12.66		50
" " "	0-2	0.12	0-4	1.12	10-14	12.82		50
murciense x erethromelan	0-4	1.36	0-8	3.74	6-13	9.58		47
erethromelan x murciense	0-4	0.72	0-8	3.62	6-14	10.02		50
murciense x reichenbachii	0-2	0.08	0-5	1.72	9-14	12.24		50
" " "	0-4	0.60	0-5	1.84	8-14	11.86		50
murciense x Stewart	0-2	0.20	0-4	1.84	10-14	12.06		50
Stewart x murciense	0-2	0.24	0-5	1.72	9-14	12.16		50
murciense x Kahla	0-2	0.20	0-6	2.36	8-14	11.54		50
Kahla x murciense	0-2	0.04	0-6	1.88	8-14	12.10		50
erethromelan x reichenbachii	0-4	0.48	1-7	3.42	7-13	10.34		50
reichenbachii x erethromelan	0-4	0.80	1-8	4.31	6-13	9.29		55
erethromelan x Stewart	0-2	0.28	0-4	1.78	10-14	12.08		50
Stewart x erethromelan	0-2	0.12	0-4	1.62	10-14	12.32		50

Table XXII (cont'd.): Metaphase I of meiosis in the hybrids - T. durum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
reichenbachii x Kahla	0-2	0.04	0-5	1.66	9-14	12.32			50
Kahla x reichenbachii	0-2	0.48	0-6	2.20	8-14	11.56			50
Kahla x Stewart	0-2	0.08	0-4	0.74	10-14	13.22			50
Stewart x Kahla			0-4	0.80	10-14	13.20			60
Camadi x "smooth-awn"	0-2	0.04	0-5	1.70	9-12	10.60	0-1	0.84	50
"smooth-awn" x Camadi	0-4	0.32	0-6	1.88	8-12	10.20	0-1	0.88	50
Camadi x Bald Medeah	0-2	0.72	0-7	3.66	6-12	8.44	0-1	0.77	47
Bald Medeah x Camadi	0-4	1.12	0-6	3.10	8-12	8.70	0-1	0.82	50
Camadi x Golden Ball	0-4	1.04	1-7	4.26	7-10	7.82	0-1	0.70	50
Golden Ball x Camadi	0-2	0.20	1-6	1.54	8-12	10.60	0-1	0.88	50
Camadi x provinciale	0-2	0.29	0-6	3.05	8-12	9.39	0-1	0.71	56
provinciale x Camadi	0-2	0.20	0-7	1.38	7-13	10.84	0-1	0.84	50
Camadi x leucurum	0-4	0.84	1-7	2.78	7-13	9.60	0-1	0.60	50
leucurum x Camadi	0-4	0.96	0-7	2.90	7-12	9.50	0-1	0.56	50
Camadi x murciense	0-2	0.60	0-5	2.88	8-11	9.26	0-1	0.78	50
murciense x Camadi	0-6	0.44	0-6	2.40	8-13	10.02	0-1	0.68	50
Camadi x erethromelan	0-2	0.38	1-7	3.32	6-11	8.62	0-1	0.84	50
erethromelan x Camadi	0-4	0.40	1-7	3.18	5-11	8.82	0-1	0.90	50

Table XXII (cont'd.): Metaphase I of meiosis in the hybrids - T. durum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
Camadi x reichenbachii	0-4	0.48	0-6	3.14	8-12	9.06	0-1	0.78	50
reichenbachii x Camadi	0-2	0.16	0-5	1.98	9-12	10.38	0-1	0.78	50
Camadi x Stewart	0-4	0.32	0-7	2.16	7-14	10.20	0-1	0.74	50
Stewart x Camadi	0-4	0.52	0-4	1.90	10-14	10.36	0-1	0.74	50
Camadi x Kahla	0-4	0.72	1-7	4.28	7-11	8.20	0-1	0.62	50
Kahla x Camadi	0-2	0.08	0-7	2.48	6-12	9.80	0-1	0.84	50
Kahla x Golden Ball			0-4	0.54	8-12	11.50	0-1	0.98	50
" "	0-2	0.04	0-4	0.92	10-12	11.14	0-1	0.96	50
Golden Ball x Kahla	0-2	0.04	0-3	0.92	11-14	13.06			50
Kahla x provinciale	0-2	0.12	0-5	0.82	9-14	11.96	0-1	0.58	50
provinciale x Kahla	0-2	0.04	0-5	1.08	9-14	12.90			50
Kahla x erethromelan	0-4	0.20	0-4	1.84	10-14	11.86	0-1	0.10	50
erethromelan x Kahla	0-4	0.28	0-7	2.46	7-14	11.40			50
reichenbachii x Stewart	0-2	0.20	0-4	1.56	10-12	10.58	0-1	0.88	50
Stewart x reichenbachii	0-2	0.08	0-5	1.28	9-14	12.60	0-1	0.04	50
" "			0-4	1.10	10-14	12.90			50
leucurum x Stewart	0-4	0.20	0-6	1.22	8-14	12.60	0-1	0.04	50
Stewart x leucurum	0-4	0.44	1-6	3.24	8-13	10.26	0-1	0.14	50

Table XXIII: Translocations - T. durum

	"s-awn"	B.med.	G.Ball	prov.	leuc.	murc.	ereth.	reich.	Stew.	Kahla	Camadi a-b
"smooth-awn"	-	II	II	II	II	II	II	II	II	II	IV 0.86
Bald Medeah		-	II	II	II	II	II	II	II	II	IV 0.80
Golden Ball			-	II	II	II	II	II	II	IV*	IV 0.79
provinciale				-	II	II	II	II	II	IV*	IV 0.78
leucurum					-	II	II	II	IV 0.07	II	IV 0.58
murciense						-	II	II	II	II	IV 0.73
erethromelan							-	II	II	IV*	IV 0.87
reichenbachii								-	IV**	II	IV 0.78
Stewart									-	II	IV 0.74
Kahla										-	IV 0.73
Camadi a-b											-

Roman numerals indicate bivalents, quadrivalents. Arabic numerals indicate the mean number of quadrivalents per cell for two plants.

* Quadrivalents when Kahla was female parent, not in reciprocals.

** Reciprocals differed considerably.

T. durum translocations (Table XXIII)

Camadi (which is morphologically rather unlike the other varieties) has one translocation with respect to all the other varieties. Apart from a few anomalous cases to be discussed below, the other crosses did not give rise to multivalents and therefore these varieties have no translocations with respect to each other.

Kahla was anomalous in producing IV's in three crosses and then only when Kahla was female parent. The reciprocals had no IV's. Kahla was quite variable morphologically, and apparently some of the plants possessed a translocation while others did not, or some were heterozygous for a translocation. It could be just a matter of chance that quadrivalents occurred only when Kahla was female parent, but possibly male gametes carrying the translocation were not viable. This might be the case if the translocation were accompanied by a deficiency.

Another anomalous cross in the T. durum group is that between var. reichenbachii and Stewart. With reichenbachii as female parent, 88% of the cells had quadrivalents, while in two plants of the reciprocal cross there were hardly any quadrivalents and a marked increase in the number of closed bivalents. The explanation may be similar to that suggested for the Kahla crosses.

The cross between leucurum and Stewart had a mean of 0.07 IV's per cell but in this case the reciprocals were similar.

Table XXIV: Metaphase I of meiosis in the hybrids - T. turgidum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		Ring or ch. VI per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
plinianum x ramoso-meg.	0-2	0.09	0-4	0.91	10-14	13.04					44
" "	0-2	0.04	0-4	0.66	10-14	13.32					50
speciosum x plinianum			0-5	1.22	9-14	12.78					50
" "	0-2	0.08	0-5	1.80	9-14	12.16					50
melanatherum x plinianum			0-4	0.54	10-14	13.46					50
" "	0-2	0.12	0-3	0.78	11-14	13.16					50
megalopol. x plinianum	0-2	0.08	0-3	0.82	10-14	13.14					50
" "	0-2	0.04	0-4	1.06	10-14	12.92					50
speciosum x ramoso-meg.	0-2	0.04	0-4	1.04	10-14	12.94					50
" "	0-2	0.04	0-5	0.92	9-14	13.06					50
melanath. x speciosum	0-2	0.08	0-3	0.70	11-14	13.26					50
speciosum x melanath.	0-2	0.08	0-4	1.10	10-14	12.86					50
melanath. x ramoso-meg.	0-2	0.12	0-5	1.24	9-14	12.70					50
" "	0-2	0.10	0-5	0.95	9-14	13.00					41
megalopol. x melanatherum	0-4	0.88	0-6	2.06	7-13	11.50					50
" "	0-2	0.04	0-4	1.12	10-14	12.86					50
dinurum x dreischianum			0-3	0.84	11-14	13.16					50
dreischianum x dinurum	0-2	0.08	0-3	0.74	11-14	13.22					50

Table XXIV (cont'd.): Metaphase I of meiosis in the hybrids - T. turgidum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		Ring or ch. VI per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
rubrialbum x dreischianum			0-2	0.39	12-14	13.61					56
dreischianum x rubrialbum			0-4	0.90	10-14	13.10					50
rubrialbum x dinurum			0-2	0.48	12-14	13.52					50
dinurum x rubrialbum			0-2	0.90	11-14	13.10					50
plinianum x dreischianum	0-2	0.04	0-3	0.78	8-11	10.20			1	1.00	50
dreischianum x plinianum			0-3	0.64	8-11	10.36			1	1.00	50
dinurum x plinianum	0-2	0.04	0-2	0.40	9-11	10.58			1	1.00	50
" "			0-4	0.78	7-11	10.22			1	1.00	50
rubrialbum x plinianum	0-2	0.04	0-4	0.76	7-11	10.22			1	1.00	50
" "			0-2	0.56	9-11	10.44			1	1.00	55
dreischianum x ramoso-meg.			0-2	0.38	9-11	10.62			1	1.00	50
ramoso-meg. x dreischianum			0-3	0.56	8-11	10.44			1	1.00	50
dinurum x ramoso-meg.			0-3	0.46	8-11	10.54			1	1.00	50
" "			0-2	0.22	9-11	10.78			1	1.00	50
rubrialbum x ramoso-meg.	0-2	0.04	0-3	0.30	8-11	10.68			1	1.00	50
" "	0-2	0.04	0-2	0.42	9-11	10.56			1	1.00	50
speciosum x dreischianum	0-2	0.08	0-3	0.90	7-11	10.06			1	1.00	50
dreischianum x speciosum			0-4	0.96	7-11	10.04			1	1.00	50
speciosum x dinurum			0-3	0.38	8-11	10.62			1	1.00	50
dinurum x speciosum	0-2	0.09	0-2	0.39	9-11	10.56			1	1.00	46

Table XXIV (cont'd.): Metaphase I of meiosis in the hybrids - T. turgidum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		Ring or ch. VI per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
speciosum x rubrialbum			0-3	0.44	8-11	10.56			1	1.00	50
rubrialbum x speciosum			0-4	0.54	7-11	10.46			1	1.00	50
melanath. x dreischianum			0-3	0.94	8-11	10.06			1	1.00	50
dreischianum x melanath.	0-4	0.12	0-5	0.96	6-11	9.98			1	1.00	50
melanatherum x dinurum			0-3	1.04	8-11	9.96			1	1.00	25
dinurum x melanatherum			0-3	0.44	8-11	10.56			1	1.00	50
melanath. x rubrialbum	0-2	0.08	0-3	0.40	8-11	10.56			1	1.00	50
" "			0-1	0.22	10-11	10.78			1	1.00	50
megalopol. x dreischianum	0-2	0.16	0-3	0.74	8-11	10.18			1	1.00	50
dreischianum x megalopol.			0-4	0.80	7-11	10.20			1	1.00	50
megalopol. x rubrialbum			0-3	0.69	6-11	10.31			1	1.00	52
" "			0-4	0.70	7-11	10.30			1	1.00	50
gentile x buccale	0-2	0.04	0-3	0.66	11-14	13.32					50
buccale x gentile	0-2	0.04	0-4	0.90	10-14	13.08					50
buccale x plinianum	0-2	0.04	0-3	1.00	9-12	11.06	0-1	0.96			50
" "			0-4	0.80	9-12	11.28	0-1	0.96			50
gentile x plinianum	0-2	0.12	0-5	1.70	7-12	10.32	0-1	0.96			50
" "			0-4	0.46	10-12	11.62	0-1	0.96			50

Table XXIV (cont'd.): Metaphase I of meiosis in the hybrids - T. turgidum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		Ring or ch. VI per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
salomonis x plinianum	0-2	0.40	0-4	1.24	8-12	10.72	0-1	0.92			50
" "			0-3	0.64	9-12	11.44	0-1	0.96			50
buccale x ramoso-meg.	0-2	0.12	0-4	1.32	8-12	10.74	0-1	0.94			50
" "	0-2	0.28	0-4	1.44	8-12	10.50	0-1	0.96			50
gentile x ramoso-meg.			0-3	1.06	9-12	11.02	0-1	0.96			50
" "			0-4	0.81	9-12	11.31	0-1	0.94			48
salomonis x ramoso-meg.	0-2	0.12	0-4	0.96	8-12	11.06	0-1	0.96			50
" "	0-4	0.25	0-4	1.04	8-12	10.95	0-1	0.94			48
speciosum x buccale	0-2	0.20	0-6	1.40	6-12	10.58	0-1	0.96			50
" "			0-3	0.80	9-12	11.40	0-1	0.90			50
speciosum x gentile	0-2	0.04	0-4	0.56	8-12	11.54	0-1	0.94			50
gentile x speciosum	0-2	0.20	0-4	0.90	9-12	11.24	0-1	0.88			50
speciosum x salomonis			0-4	0.74	10-12	11.38	0-1	0.94			50
salomonis x speciosum	0-2	0.09	0-4	0.49	10-12	11.55	0-1	0.96			45
melanatherum x buccale	0-2	0.24	0-4	1.40	7-12	10.48	1	1.00			50
buccale x melanatherum	0-2	0.04	0-4	0.84	8-12	11.14	1	1.00			50
melanatherum x gentile			0-2	0.26	10-12	11.74	1	1.00			50
gentile x melanatherum	0-4	0.16	0-5	1.24	8-12	10.80	0-1	0.94			50

Table XXIV (cont'd.): Metaphase I of meiosis in the hybrids - T. turgidum

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		Ring or ch. VI per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
melanatherum x salomonis			0-3	0.86	9-12	11.30	0-1	0.92			50
salomonis x melanatherum			0-3	0.64	10-12	11.44	0-1	0.96			50
dreischianum x buccale	0-2	0.04	0-2	0.28	7-9	8.70	1	1.00	1	1.00	50
buccale x dreischianum	0-2	0.08	0-3	0.49	6-9	8.55	0-1	0.96	1	1.00	47
dreischianum x gentile			0-4	0.78	6-9	8.30	0-1	0.96	1	1.00	50
gentile x dreischianum			0-2	0.30	7-9	8.70	1	1.00	1	1.00	50
dreischianum x salomonis	0-2	0.04	0-3	0.70	9-12	11.32	0-1	0.98			50
salomonis x dreischianum	0-2	0.10	0-5	1.10	7-12	10.85	1	1.00			50
dinurum x buccale			0-2	0.26	7-9	8.74	1	1.00	1	1.00	50
" " "			0-2	0.28	7-9	8.72	1	1.00	1	1.00	50
dinurum x gentile			0-1	0.22	8-11	8.78	1	1.00	1	1.00	50
gentile x dinurum			0-2	0.36	7-11	8.64	1	1.00	1	1.00	50
dinurum x salomonis			0-4	0.56	8-12	11.48	0-1	0.98			50
salomonis x dinurum	0-2	0.08	0-3	0.56	9-12	11.44	0-1	0.98			50
rubrialbum x buccale			0-3	0.32	6-9	8.68	1	1.00	1	1.00	50
buccale x rubrialbum			0-4	0.64	7-9	8.52	0-1	0.92	1	1.00	50
rubrialbum x gentile			0-3	0.32	7-9	8.72	0-1	0.98	1	1.00	50
gentile x rubrialbum			0-2	0.32	8-9	8.76	0-1	0.96	1	1.00	50

Table XXIV (cont'd.): Metaphase I of meiosis in the hybrids - *T. turgidum*

	Univalents per cell		Open II per cell		Closed II per cell		Ring or ch. IV per cell		Ring or ch. VI per cell		No. of cells
	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	
rubrialbum x salomonis			0-3	0.62	9-12	11.38	1	1.00			50
salomonis x rubrialbum			0-1	0.29	11-12	11.71	1	1.00			35
buccale x salomonis	0-2	0.12	0-5	0.98	7-10	9.24	1-2	1.86			50
salomonis x buccale			0-3	0.36	7-10	9.64	2	2.00			50
gentile x salomonis			0-3	0.38	8-10	9.66	1-2	1.98			50
salomonis x gentile			0-3	0.60	8-10	9.52	1-2	1.94			50
megalopol. x ramoso-meg.			0-3	0.72	9-12	11.36	0-1	0.96			50
" " "			0-3	0.34	10-12	11.70	0-1	0.98			50
megalopol. x speciosum	0-6	1.16	0-6	2.22	5-12	9.14	0-1	0.74			50
speciosum x megalopol.	0-2	0.16	0-6	1.40	8-12	10.84	0-1	0.84			50
megalopol. x dinurum			0-2	0.26	7-9	8.74	1	1.00	1	1.00	50
dinurum x megalopol.			0-2	0.22	9-11	10.78			1	1.00	50
megalopol. x buccale			0-3	0.76	9-12	11.28	0-1	0.98			50
buccale x megalopol.			0-4	0.72	6-12	9.78	0-2	1.75			32
megalopol. x gentile	0-2	0.06	0-4	0.55	8-10	9.54	1-2	1.94			31
gentile x megalopol.			0-3	0.56	7-10	9.58	1-2	1.93			45
megalopol. x salomonis	0-6	0.92	0-6	2.20	5-11	8.74	0-2	1.30			50
salomonis x megalopol.			0-2	0.42	8-10	9.62	1-2	1.98			50

Table XXV: Translocations - T. turgidum

	plin. a-b	ramoso. a-b	spec. a-b	mela. a-b	megal. a-b	dreis. b-c	dinurum b-c	rubri. b-c	buccale a-b,d-e	gentile a-b,d-e	salom. -
plinianum a-b	-	II	II	II	II	VI 1.00	VI 1.00	VI 1.00	IV 0.96	IV 0.96	IV 0.94
ramoso-meg. a-b		-	II	II	*	VI 1.00	VI 1.00	VI 1.00	IV 0.95	IV 0.95	IV 0.95
speciosum a-b			-	II	*	VI 1.00	VI 1.00	VI 1.00	IV 0.93	IV 0.91	IV 0.95
melanatherum a-b				-	II	VI 1.00	VI 1.00	VI 1.00	IV 1.00	IV 0.97	IV 0.94
megalopol. a-b					-	VI 1.00	*	VI 1.00	*	*	*
dreischianum b-c						-	II	II	IV 0.98 VI 1.00	IV 0.98 VI 1.00	IV 0.99
dinurum b-c							-	II	IV 1.00 VI 1.00	IV 1.00 VI 1.00	IV 0.98
rubrialbum b-c								-	IV 0.96 VI 1.00	IV 0.97 VI 1.00	IV 1.00
buccale a-b,d-e									-	II	2IV 1.93
gentile a-b,d-e										-	2IV 1.96

Roman numerals indicate bivalents, quadrivalents, etc. Arabic numerals indicate the mean number of quadrivalents, etc. per cell for two plants.

* Some plants had one more quadrivalent per cell than expected.

T. turgidum translocations (Table XXV)

These crosses were remarkable in that where multivalents occurred, they occurred in a very high proportion of the cells.

The varieties can be treated as groups, i.e. group 1 (varieties 1-5), group 2 (varieties 6-8), and group 3 (varieties 9 and 10). The eleventh variety, salomonis, differs cytologically from all the others. The varieties within each group, when crossed with each other, did not produce any multivalents, i.e. either they possessed the same translocation or no translocation at all. The varieties of group 1, when crossed with the varieties of group 2, formed VI's (two translocations with one chromosome in common). Group 1 by group 3 gave rise to IV's, but group 2 by group 3 produced IV's and VI's. The following translocations are postulated: The varieties in group 1 are a-b, and the varieties in group 2 are b-c. The varieties in group 3 have two translocations, a-b and d-e. These translocations would explain the cytological data.

The eleventh variety, salomonis, can be regarded as lacking translocations since the translocations already postulated would account for one quadrivalent per cell with groups 1 and 2, and two quadrivalents per cell with group 3.

Six of the ten crosses involving var. megalopolitanum were anomalous in having one more quadrivalent per cell than expected. In two of these crosses, the reciprocals differed

from each other. Apparently some of the parent plants had an extra translocation though no morphological variation was observed within this variety.

Table XXVI: A comparison of numbers of univalents and open bivalents in both parents and hybrids

Species	Parents				Hybrids				Difference between parents and hybrids	
	Univalents		Open II		Univalents		Open II		Univalents	Open II
	Range	Mean	Range	Mean	Range	Mean	Range	Mean		
<u>T. dicoccoides</u>	0-2	0.02	0-5	0.71	0-4	0.17	0-7	1.60	0.15	0.89
<u>T. dicoccum</u>	0-4	0.18	0-9	1.35	0-6	0.21	0-8	1.46	0.03	0.11
<u>T. persicum</u>	0-4	0.07	0-5	1.40	0-4	0.21	0-7	1.81	0.14	0.41
<u>T. orientale</u>	0-4	0.06	0-5	0.93	0-4	0.30	0-7	1.51	0.24	0.58
<u>T. pyramidale</u>	0-4	0.21	0-10	1.89	0-12	0.51	0-11	2.41	0.30	0.52
<u>T. durum</u>	0-2	0.07	0-8	1.31	0-6	0.28	0-8	2.07	0.21	0.76
<u>T. turgidum</u>	0-2	0.02	0-5	0.66	0-6	0.07	0-6	0.74	0.05	0.08

Comparison of parents and hybrids

It is difficult to find a basis for comparison between parents and hybrids, and between the different species. The presence of multivalents complicates the situation. Table XXVI is a brief comparison of the mean numbers of univalents and open bivalents per cell for both parents and hybrids. These values may be influenced by the fact that while in some hybrids multivalents are formed in 100% of the cells, in others the percentage is quite low, with possibly a corresponding increase in univalents and open bivalents.

In every case there are more univalents and open bivalents per cell in the hybrids than in the parents, but in some cases e.g. T. dicoccum and T. turgidum, the differences are very small. The actual values are highest for T. pyramidale and lowest for T. turgidum, for both univalents and open bivalents and in both parents and hybrids.

Morphology

The morphological characters of the parent varieties are presented in Table II in the section on materials and methods. Twenty-four of the 49 varieties used in this study are mentioned by Percival (7), and on checking their characteristics, five were found to differ from Percival's descriptions. Four varieties were found to have pubescent glumes when according to Percival they should have been glabrous. Another variety had black awns instead of red awns (Table II). This throws some doubt on the identity of the parent material. Five of the varieties were variable morphologically and this, too, raises the question of identity. It is not known which of the variants truly represents the variety.

Notes were made on the morphological characteristics of the F₁ plants, but since there were 175 different crosses, the descriptions will not be presented here. Most of the characters studied were common to some varieties of all seven species.

Inheritance of parental characters as seen in the F₁ plants

As this study was not continued beyond the F₁ generation, not much can be said about the mode of inheritance of the various characters. The F₁ plants were compared with their parents and the following observations were recorded:

Glume pubescence - in all crosses the F₁ plants were intermediate between the parents.

Glume colour - colour was not always very well developed in the greenhouse, but many F₁ plants had black glumes, i.e. this character appears to be dominant.

Glaucousness of glumes - this character seemed to be recessive, but as most of the parent varieties were at least somewhat glaucous, there were not many crosses in which this could be studied.

Glume shape and size, and shape of the apical tooth - comparison of the F₁ plants with the parent varieties showed that the F₁'s were always intermediate between their parents.

Awn colour - like glume colour, this was poorly developed under greenhouse conditions, but black awns appeared to be dominant.

Head density - comparison of F₁ plants with their parents showed the F₁'s to be intermediate in head density. An exception was the dicoccum variety known as "compact". Heads in the F₁ hybrids with this variety were as lax as those of the more lax parent. There was no possibility of self-pollination since heads were lax even when "compact" was the female parent. This head type must be controlled by a different gene and it must be a recessive gene.

Pubescence of leaves and/or leaf sheaths - F₁ plants were more or less intermediate. This is exemplified by T. dicoccoides var. aaronsohni (1) which has conspicuous, erect hairs scattered over the surface of the lower leaf-sheaths. Hairs on the sheaths of the progeny were shorter and more sparsely distributed.

Cilia on auricles - this character varies somewhat in expression, but it appears to be dominant.

Purple seeds - Camadi (T. durum) and Nero (T. dicoccum) are both purple-seeded. Although here classified as two different species, Camadi and Nero are very much alike in general appearance. When these varieties were crossed with other varieties, the F₁ plants had purple seeds irrespective of whether the purple-seeded variety was male or female parent. Purple seeds must be due to a dominant endosperm (probably aleurone) character.

Awnlessness - Bald Medeah was the only awnless variety used. All F₁ progeny were awnless or had just a few, very short, awns, so this character was dominant as expected.

Branched heads - two varieties of T. turgidum (var. plinianum and var. ramoso-megalopolitanum) had large, conspicuously branched heads. T. dicoccoides var. tumanjani and T. dicoccum var. arras had slightly branched heads. The heads of F₁ plants were never branched, so this character must be recessive.

GENERAL DISCUSSION AND CONCLUSIONS

The cytological and morphological examination of the intraspecific crosses in this study was intended as a first step in a programme to find out if the existing classification of the tetraploid species of wheat is an adequate one.

The cytological results have been summarised in various ways, including:-

(a) differences within heads of the parent varieties
(Table X)

(b) differences between parents and hybrids (Table XXVI)

These two tables can now be compared in part, though it should be borne in mind that Table X is based on a very small sample. Table XXVI showed that in each species there were slightly more univalents and open bivalents in the hybrids than in the parents.

Species	Mean differences within heads		Mean differences between parents and hybrids	
	Univalents	Open II	Univalents	Open II
<u>T. dicoccoides</u>	0.03	0.34	0.15	0.89
<u>T. orientale</u>	0.10	0.32	0.24	0.58
<u>T. durum</u>	0.06	0.85	0.21	0.76

This shows that differences between parents and hybrids are of the same order as differences within single plants. Therefore in general the presence of univalents and open bivalents in the hybrids does not indicate any lack of homology between the parental chromosomes, though there may be a few crosses where there is some lack of homology.

Translocations

The most unexpected feature of this study is the large number of translocations disclosed. In 104 out of 175 crosses (59.4%) there were one or more multivalent associations per cell. It is assumed that translocations were responsible because the multivalents were mostly in the form of rings and the number of rings per cell in any one cross was practically constant, i.e. one per cell in some crosses and two per cell in others. Multivalent associations due to causes other than translocations probably would not have formed rings so consistently and the number of multivalents per cell would not have been so constant.

It must be admitted that there were some exceptions to this regular pattern. In a few crosses the proportion of chains was fairly high. In some plants there were two or three (III - I)'s or (V - I)'s and these have been included with the IV's and VI's respectively. In a few plants, otherwise lacking in multivalents, there appeared to be an occasional chain of four chromosomes. Unless these chains occurred in more than 5% of the cells, or in both reciprocals, they were disregarded. Probably the chromosomes were not really attached but only apparently so.

Many plants had a multivalent in almost every cell but a few had a multivalent in only a small proportion of the cells. The reasons for this are not known, but there are many possibilities. In the previous section very small translocations have been postulated. If this were the case, the pachytene

cross would have two very short arms and might break up into two open bivalents at terminalisation. An interstitial translocation, not involving the ends of the chromosomes would make pairing difficult and would probably yield very few multivalents. Unfortunately there was no time to examine the pachytene configurations so the real reasons are unknown.

Fertility

Table XXVI shows that, on the average, there were only slightly more univalents and open bivalents in the hybrids than in the parents. Regular pairing at meiosis in a hybrid is usually considered to indicate fairly close homology between the parental chromosomes. Sachs (8) found that in a dicoccoides - timopheevi cross despite good pairing no seed was produced. This he attributed to lack of homology or "cryptic structural hybridity". In this study some of the hybrids were sterile, but this could have been due to low light-intensity in the greenhouse during the winter, and to the presence of translocations. In view of these difficulties, seed-set was not recorded, but general observation showed that a number of the plants were fairly fertile.

Classification

As mentioned in the section on results, some of the varieties differed from the descriptions given by Percival (7) and this casts some doubt on their identity. Species classification is also questionable. Consider Camadi (T. durum) and Nero (T. dicoccum). These two varieties are very much

alike in general appearance and are what Percival has described as Abyssinian emmers. He classified the Abyssinian emmers as T. dicoccum. Flaksberger classified them as T. abyssinicum. Golden Ball (T. durum) and T. turgidum var. melanatherum are indistinguishable as to head type. T. dicoccoides var. tumanjani and T. dicoccum var. arras are identical in appearance. One wonders why they have been classified as different species. These examples are given to show that some of the so-called intraspecific crosses in this study may be interspecific - it seems to be largely a question of classification.

Relationships in the tetraploid group ought to be much clearer when a series of interspecific crosses have been made. The varieties used in this study are only a small sample of the existing tetraploid material, but a series of interspecific crosses could be made using a selection from these varieties. The results of the present study show that some of the varieties can be grouped according to translocations. One member of each of these groups should be used for interspecific crosses. Where there are no well defined cytological groups all the varieties should be used. Varieties which are variable morphologically or cytologically should be omitted and a selection could be made from the following:

T. dicoccoides all five varieties

T. dicoccum (cont'd.)

One of the following: (Khapli
(nigro-ajar
(rufum

All of the following: (arras
(Yaroslav
(Nero
("compact"

T. persicum

One of the following: (fuliginosum
(stramineum

T. persicum (4)

T. orientale

One of the following: (notabile (1)
(notabile (2)
(Gigante ingles

insigne

T. pyramidale

One of the following: (pseudo-copticum
(nigritans
(recognitum
(Beladi

thebaicum

T. durum

One of the following: (Bald Medeah
(Golden Ball
(provinciale
(leucurum
(murciense
(erethromelan

Camadi

T. turgidum

One of the following: (plinianum
(ramoso-megalopolitanum
(speciosum
(melanatherum
(megalopolitanum

One of the following: (dreischianum
(dinurum
(rubrialbum

One of the following: (buccale
(gentile

salomonis

Thus it can be seen that 22 varieties from the 49 used in this study should be crossed in diallel to determine their interspecific relationships from the point of view of translocations. Thirty of these crosses have been made in the present study so 160 more crosses would complete the series. It may well be that the interspecific differences will be no greater than the intraspecific differences already disclosed. A thorough examination of all the existing tetraploid varieties will require a very large number of crosses.

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APPENDIX I

The following key, translated from Flaksberger et al. (4) and reproduced by Clark and Bayles (3), distinguishes the species of Triticum. Details of the diploid and hexaploid species have been omitted.

Key to the species of Triticum

- I. Spike does not disarticulate at maturity; grain more or less easily threshed by ordinary methods. Free-grained wheats.
 - A. Glumes coriaceous (firm), shorter than or almost equal to the lemmas; palea of all florets slightly shorter than or equal to the lemma; terminal floret (usually rudimentary) of each spikelet projects beyond the glumes.
 1. Spikes awned or awnless; the imbricate (face) surface wider than or equal to the distichous (lateral) surface; glumes with an indistinct, narrow carina (keel), which sometimes disappears at the base of the glume; carina tooth of the glume from short and acute to long and awn-like or tapering into a short awn.
 - a. (T. vulgare)
 - b. (T. compactum)
 - c. (T. sphaerococcum)

2. Spikes awned, rarely awnless; the distichous surface wider than the front surface, or spikes square in cross section; in Abyssinian forms and in Caucasian wheat the imbricate surface wider than the distichous surface. Glumes firmly coriaceous, distinctly carinate to the base where there are never any longitudinal folds or transverse depressions, so that the characteristic texture and consistency of glumes remain the same to the very base; tooth of the glume from broad, short, somewhat obtuse to acute, or tapering into an awnlike tooth or even an awn.

a. In general appearance spikes resemble those of soft wheats; the front surface wider than or almost equal to the distichous surface; carina of the glume comparatively narrow; carina tooth acute, awnlike, or tapering into an awn which is somewhat shorter than or equal to the awn of the lemma.

x. Rachis joints of normal width, as in soft wheats (about 2 to 3 mm.); carina tooth of the glume acute or awnlike, tapering into a somewhat shortened awn.

Abyssinian hard wheats - T. abyssinicum Vav.

xx. Rachis joints approximately half as wide as in soft wheats (about 1.5 mm. or less), which

makes the spike very flexible; carina tooth of the glume tapers into an awn of the same length or somewhat shorter (by about one-half) than the awn of the lemma; therefore the number of awns on the spike is doubled and it appears densely aristate (awned). Awnless forms unknown.

Persicum or Caucasian wheat - T. persicum Vav.

- b. Spikes clearly distinguished from those of soft wheats; the distichous surface wider than or equal to the front surface (compare with soft wheats); awns long, usually longer than the spike, parallel to it or somewhat divergent; awnless forms rare; carina of the glume broad, distinct and strong to the base; carina tooth of the glume broad, comparatively short, somewhat obtuse or acute, but not tapering into an awnlike point.
- x. Glumes oval, elongate-oval, slightly convex, of approximately the same length as lemmas; lemmas navicular (boat-shaped), at the apex gradually tapering into a long awn (rarely into an awnlike point in awnless forms); rachis joints at the place of attachment of spikelets usually almost glabrous or slightly pubescent.

Hard wheats - T. durum Desf.

xx. Glumes shortened, oval, definitely convex, shorter than the lemmas, covering approximately two-thirds of the latter; main lateral nerve distinct; awns long, longer than the spike, attached directly to the convex glume without gradual tapering, which causes them to break off easily together with a small section of the glume; awnless forms rare; spikes simple or branching; rachis joints of typical forms definitely pubescent at the place of attachment of spikelets; rachis joint bearing the terminal spikelet has a crown of hairs.

Turgidum or English wheats - T. turgidum L.

B. Glumes membranous or herbaceous (in consistency resembling glumes of oats), of the same length as or longer than lemmas, long, lanceolate, distinctly many-nerved, indistinctly carinate; spikes more or less large, comparatively short awned; the distichous surface wider than or as wide as the front surface.

Polonicum or Polish wheat - T. polonicum L.

II. Spikes disarticulate at maturity; usual methods of threshing not effective. Membranous or "polba" wheats.

A. Spikes compact or lax; the distichous surface wider than the front surface, i.e. spikes compressed, not long in relation to width, awned; awnless forms rare; awns usually long, parallel to the spike; when

spike disarticulates the rachis joints remain attached to the spikelets by their upper ends in a handlelike arrangement.

1. The bicarinate (two-keeled) palea does not split into two sections at maturity.
 - a. Glumes of different shapes, resembling those of hard wheats but less strongly carinate, compressed; density (D) from 21 to 46; when green spikes resemble those of hard wheats; usually simple but many branching forms are also known; rachis joints pubescent on the edges or almost glabrous; spikelets usually contain two grains; surface lying against the joint convex.

"Polbas", Emms - T. dicoccum Schubl.

- b. Glumes wing-shaped, indistinctly carinate (keeled), with the surface of the glume gradually rising into a ridge (here arbitrarily called carina) especially in the upper part of the glume; tooth of the glume broad, triangular, usually in the shape of an equilateral triangle, straight or reflexed, acute, with a smaller tooth next to it; between the teeth there is a more or less acute notch; the bicarinate palea does not split at maturity into two longitudinal sections.
 - x. Spikes not long in relation to width, of somewhat pyramidal shape; density (D) from 30 to 54; teeth somewhat reflexed; at the base of

the tooth the ridge is depressed; instead of a lateral tooth there is a knob; rachis joints pubescent on the edges; glumes comparatively thin with a prominent lateral nerve; on the side lying against the rachis spikelets convex or somewhat concave.

Timopheevi wheat - T. timopheevi Zhuk.

xx. Spikes narrow in relation to length; lax (D) from 16 to 20; carina tooth triangular; acute or sub-obtuse, with a smaller tooth next to it; between the teeth there is a more or less acute notch; glumes firm; rachis joints densely pubescent on the angles with long hairs directed upwards and forming dense beards at the base of spikelets (in some forms pubescence is less pronounced); spikelets depressed on the side lying against the rachis, in cross section trapeziform.

Wild "Polbas" - T. dicoccoides Korn.

2. The bicarinate palea splits at maturity into two longitudinal sections; spikes small, flat, always awned; density (D) from 30 to 55; carina tooth triangular, acute, with a small lateral tooth next to it; between the teeth there is an acute notch; broad surface of the spike convex on one side, more or less flat on the other; spikelets usually contain one developed grain (occasionally two grains).

- a. (T. spontaneum Flaksb.)
 - b. (T. monococcum L.)
- B. Spikes lax or compact; glumes broad, broad-cuneate, spatulate; when spikes disarticulate, spikelets remain attached to the lower end of the rachis joints, which lie against the spikelet and do not form a "handle"; however, it sometimes happens that the break occurs in the lower third of the rachis joint; in that case the spike breaks up as in soft wheats; occasionally the spike disarticulates partly as in "polbas", i.e., with the rachis joint forming a "handle" to the spikelet.
1. (T. spelta L.)
 2. (T. macha Dek. et Men.)

APPENDIX II

As some of the varieties used in this study are variously classified by different authorities, it is difficult to know which classification is the correct one. The names in the left-hand column are those under which the seed was received by the University of Manitoba. (Some descriptive terms used to distinguish unnamed varieties are given in the right-hand column.)

<u>Variety</u>	<u>Source*</u>	<u>U. of Man. Number</u>	<u>Other classifications and remarks</u>
<u>T. dicoccoides</u>			
<u>aaronsohni</u> Perc.	Percival	55B4.15	also spelt <u>aaronsohni</u> (called <u>aaronsohni</u> (1) in this study)
<u>aaronsohni</u> Flaksb.	Max Planck	55B4.152	(called <u>aaronsohni</u> (2) in this study)
<u>kotschyanum</u> Perc.	Bell	57B4.59	<u>kotschyanum</u> Schulz (16, p.5)
<u>pseudo-rufovillosum</u> Jakubz.	Max Planck	55B4.153	
<u>tumanjani</u> Jakubz. f. <u>straussianum</u> Schulz	"	55B4.154	
<u>T. dicoccum</u>			
<u>arras</u> Hochst.	"	55B4.156	
<u>nigro-ajar</u>	Percival	55B4.31	

* See list of sources at the end of this section.

APPENDIX II (cont'd.)

<u>Variety</u>	<u>Source*</u>	<u>U. of Man. Number</u>	<u>Other classifications and remarks</u>
<u>T. dicoccum (cont'd.)</u>			
<u>rufum</u> Schubl.	Zhukovsky	57B4.5	<u>rufum</u> Korn. (7, p. 192)
- (Khapli)	U.S.D.A.	55B4.396	(<u>ajar</u> Perc. (7, p. 194) (<u>arras</u> (7, p. 436) (<u>arras</u> Hochst. (16, p.5)
- (Nero)	U. of Sask.	54B4.1	
- (Yaroslav)	U.S.D.A.	55B4.323	
- -	"	55B4.353	(called "pubescent" in this study)
- -	"	55B4.411	(called "compact" in this study)
<u>T. persicum</u>			
<u>fuliginosum</u>	"	55B4.260	<u>fuliginosum</u> Zhuk.
<u>rubiginosum</u>	"	55B4.270	<u>rubiginosum</u> Zhuk.
<u>stramineum</u>	"	55B4.263	<u>stramineum</u> Zhuk.
-	"	55B4.259	(called <u>T. persicum</u> (14) in this study)

* See list of sources at the end of this section.

APPENDIX II (cont'd.)

<u>Variety</u>	<u>Source*</u>	<u>U. of Man. Number</u>	<u>Other classifications and remarks</u>
<u>T. orientale</u>			
<u>insigne</u> Perc.	Max Planck	55B4.157	
<u>notabile</u> Perc.	Bell	55B4.187	(called <u>notabile</u> (1) in this study)
"	U.S.D.A.	55B4.283	(called <u>notabile</u> (2) in this study)
- (Gigante ingles)	"	55B4.292	
<u>T. pyramidale</u>			
<u>alborubrum</u>	Percival	55B4.144	
<u>nigritans</u>	"	55B4.145	
<u>pseudo-copticum</u> Perc.	"	55B4.141	
<u>recognitum</u>	U.S.D.A.	55B4.304	recognitum Perc. (7, p. 263)
<u>thebaicum</u>	Percival	55B4.143	
- (Beladi 164)	U.S.D.A.	55B4.322	

* See list of sources at the end of this section.

APPENDIX II (cont'd.)

<u>Variety</u>	<u>Source*</u>	<u>U. of Man. Number</u>	<u>Other classifications and remarks</u>
<u>T. durum</u>			
<u>erethromelan</u> Korn.	Percival	55B4.49	
<u>leucurum</u> Korn.	"	55B4.40	<u>leucurum</u> Alef. (15) " " (14)
<u>murciense</u> Korn.	"	55B4.48	
<u>provinciale</u> Korn.	"	55B4.53	<u>provinciale</u> Alef. (15) " " (14)
<u>reichenbachii</u> Korn.	"	55B4.43	
- (Bald Medeah)	C.D.A.	57B4.40	<u>australe</u> Perc. (7, p. 229)
- (Camadi)	"	57B4.47	
- (Golden Ball)	"	56B4.109	<u>melanopus</u> Alef. (3, p. 125)
			Other authorities for <u>melanopus</u> : <u>melanopus</u> Korn. (7, p. 211) " Alef. (15) " " (14) " (Alef.) Korn. (16, p. 6)
- (Kahla)	"	57B4.42	<u>taganrogense</u> Desv. (3, p. 125)

* See list of sources at the end of this section.

APPENDIX II (cont'd.)

<u>Variety</u>	<u>Source*</u>	<u>U. of Man. Number</u>	<u>Other classifications and remarks</u>
<u>T. durum</u> (cont'd.)			
- (Stewart)	U. of Sask.	55B4.498	<u>hordeiforme</u> (Host) Stol. (1, p. 152) Other authorities for <u>hordeiforme</u> : <u>hordeiforme</u> Korn. (7, p. 212) " (Host) Korn. (15) " " " (16, p. 6)
- -	C.D.A.	57B4.55	(called "smooth-awn" in this study)
<u>T. turgidum</u>			
<u>buccale</u> Korn.	Percival	55B4.69	<u>buccale</u> Alef. (15) " " (14)
<u>dinurum</u> Korn.	"	55B4.79	<u>dinurum</u> Alef. (15) " " (14)
<u>dreischianum</u> Korn.	"	55B4.72	
<u>gentile</u> Korn.	"	55B4.65	<u>gentile</u> Alef. (15) " " (14)
<u>megalopolitanum</u> Korn.	"	55B4.67	
<u>melanatherum</u> Korn.	"	55B4.198	

* See list of sources at the end of this section.

APPENDIX II (cont'd.)

<u>Variety</u>	<u>Source*</u>	<u>U. of Man. Number</u>	<u>Other classifications and remarks</u>
<u>T. turgidum (cont'd.)</u>			
<u>plinianum</u> Korn.	Percival	55B4.76	
<u>ramoso-megalopolitanum</u>	"	55B4.68	
<u>rubrialbum</u>	"	55B4.84	
<u>salomonis</u> Korn.	"	55B4.70	also spelt <u>salamonis</u> (15)
<u>speciosum</u> Korn.	"	55B4.74	<u>speciosum</u> Alef. (15) " " (14)

* See list of sources at the end of this section.

APPENDIX II (cont'd.)

Sources of material used in this study:

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| C.D.A. | Canada Department of Agriculture Research
Laboratory, Winnipeg, Manitoba. |
| Bell | Dr. G. D. H. Bell, Plant Breeding Institute,
Cambridge, England. |
| Max Planck | Professor Dr. W. Rudorf, Max-Planck-Institut,
Koln-Vogelsang, Germany. |
| Percival | Percival Collection, Reading University,
Berkshire, England. |
| U. of Sask. | University of Saskatchewan, Saskatoon, Sask. |
| U.S.D.A. | Mr. D. J. Ward, Plant Industry Station, U.S.D.A.,
Beltsville, Maryland. |
| Zhukovsky | Professor P. Zhukovsky, Institute of Plant
Industry, U.S.S.R. |

