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by

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CONTENTS

I. INTRODUCTION

The phylogenetic relationship between species of *Triticum* and its closely related genus *Aegilops* has been well clarified by the genome analytical method established by Kihara and his co-workers (Kihara and Nishiyama 1930 *etc*.). The evolutionary process of *Triticum* and *Aegilops* consists of two basic steps; the differentiation of the genomes at the diploid level and the formation of tetra- and hexaploid species through allopolyploidization (for a review, see Lilienfeld 1951; Kihara 1954). However, tetraploid species in *Triticum* and *Aegilops* are rarely simple allopolyploid between two ancestral species. In his review on the evolution of *Aegilops*, Kihara (1954) reported that, in most of the tetraploid species, one genome is homologous to that of the diploid analyzers but that the other genome is modified variously (see also Lilienfeld 1951).

Such a diverse modification of genomes is also recognized in *Triticum*. The tetraploid wheats belong to two groups, the emmer group which has the AABB genome and the timopheevi group which has the AAGG genome. The A genome of the tetraploid wheats is homologous to that of the diploid wheats. The donor(s) of the second genome to the tetraploid wheats has been and is still one of the most controversial problems among wheat studies. But the B and G genomes are generally considered to have derived from the S genome of *Ae*. *speltoides* Tausch. (The literature dealing with the genomes of the tetraploid wheats and their origin will be reviewed in the following section.)

From their genome-analysis and studies on morphological continuity, Zohary and Feldman (1962) and Zohary (1966) concluded that polyploid Triticum and Aegilops had three species clusters which shared either the A (T. boeoticum Boiss.), D (Ae. squarrosa L.) or C^u (Ae. umbellulata Zhuk.) genome.

To explain the origin of the modified genomes, Kihara (1954, see also Lilienfeld 1951) proposed that a now extinct or yet unknown diploid species was the donor and also assumed that chromosome differentiation had occurred independently within the genome concerned. Zohary and Feldman (1962) and Zohary (1966) proposed an alternative hypothesis to explain the varying degree of differentiation between ancestral genomes of diploid species and corresponding genomes in polyploid species. According to their model, introgressive hybridization between amphidiploids sharing a common genome would have produced a new genomic constitution in which the genome in common remains unchanged while the other genome is modified through segmental replacement of chromosomes. They further assumed that such a process would also cause intraspecific chromosomal differentiations and predicted that extensive structural variation would be found in chromosomes belonging to the modified genomes of the tetraploid species. However, the possibility of modification of genomes by recombination of two different genomes has been criticized by Kihara (1963) who emphasized that differentiation occurred independently within the genome.

Thus, in considering the origin of the tetraploid wheats, the process by which one genome became structurally modified while the other remains unchanged must be studied more extensively. Recently, Larsen (1973) reported that most of the translocations identified in the hexaploid wheats involved chromosomes belonging to the B genome. This suggested that the B genome is more variable than the other genomes.

Therefore, I attempted to test the above hypotheses on the modified genomes by analyzing the intraspecific structural differentiations in chromosomes. In the present study, I examined intraspecific variation in chromosome structure, especially that due to translocations, in the two wild tetraploid wheats, *T. dicoccoides* (Körn.) Schweinf. and *T. araraticum* Jakubz. This was done to obtain information concerning the origin and the course of dissemination and, further, information concerning the degree of structural variation in different genomes. Such information would be of value in clarifying the origin and the evolution of the tetraploid wheats.

II. REVIEW OF LITERATURE

1. Genomes of the tetraploid wheats and their origin

In 1913, Schulz classified wild and cultivated wheats (genus *Triticum* L.) into three groups, *i. e.*, Einkorn, Emmer and Dinkel, based on their morphological characteristics (see Kihara 1924). These three groups were then revealed to form a polyploid series (Sakamura 1918; Sax 1918; Kihara 1919, 1924). Einkorn has 2n = 14 chromosomes, Emmer or two-grained wheats, 2n = 28 chromosomes and Dinkel, 2n = 42 chromosomes, the basic chromosome number of these groups being seven. The genome of the diploid group consisting of seven chromosomes was designated as A and the whole genome formula of the diploid wheats as AA (Sax 1922; Kihara 1924; Kihara and Nishiyama 1930). Tetraploid emmer wheats have the A genome of diploid wheats and another genome designated with B (*loc. cit.*). Genomes of the hexaploid wheats consists of three different genomes; the two (AB) of the tetraploid emmer wheats and another genome designated D (Kihara 1924; Kihara and Nishiyama 1930).

In 1928, Zhukovsky reported a new cultivated two-grained wheat *T. timopheevi* Zhuk. which he found in 1923 in Western Georgia, Transcaucasus and at first classified it as a variety of a cultivated emmer wheat, *T. dicoccum* Schübl. (Zhukovsky 1928). Cytogenetical studies by Lilienfeld and Kihara (1934) revealed that this species has the A genome in common with the diploid wheats and the tetraploid emmer wheats but the second genome was structurally different from the B genome of the other tetraploid species. By giving this second genome the symbol G, they emphasized its identity. Namely, Lilienfeld and Kihara (1934) established the fourth group, Timopheevi, which has 2n = 28 chromosomes and the genome formula AAGG. At about the same time, two-grained wild wheat was also found in Transcaucasus (Tumanyan 1930; Jakubziner 1932) and it was classified as a subspecies of wild emmer wheat; *T. dicoccoides* Körn. subsp. *armeniacum* (Jakubziner 1932). Makushina (1938) observed irregular meiosis and sterility in hybrids of this subspecies with other emmer wheats and Svetozarova (1939) showed that it has the same genomic constitution, AAGG, as *T. timopheevi*. Based on these studies, Jakubziner named this taxon *T. araraticum* Jakubz. in 1947 (see Jakubziner 1959). Kostoff (1936) pointed out a certain degree of homology between the B genome and the second genome of *T. timopheevi* and proposed to designate the second genome by the symbol β. However, in spite of his proposal and several other studies which indicated a close relationship between the emmer and the timopheevi group (Love 1941; Sachs 1953; Wagenaar 1961, 1966; Feldman 1966), the genome formula AAGG is generally accepted for the timopheevi group.

Thus, the tetraploid wheats are divided into two groups, the emmer group (AABB) and the timopheevi group (AAGG). The emmer group contains one wild species, *T. dicoccoides* and several cultivated species, *T. dicoccum*, *T. durum* Desf., *etc.* It played an important role in the evolution of cultivated wheat: The hexaploid wheats, *T. aestivum* L., *T. spelta* L., *etc.*, were originated from an amphidiploid between the cultivated Emmer and the wild diploid *Aegilops squarrosa* (Kihara 1944; McFadden and Sears 1944). Genetical and morphological evidence show that the cultivated Emmers were derived from wild *T. dicoccoides*. Members of this group produce fertile hybrids when crossed to each other. In the timopheevi group, complete sterility has been reported in hybrids between wild *T. araraticum* and cultivated *T. timopheevi* (Svetozarova 1939; Sachs 1953; Wagenaar 1961, 1966). However, recent studies (Tanaka and Ichikawa 1972; Tanaka and Ishii 1973, 1975; Kawahara and Tanaka 1977) have revealed that several *araraticum* strains produce fertile or semi-fertile hybrids when crossed to *T. timopheevi*. These studies provided genetical evidence to the generally accepted theory that *T. timopheevi* had originated from *T. araraticum*. Consequently, the two wild tetraploid wheats, *T. dicoccoides* and *T. araraticum* are the ancestral species of the emmer and the timopheevi group, respectively.

As mentioned above, many workers have shown that one genome of the tetraploid wheats pairs quite well with the chromosomes of the diploid wheats (Sax 1922; Kihara 1924, 1929; Thompson 1926; Kihara and Nishiyama 1930; Lilienfeld and Kihara 1934; Kostoff 1936; Matsumura 1950). Thus, it is clear that the diploid wheats had donated one of the genomes of the tetraploid wheats, namely A. Apparently, one of the ancestral species of the wild tetraploid wheats would be a wild and not a cultivated species. Riley and Bell (1959) indicated a closer similarily between the gene content of the A genome of tetraploid wheats and that of wild *T. thaoudar* Reut. than that of the cultivated *T. monococcum* L. or wild *T. boeoticum*.

Jenkins (1929) observed that in a hybrid between *T. turgidum* L., a cultivated emmer species, and *Ae. speltoides*, seven pairs of chromosomes usually mate and suggested that the chromosomes of *Ae. speltoides* are homologous with a set of chromosomes in *T. turgidum*. At the same time, he found that *Ae. speltoides* possesses several characters which distinguish *T. aestivum* from the emmer wheats and considered that the situation was more complex than was indicated by the amount of pairing. Thompson (1931) also considered on a cytogenetical basis that *Ae. speltoides* has a genome in common with the emmer wheats. While, no homology was recognized by Kihara and Nishiyama (1930) nor by Lilienfeld and Kihara (1934). between the S genome of *Ae. speltoides* and the B or G genome in polyploid wheats, the theory that *Ae. speltoides* had donated the B genome to the emmer wheat has been supported by many authors since then. Pathak (1940) observed similarity between the satellites of the chromosomes of *Ae. speltoides* and the emmer wheats. The morphological characters have been critically applied to this problem by Sarkar and Stebbins (1956). By using Andernos's (1949) "Method of extraporated correlates", they suggested that *Ae. speltoides* var. *ligustica* could be the donor of the B genome. On the basis of synaptic, karyotypic and geographical evidence, Riley *et al*. (1958) also concluded that *Ae. speltoides* might have donated the B genome.

The suggestion of McFadden and Sears (1946, 1947) that the emmer wheats might have arisen as an amphidiploid between *T. monococcum* and *Agropyron tiriceum* Gaertn. has been discarded in later studies. Karyomorphological studies by Sarkar (1955) and Matsumura and Sakamoto (1955) indicated that *Ag. triticeum* does not have the expected type of chromosomes.

Tanaka (1956) recognized similarity in the morphological characteristic of the culum between *Ae. longissima* Schw. et Musch. and the emmer wheat and produced an amphidiploid between *Ae. longissima* and *T. boeoticum*. However, he failed to obtain cytogenetical evidence in hybrids between the amphidiploid and the emmer wheats. Sears (1956) proposed *Ae. bicornis* (Forsk.) Jaub. et Sp. to be the B genome donor on the basis of the morphological similarity of the amphidiploid between *Ae. bicornis* and *T. monococcum* to the emmer wheats. But the chromosomes of the B genome belong to a karyotype different from that of *Ae. bicornis*, *Ae. sharonensis* Eig and *Ae. longissima* (Riley *et al*. 1958). By the measurement of the DNA contents of the genome, Rees (1963) and Rees and Walters (1965) concluded that *Ae. speltoides* is a more likely contributor of the B genome than either *Ae. bicornis* or *Ae. longissima*.

The origin of the G genome was studied by several authors together with its relationship to the B genome. As mentioned above, Kostoff (1936) and Love (1941) suggested partial homology between the B and G genomes and that the latter was derived from the former through a process of structural differentiation of chromosomes. Sachs (1953) crossed two varieties of _T. dicoccoides_ to _T. timopheevi_ and found that one of them, var. _kotschanum_, showed irregular meiosis with univalents but that the other, var. _nudiglumis_ collected by J. B. Gillet in Iraq, showed regular meiosis with 14 bivalents in their hybrids. Since the specimens designated as var. _nudiglumis_ was not morphologically identical with _T. araraticum_, he regarded these two varieties as two types of _T. dicoccoides_ that differ in their chromosome structure. Consequently, he concluded that the cytologically different 4x _Triticum_ species could have been derived from an original tetraploid prototype. However, var. _nudiglumis_ used by Sachs (_loc. cit._) was apparently a form of _T. araraticum_ cytogenetically (Wagenaar 1961, 1966). Wagenaar (1961, 1966, 1970) suggested that the two genomes of the timopheevi wheats are basically the same as the AB genomes of the emmer wheats and that the irregular meiosis in F_1 hybrids between these two groups was due primarily to a genetic system which induced asynapsis. Since normal meiosis was observed in hybrids within each group, he assumed that the genetic system induces asynapsis in the hybrids when in a heterozygous condition; _i. e._, complementary genes.

If so, the amphidiploid between the two groups would also show irregular meiosis. However, amphidiploids between T. timopheevi and several species of the emmer wheats showed almost normal meiosis (Sachs 1953). Therefore, irregular meiosis in hybrids between the two groups of tetraploid wheats would be due primarily to structural differentiations between their genomes but not to a genic system as Wagenaar had assumed. Wagenaar's hypothesis was further disapproved by Feldman (1966) who studied the amount of the relative chromosomal differentiation of the two genomes of T. timopheevi using telocentric chromosomes as cytogenetical markers. He found that most of the pairing failure in aestivum-timopheevi hybrids involved chromosomes of the B genome and the corresponding genome of T. timopheevi. This and the variation between chromosomes led him to suggest that structural differences, rather than genes causing asynapsis when heterozygous, were responsible for the lack of pairing. At the same time, he considered that the second genome of T. timpheevi was closely related enough to the B genome to be designated B^t, and it had differentiated from the B genome by introgression of alien chromosomal segments following interspecific hybridization.

Kimber and Athwal (1972) showed the variation in the genetic mechanism in Ae. speltoides that affected the amount of homoeologous chromosome pairing in interspecific hybrids. In hybrids with T. aestivum, they recognized three groups; high, intermediate and low pairing types. Chromosomal affinity deduced by the amount of pairing in intermediate and low pairing types of hybrids was well below that expected if the chromosomes of *Ae. speltoides* were homologous to the B genome of *T. aestivum*. Therefore, they concluded that *Ae. speltoides* could no longer be considered as the donor of the B genome of the polyploid wheats and proposed that the B genome had originated through intercrossings of two or more amphidiploids originated as a result of hybridization between diploid wheat and other species. On the other hand, Kimber (1973) and Shands and Kimber (1973) suggested that *Ae. speltoides* had donated the second genome of the timopheevi wheats and the genomic formula should be AASS, but Sano and Tanaka (1980, 1982) could not detect any chromosomal homology between the genome of *Ae. speltoides* and the B or G genome in their study to estimate the chromosomal homology by using the B-chromosomes of *Ae. speltoides*.

Recently, Johnson and Dhaliwal (Johnson 1972, 1975; Johnson and Dhaliwal 1976, 1978; Dhaliwal and Johnson 1976, 1982) proposed the autotetraploid origin of the two groups of tetraploid wheats from the diploid wheats. The autotetraploid origin of tetraploid wheats has already been suggested by Câmara (1935) in his studies on the effects of X-rays on chromosomes of *T. monococcum*. Based on the protein profiles revealed by electrophoresis and some other morphological and genetical evidences, Johnson and Dhaliwal (*loc. cit.*) proposed wild diploid *T. urartu* Tum. as the donor of the second genomes (B and G) of the tetraploid wheats. However, this hypothesis was soon disapproved. Chen et al. (1975) observed the variation in Fraction 1 protein large subunit in several species of Triticum and Aegilops. They revealed that polyploid wheats have large subunits with higher isoelectric points while the diploid wheats have those with lower isoelectric points. Both types were recognized in Aegilops. Since large subunits are inherited maternally, they concluded that the tetraploid wheats originated from the hybridization between unknown species with the large subunits of higher isoelectric points as female parent and the diploid wheats as male parent. Chapman et al. (1976) and Dvořák (1976) observed chromosome pairings in hybrids between T. urartu and telosomics of T. aestivum cv. Chinese Spring and found that chromosomes of T. urartu pair with the A genome but not with the B genome chromosomes of T. aestivum.

Tanaka et al. (1978, 1979a, b) reported that an amphidiploid of Ae. speltoides and T. boeoticum at the F_{11} generation produced fertile hybrids with T. durum. This and other evidence on distribution and variation of the wild tetraploid wheats and on the close similarity of the B and G genomes led them to conclude that the tetraploid wheats had been derived from an amphidiploid (SSAA) between Ae. speltoides and T. boeoticum through disruptive differentiation of species.

Recent studies on several isozymes (Jaaska 1976, 1978, 1980; Nakai 1978, 1979) revealed that Ae. speltoides is the most probable donor of the B and G genomes. Studies on nucleo-cytoplasmic interactions have supported the assumption that *Ae. speltoides* or a closely related species is the donor of the B and/or G genomes (Suemoto 1968, 1973, 1979; Tsunewaki *et al*. 1976, 1979; Tsunewaki 1980).

By using the Giemsa C-banding technique, Natarajan and Sarma (1974) showed closer similarity of *speltoides* chromosomes than those of *bicornis*, *sharonensis* and *longissima* to B genome chromosomes. On the other hand, Gill and Kimber (1974) emphasized the differences in banding pattern between *speltoides* chromosomes and B genome chromosomes.

Feldman (1979) found that the B genome chromosomes of *T. aestivum* paired at a higher frequency in hybrids with *Ae. longissima* than in hybrids with *Ae. speltoides*. However, *longissima* was not considered to be the donor of the B genome. Instead, based on karyological and geological evidence, he concluded that *Ae. searsii* Feldman and Kislev, a closer relative to *Ae. longissima* could have donated the B genome. Kushnir and Halloran (1981, 1982) suggested on the basis of morphological and karyological evidence that *Ae. sharonensis* might have donated the B genome of polyploid wheats. But the isoelectric pattern of the Fraction 1 protein of *searsii*, *longissima*, *sharonensis* and *bicornis* is not the same as that expected from the tetraploid wheats (unpublished data by Wildman and by Edelman, cited by Feldman 1979). *Ae. speltoides* has the expected pattern of the Fraction 1 protein (Chen *et al*. 1975).

Thus there seems to be a good agreement in the opinions that the B and G genomes had originated from some species or varieties of the section Sitopsis of _Aegilops_, most probably from _Ae_. _speltoides_. It is also clear that the B and G genomes are unique to the polyploid wheats and that no diploid species in _Triticum_, _Aegilops_ or their related genera has the B or G genome. Consequently, the B and G genomes would have structurally differentiated after the formation of amphidiploids to such an extent that no homology could be recognized between their ancestral genome(s) as suggested by Tanaka _et al_. (1978, 1979a, b). This is in sharp contrast to the A genome of the polyploid wheats that is also found in the diploid wheats.

To explain such differential genome modifications, several hypotheses have been proposed. The differential introgression model (Zohary and Feldman 1962; Zohary 1966) assumed that hybridization between two amphidiploids of, for example, genomic constitution AABB and AACC would allow the A genome to act as a buffer while the B and C genomes recombined. They further assumed that intraspecific chromosome differentiations as well as species differentiations would occur through this process. However, Furuta and Tanaka(1970) and Furuta (1982) could not obtain evidence supporting this theory in their studies on experimental introgression in natural tetraploid _Aegilops_ species. Another possibility is that several genomes of _Triticum_ and _Aegilops_ are unstable while others are stable, and some tetraploid species had differentiated from an amphidiploid with a stable and an unstable genome (Tanaka 1963 and personal communication). If one of the two genomes of a tetraploid is structurally less stable than the other, intraspecific chromosomal differentiation would be more frequent in the unstable than in the stable genome. However, decisive evidence supporting either of these hypotheses is not obtained yet. The present studies were aimed at analyzing the nature of intraspecific chromosomal differentiation in tetraploid species and obtaining information to access the validity of the hypotheses on genome modifications.

2. Geographical distribution and the center of diversity of the wild tetraploid wheats.

According to Percival (1921), *T. dicoccoides* is found in the neighbourhood of Mount Hermon and other parts in Syria and Palestine and in Western Iran. Flaksberger (1939, cited by Hosono 1954) reported that *T. dicoccoides* ssp. *syrio-palestinicum* Flaksb. occurs in Syria, Palestine, Transjordan, Iraq and in Taurus in Turkey. The other subspecies, ssp. *armeniacum* Jakubz. (= *T. araraticum* Jakubz.) is found in Armenia, Azerbaijan in U.S.S.R. and in Iran (loc. cit.). According to Jakubziner (1959), *T. araraticum* is also found, in addition, in Nachichevan in U.S.S.R.

Cytogenetical studies by Sachs (1953) and Wagenaar (1966) showed that the wild wheat collected by J. B. Gillet in Northern Iraq (identified as *T. dicoccoides* var. *nudiglumis* Nabalek) was identical to *T. araraticum*. Consequently, the two wild tetraploid wheats have been considered to have a distinct distribution area; *T. dicoccoides* in Palestine and its adjacent areas in Syria and Jordan and *T. araraticum* in Transcaucasus, Southern Turkey, Northern Iraq and Western Iran. Harlan and Zohary (1966) described two main races of the wild tetraploid wheats; the Palestine race growing in Israel, Syria and Jordan and the Turkish-Iraqi race in Turkey, Iraq, Iran and U.S.S.R. They considered that the Palestine race is *T. dicoccoides* and that the Turkish-Iraqi race corresponds to *T. araraticum*.

More recent studies, however, indicated that *T. dicoccoides* also grows in the Zagros-Taurus Mountain area in Turkey, Iraq and Iran. Rao and Smith (1968) reported four *dicoccoides* accessions from Turkey which show cytogenetic behavior similar to that of *T. dicoccum* and *T. turgidum* L. Also, Dagan and Zohary (1970) showed that the two samples of wild tetraploid wheats collected in the western flants of the Zagros Mountains, Northern Iraq, are cytogenetically identical with Israeli *T. dicoccoides*. They further reported that both *T. dicoccoides* and *T. araraticum* occur sympatrically in Southeastern Turkey, Northern Iraq and Western Iran occupying the oak park-forest belt of this region. Morphologically these sympathric wheats were similar. In this region, Tanaka and Ishii (1973) reported four sites where the two species grow together and three sites where only *T. dicoccoides* grows and that *T. araraticum* was found abundantly in this region.

Samples reported by them were identified cytogenetically (Tanaka and Ishii 1973 and in the present study). They also pointed out that little morphological difference exists between them except for hairiness of leaf surface. Johnson (1975) collected more than one hundred *dicoccoides* accessions in Southeastern Turkey and two in Western Iran though without cytogenetical identification. Rawal and Harlan (1975) crossed several accession of wild tetraploid wheats from Israel and Turkey to *T. timopheevi* from Georgia, U.S.S.R., and observed chromosome pairings in the hybrids. They found that all the four accessions from Israel were *T. dicoccoides* but those from Turkey consisted of two species; four *dicoccoides* accessions, one *araraticum* accession and one mixed accession of *dicoccoides* and *araraticum*. Tanaka (1978) reported a mixed population of T. *dicoccoides* and *T. araraticum* in Southcentral Turkey and a pure stand of *T. dicoccoides* or *T. araraticum* in Southeastern Turkey. Thus, the distribution of the two wild tetraploid wheats overlaps in Southern Turkey, Northern Iraq and Western Iran, the mid point of tetraploid distribution range. Moreover, those in this area have almost the same morphological characteristics. Therefore, hybridization of samples collected in this area with strains of *T. dicoccoides* from Palestine or of *T. araraticum* from Transcaucasus would be of practical value in the identification of species.

As to the center of diversity of *T. dicoccoides* and *T. araraticum*, little is known because many accessions of these species became available only recently. Tanaka and Sakamoto (1979) observed several morphological and physiological characteristics and found that almost all of the variations of ~~the~~ wild tetraploid wheats, especially of *T. araraticum*, were concentrated in the Sulaymaniyah, Rowanduz and Amadiyah regions in Northern Iraq. Saito and Ishida (1979) investigated variations in susceptibility to leaf rust, *Puccinia recondita* Roberge et Desm. f. sp. *tritici*. In *T. dicoccoides*, all the strains from Palestine, Iraq and Iran were susceptible but those from Turkey showed the variation from susceptible to resistant. In *T. araraticum*, strains from Transcaucasus were resistant but those from the Zagros-Taurus Mountain area had various degree of susceptibility. They concluded that Mesopotamia, especially the Zagros Mountains, is the center of genes controlling susceptibility to leaf rust. Nakai (1978, 1979) observed variations in esterase isozymes and found that *T. dicoccoides* in Palestine and *T. araraticum* in Transcaucasus was monotypic in regard to isozyme variation but those in Zagros-Taurus area (Turkey, Iraq and Iran) showed variations. Nevo *et al.*(1982) observed genetic variations in natural populations of *T. dicoccoides* by using 38 isozymes but the sampling sites were all in Israel.

Consequently, it is clear that the Zagros-Taurus Mountain area is the center of diversity of *T. dicoccoides* and *T. araraticum*. However, newly introduced samples from Turkey (Tanaka 1978) had not yet been examined in regard to their variation. By examining many samples from this area using a different method from those cited above, more information concerning the center of diversity of the wild tetraploid wheats would be obtained.

3. Reciprocal translocations in *Triticum* and *Aegilops*

In *Triticum* and *Aegilops*, translocations have been found by many authors (see Burnham 1956). But most of the translocations studied were artificially induced by X-rays or other methods. Here, studies on spontaneous translocations are reviewed.

a. Diploid species

Kihara (1937) reported a reciprocal translocation between *Ae. comosa* Sibth. et Sm. and *Ae. heldreichii* Holzm. These two species have an identical genome M (*loc. cit.*).

Between *Ae. longissima* and *Ae. sharonensis*, structural differentiation due to translocations has been reported (Kihara 1954; Tanaka 1955). Here also the two species have the same genome S^l (Tanaka 1955). The presence of a translocation between *longissima* and *sharonensis* was further confirmed by Kimber (1961) and Ankori and Zohary (1962). Structural differentiation due to a reciprocal translocation was also found between *longissima* and *speltoides* (Kihara 1949; Riley *et al*. 1961) and between *longissima* and *bicornis* (Kimber 1961). While, no multivalent was observed in hybrids between *sharonensis* and *speltoides* nor between *sharonensis* and *bicornis* (Tanaka 1955). Therefore, *Ae.*

speltoides, *Ae*. *sharonensis* and *Ae*. *bicornis* would have the same chromosomal arrangements but *Ae*. *longissima* differs from these species by one reciprocal translocation. Feldman *et* *al*. (1979) reported a translocation between *Ae*. longissima and *Ae*. *searsii*. *Ae*. *searsii* was described as a new species by Feldman and Kislev (1977, 1978) but it appears to be the same as a new variety of *Ae*. *longissima* reported by Yamashita and Tanaka (1967) (Waines 1978).

Smith (1936) found a reciprocal translocation between varieties of diploid *T.* *monococcum*

Although these studies were based on a few hybrid combinations, they may suggest an important role of structural differentiation of chromosomes in intraspecific differentiation of species

In *Ae*. *squarrosa*, chromosome pairings in hybrids between more than 20 strains from various regions were observed (Kihara *et* *al*. 1965). Of these, one strain, No 2107 from Iran had a translocation relative to others. Two other strains from the same site as 2107 had no translocation. This may indicate that spontaneous translocation is very rare in this species.

b. Tetraploid species

Kihara (1937) observed one (or rarely two) quadrivalent in hybrids between *Ae*. *variabilis* Eig and *Ae*. *kotschyi* Boiss. He concluded that the genome ($C^uC^uS^vS^v$) of these two species are segmentally differentiated but they are better recognized as two varieties rather than two species.

Feldman (1963) found up to two translocations between six Israeli collections of *Ae. variabilis*. Further analysis to locate the translocation on specific genomes indicated the concentration of the differences in the S^v genome (*loc. cit.*). Tanaka and Kawahara (1980) intercrossed 24 strains of *Ae. variabilis* and *Ae. kotschyi* and grouped them into four chromosome types, K_1, V_2, K_3 and V_4, differing with reciprocal translocations. K1 and K3 were found in *Ae. kotschyi*, V_4 in *Ae. variabilis* and V_2 in both species. The greatest variation was found in Palestine, where both of the two species grow. It was assumed that the fundamental type of the two species was V2 and that these species were originated monophyletically. Furuta (1981b) examined intraspecific variation by observing chromosome pairings in 83 hybrids of strains of *Ae. variabilis* and *Ae. kotschyi* with a tester strain of *Ae. variabilis*. He observed quadrivalents and sexivalents at various frequencies and concluded that the main factor of variation in chromosome structure of these species was reciprocal translocation.

Furuta (1981a) also reported structural differentiations in chromosomes in *Ae. ovata*. L. ($C^uC^uM^oM^o$). He crossed a tester strain, KU-9-1, to 73 *ovata* strains and classified them into four types, I - IV, by the occurrence of multivalents in the hybrids. Most of the strains (55) were of type II which produced a quadrivalent in hybrids with 9-1. Fourteen strains produced a sexivalent (Type III), three formed two quadrivalents (type IV) and one hybrid combination produced no multivalent (Type I). The common pollen parent in his study had been used earlier in genome analysis by Kihara and his co-workers (*loc. cit.*). Furuta's study clearly indicated that the chromosome structure of 9-1 was not typical of *Ae. ovata* in regard to translocations.

In *Ae. triuncialis* L., Matsumura and Kondo (1942) found no multivalents in the hybrids between two strains of var. *typica* nor in those between strains of var. *persica* but observed trivalents and quadrivalents in almost all the intervarietal hybrids. Since two multivalents were frequently formed in a cell, they concluded that the two varieties differs by two translocations. Koshikawa *et al.* (1978) crossed a tester strain of *Ae. triuncialis* to 55 *triuncialis* strains from Iran and Afghanistan and observed meiosis in the F_1 hybrids. Of these, five produced a quadrivalent per cell. No multivalent was observed in the remaining hybrids.

Studies on intraspecific variation in tetraploid *Aegilops* (Koshikawa *et al.* 1978; Tanaka and Kawahara 1980; Furuta 1981a,b) indicate that translocations are more common in *Ae. ovata*, *Ae. variabilis* and *Ae. kotschyi* than in *Ae. triuncialis*.

In *Ae. ventricosa* Tausch (DDM^vM^v), Kihara and Lilienfeld (1932) reported a translocation between var. *comosa* and var. *fragilis*.

Hosono (1935) reported that in most of the hybrids in the emmer group, a quadrivalent or two quadrivalents were observed. The frequency of cells with quadrivalents was high in hybrids involving *T. dicoccum* ranging from 22.5 per cent to 35.1 per cent. Sizova (1939) found that two subspecies of *T. durum* differed by a translocation involving one of the two chromosome pairs with a satellite. A quadrivalent was observed in every PMC in a hybrid *T. durum* x *T. percicum* (Smith 1947). Nishikawa (1962) examined reciprocal translocations in the emmer wheats using five varieties, *T. dicoccoides spontaneo-nigrum*, *T. dicoccum liguiforme*, *T. dicoccum arras* (Khapli), *T. dicoccum* (Vernal) and *T. durum reichenbachii*. Four cultivated varieties of the Emmer had at least one reciprocal translocation in common which was not found in the variety of wild Emmer, *T. dicoccoides spontaneo-nigrum*, and in addition to this one, *liguiforme* carried another reciprocal translocation. Jinahyon (1960) observed that hybrids of *T. dicoccum* cv. *Khapli* and *T. carthlicum* Nevski were heterozygous for a reciprocal translocation. Later, Dalal and Sadanaga (1965) identified the chromosomes involved in the translocation. By using *T. aestivum* cv. *Chinese Spring* as a standard, they found no detectable chromosomal rearrangement in cv. *Khapli* but found a translocation involving 2B and 3A in *T. carthlicum*.

Rao and Smith (1968) observed quadrivalents in hybrids between Turkish *dicoccoides* accessions and *T. dicoccum*, *T. turgidum* or an Israeli *dicoccoides* accession; the frequency being 0.07 to 0.34 per cell. Similarly, quadrivalents (and also quinque- or sexivalents) were recognized by Dagan and Zohary (1970) in hybrids involving two dicoccoides lines from Iran, one from Israel and an Israeli durum cultivar.

Svetozarova (1939) observed the presence of quadrivalents at meiosis in hybrids between T. araraticum and T. timopheevi and assumed that reciprocal translocations had a definite significance in the evolution of T. timopheevi and T. araraticum. This assumption was disapproved by Wagenaar (1961, 1966) who found no multivalent in several hybrids between T. araraticum and T. timopheevi nor in hybrids among strains of T. timopheevi. However, various kinds of multivalents were recognized in other hybrids between T. araraticum and T. timopheevi and in a hybrid between T. araraticum and T. dicoccoides var. nudiglumis. From the distribution of the samples used, he assumed that chromosome differentation in the T. timopheevi complex (T. araratucum and T. timopheevi) was localized to the more northern regions of the distribution area, Southern Soviet Union and northeastern tip of Turkey. Tanaka and Ichikawa (1972) found that an araraticum strain from Transcaucasus differs from other araraticum and timopheevi strains from Transcaucasus by one reciprocal translocation. Further, Tanaka and Ishii (1975) found another strain of T. araraticum that differs from these strains by one or two translocations. On the other hand, they observed no translocation between timopheevi strains. By examining the hybrids obtained by crossing with a tester strain of T. timopheevi, they recognized two groups of T. araraticum; one gave semi-fertile hybrids with normal meiosis and the other gave sterile hybrids with multivalents at meiosis. All the araraticum strains examined by them had been collected in Transcaucasus. Tanaka and Ishii (1973) reported extensive chromosomal differentiations including translocations among strains of *T. araraticum* from the eastern part of the Fertile Crescent; Southeastern Turkey, Northern Iraq and Western Iran. Thus, translocations are rather common in the wild tetraploid wheats but systematic analysis has not been made except by Tanaka and his co-workers on *T. araraticum* in Transcaucasus.

c. Hexaploid species

Reciporcal translocations have been observed between many hexaploid wheat species and varieties (Ellerton 1939; Sears 1953; Baker and McIntosh 1966; Riley *et al*. 1967; Röbbelen 1968; Zeller and Sastrosumarjo 1972; Larsen 1973; Baier *et al*. 1974; Vega and Lacadena 1982; and see also Burnham 1956). Crossing with monosomic or other aneuploid lines of *T. aestivum* cv. Chiese Spring have shown that most of these translocations are localized to specific chromosomes. These identified translocations will be summarized later (Table 26).

Riley *et al*. (1967) showed the existence of hexaploid wheats with the primitive chromosome structure by tracing the distributions of translocations. They presumed that in the initial hexaploid wheat, the structure of the chromosomes of the A and B genome were identical with that of the chromosomes of the tetraploid from which it was derived.

Similarly, the structure of D genome chromosomes must have been identical with that of the chromosomes of the parental form of *Ae. squarrosa*. In hybrids of *T. aestivum* cv. Chinese Spring with a strain of *Ae. squarrosa* (Riley and Chapman 1960) and with a strain of *T. dicoccoides* (Riley *et al*. 1967), no multivalent was recognized. Based on these observations, they concluded that cv. Chinese Spring had the primitive chromosome structure of the hexaplid wheats. The chromosomes of other hexaploid wheats were compared with those of Chinese Spring to determine whether or not deviation from the primitive structure have occurred. The results they obtained revealed that the two strains of *T. aestivum* and of *T. spelta* have the primitive hexaploid chromosome structure but the other hexaploid, including other strains of *aestivum* and *spelta*, as well as one representative of each of *T. compactum* Host., *T. sphaerococcum* Perc., *T. macha* Dek. et Men. and *T. vavilovi* Jakubz. differed from the primitive structure by one or two translocations. They concluded that the first hexaploid wheat must have been either *T. aestivum* or *T. spelta*.

Larsen (1973) assembled the data on identified translocations in *Triticum*. According to him, chromosomes from the A genome and especially from the B genome are much involved in translocations in the hexaploid wheats, while the D genome chromosomes are less involved. The A genome were involved in 9 different translocations, the B genome chromosomes in 15, while the D genome chromosomes were involved in only 5 different translocations. He assumed that the B genome was so much split up that the donor of this genome could not be found. In hybrids between a synthetic hexaploid wheat and Chinese Spring monosomics, Larsen (*loc. cit.*) observed multivalents, bridges and low pairings at meiosis. In the mitosis of the hybrids, morphological differences were recognized in chromosome 5D. These data led him to conclude that Chinese Spring was not so primitive in its chromosome structure as is generally assumed.

In these two studies (Riley *et al.* 1967; Larsen 1973), however, only one strain of *Ae. squarrosa*, *T. dicoccoides* or synthetic hexaploid wheat was used without examining cytogenetical relationships to other strains. Therefore, further study is needed to find out the primitive chromosome structure of the hexaploid wheats. Especially, the primitiveness of the Chinese Spring chromosome structure must be reexamined because it is widely used as a standard chromosome structure of the hexaploid wheats.

III. METHODS

Most of the crossings were performed in the experimental field but some were conducted in a glasshouse. The hand emasculated spikes were enclosed in paraffin-paper bags and pollination was carried out three or four days later by brushing the stigma with newly broken anthers of the male plant.

For cytological observations, young anthers were fixed in Farmer's solution (ethanol: gracial acetic acid = 3:1) and stored in a refrigerator. Preparations were made by the aceto-carmine or aceto-orcein squash technique. Chromosome pairings were observed at first metaphase (MI) or at first anaphase (AI) of meiosis in the pollen mother cells (PMCs). Chiasma frequency was calculated from the number of paired arms of chromosomes. Photographs were taken from temporary preparations.

Seed fertilities were calculated from seed settings on the lower two florets of the spikelets on three bagged spikes.

IV. DIFFERENTIATION OF CHROMOSOME STRUCTURES IN *TRITICUM DICOCCOIDES* (KÖRN.) SCHWEINF.

In *T. dicoccoides*, differentiation in chromosome structure has been reported by several authors (Section II). However, the number of strains used in these studies was too small to discuss either the geographical distribution of translocations or the fundamental chromosome structure with regard to translocations. The first attempt to clarify the fundamental chromosome structure was made by Kawahara and Tanaka (1978) by examining hybrids among 22 strains of *T. dicoccoides*. Based on the data obtained by them, further analysis on translocations in *T. dicoccoides* were made in the present study. Structural differentiations other than translocations found in the course of this study were also reported.

1. Materials

The materials used in the present study were 46 strains of *T. dicoccoides* as listed in Table 1. Of these, 20 strains were collected by the members of the Kyoto University Botanical Expedition to the Northern Highlands of Mesopotamia, 1970 (abbreviation: BEM), in Turkey, Iraq and Iran. Seventeen were from the collection of the Kyoto University Scientific Exploration to the Eastern Turkey, 1976 (KUET: Tanaka 1978). Two were collected in Syria by the Botanical Mission of the University of Kyoto to the Eastern Mediterranean Countries in 1959 (BMUK: Yamashita and Tanaka 1960). The other strains were from the collection of MacKey, Vavilov or Aaronsohn or the All Union Institute of Plant Industry, Leningrad, U.S.S.R.

The species of each strain collected by BEM, KUET and BMUK was identified by Dr. M. Tanaka, Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University by morphological characteristics and was further confirmed cytogenetically by Tanaka and Ishii (1973) or in the present study.

All these strains have been established from a single plant of the original sample and maintained by selfing at the Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University. Therefore, each strain was considered to be a structural homozygote.

In the crossings, a Syrian strain, 108-3, was arbitrary chosen as a standard (Kawahara and Tanaka 1978) and later several other strains were also used as testers.

2. Results and Discussions

a. Cytogenetical analysis at MI

Detailed data on the occurrence of multivalents in F_1 hybrids between strains of <u>T. dicoccoides</u> are listed in Table Ia (Appendix I) and mean chromosome pairings in them are shown in Table IId (Appendix II). As is shown in Table IId, multivalents, especially association of even numbers of chromosomes, were frequently observed but the mean univalent

Table 1. List of *T. dicoccoides* used

Stock No. (KU-)*	Source and locality**
108-1	unknown
108-2, 108-3	BMUK, 20 km NW of Sueida(Cheikh Meskine-Sueida), Syria
108-4, 108-5	Collection of MacKey, by Yamashita(1964)
109	Vavilov(1930), Palestine
110	Vavilov(1930), Suburbs of Tiberia, Palestine
195	Collection of All Union Institute of Plant Industry, Leningrad, U.S.S.R.(1964), Palestine(20403)
198	Aaronsohn(1906), Mt. Canaan, Palestine
1921	KUET, 155 km W of Mardin(Urfa-Mardin), Turkey
1945, 1947, 1948, 1949, 1951, 1952, 1953, 1955, 1957, 1959A, 1959B, 1972B, 1974, 1976B, 1978B, 1991	KUET, 45 km SE of Maras(Maras-Gaziantep), Turkey
8536, 8539, 8541	BEM, 20.3 km S from Sulaymaniyah to Qara Dagh, NE slope of Shakh i Baranan, Iraq
8736A, 8736B, 8737	BEM, SSW of Rowanduz, Iraq(alt. 850 m)
8804, 8808, 8816A, 8816B, 8817	BEM, North slope of Jabal Sinjar, South of Kursi, Iraq

Table 1. List of *T. dicoccoides* used (continued)

Stock No. (KU-)*	Source and locality**
8821A, 8821C	BEM, 15.3 km ENE from Dohuk to Amadiyah, Iraq (alt. 780 m)
8915A, 8915B	BEM, 17.3 km E from Silvan to Bitlis, Turkey (alt. 660 m)
8935, 8937B	BEM, 9.3 km SE from Ergani to Diyarbakir, Turkey (alt. 780 m)
8941, 8942, 8943	BEM, 58.8 km N from Kermanshah to Ravansar, Iran (alt. 1610 m)

* Stock No. of the Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University.

** The following abbreviations were used.

BMUK: The Botanical Mission of the University of Kyoto to the Eastern Mediterranean Countries, 1959;

KUET: The Kyoto University Scientific Exploration to the Eastern Turkey, 1976;

BEM: The Kyoto University Botanical Expedition to the Northern Highlands of Mesopotamia, 1970.

frequencies per cell were low. Table 2 shows the frequency of mean univalent per cell in 133 hybrids of _T. dicoccoides_. The average was 0.102 in hybrids without multivalents and 0.149 in those with multivalents. Most of the hybrids (88.0%, 117 hybrids) had a univalent frequency lower than 0.30. High frequencies of even valency of multivalents and low frequencies of univalent show that most of the irregularities observed at MI in hybrids among strains of _T. dicoccoides_ could be explained by the structural heterozygosity due to reciprocal translocations. The higher univalent frequencies in hybrids with multivalents than in hybrids without multivalent are, most probably, caused by the breakdown of multivalents into smaller chromosome configurations.

The frequency of multivalents observed at MI can be taken as an indication of the length of the chromosome segments involved in the translocation of the hybrid combination. The higher the frequency of, for exapmle, quadrivalents, the longer segments would be involved. The frequencies of quadrivalents in hybrids inferred to be heterozygous for one translocation, _i.e._, that formed only one quadrivalent or one trivalent per cell, are shown in Fig. 1. In intraspecific hybrids of _T. dicoccoides_, 59 produced one quadrivalent per cell. Of these, 39 hybrids (66.1%) formed a quadrivalent at frequencies ranging from 0.02 to 0.30, 13 (22.0%) from 0.71 to 1.00 and the quadrivalent frequencies of the remaining 7 hybrids (11.9%) were of the range 0.31 -

Table 2. Frequency of mean univalent per cell in F_1 hybrids between strains of *T. dicoccoides*

Mean univalent per cell	No. of hybrids	
	without multivalent	with multivalents
0.00	14	28
0.01 - 0.10	5	26
0.11 - 0.20	11	19
0.21 - 0.30	1	13
0.31 - 0.40	1	4
0.41 - 0.50	-	3
0.51 - 0.60	-	2
0.61 - 0.70	-	3
0.71 - 0.80	1	1
0.81 - 0.90	-	1
Total	33	100
Average	0.102(0.00-0.76)*	0.149(0.00-0.90)

* Range of means.

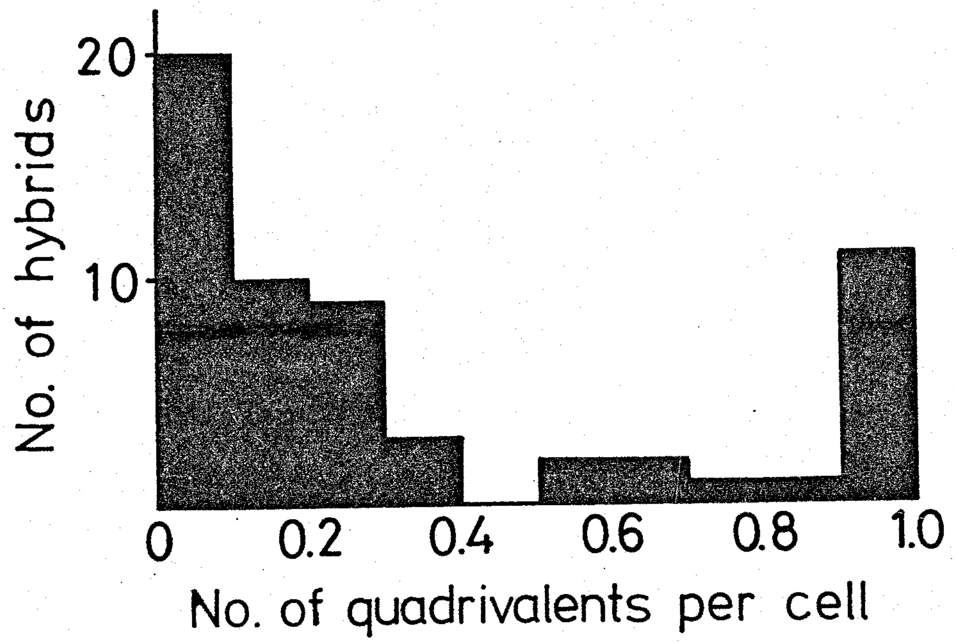

Fig. 1. Frequency distribution of quadrivalents in intraspecific hybrids of *T. dicoccoides*. (for details, see text)

0.70. Further, the frequency distribution of quadrivalent shows a clear gap in the class of 0.41 - 0.50. Therefore, translocations found among dicoccoides strains were classified into two groups by the frequency with which multivalents occur. Quadrivalent formations at a low frequency (less than half) were inferred to be caused by minor translocations but those at a high frequency (more than half) were attributed to major translocations. This was in contrast with the results obtained in *Ae. ovata* by Furuta (1981a, Fig. 3) who found that the frequency of quadrivalents varied continuously.

In several hybrids, chromosome arrangements in quadrivalents were observed and the results are shown in Table 3. These hybrid combinations were chosen randomly in these which produced only quadrivalents or trivalents (or rarely produced quinquevalents or sexivalents, in addition) to avoid the possibility that the quadrivalents observed were the result of the breakdown of higher chromosome associations. So far as the present data are concerned, most of the quadrivalents were chain shaped when their frequency was very low (less than 0.20). When the frequency of quadrivalents was high, no clear tendency was recognized between the frequency of quadrivalents and that of ring quadrivalents. In two hybrids, 195 x 8808 and 108-3 x 1957, the frequencies of ring quadrivalents were low, 25.0% and 27.0%, respectively. But in two other hybrids, 1978B x 1957 and 1978B x 8915A, the values were high, 85.7% and 87.9%, respectively.

Table 3. Type of quadrivalents in F_1 hybrids between strains of *T. dicoccoides*

Cross combination	No. of cells observed	Mean frequency of quadrivalents	Per cent of ring quadrivalents	Per cent of zigzag arrangements
1957 x 1952	33	0.06	0.0	100
108-3 x 1978B	54*	0.09	20.0	-
198 x 108-2	23	0.17	25.0	75.0
108-3 x 8808	66*	0.20	15.4	76.9
8536 x 8915B	50	0.38	73.7	-
1978B x 1957	33	0.64	85.7	33.3
109 x 8808	33	0.79	38.5	65.4
1978B x 8915A	33	1.00	87.9	15.2
195 x 1978B	33	1.06	71.4	-
195 x 8808	33	1.09	25.0	75.0
108-3 x 1957	33	1.12	27.0	-
1957 x 1945	33	1.91	66.7	54.0
1957 x 195	55*	2.05	60.2	60.2

* Two plants were observed.

The frequency of zigzag or alternate arrangement were examined in nine hybrids (Table 3). Of these, seven showed rather high values, 54.0% - 100%. But the frequency in the remaining two hybrids was low; 33.3% in 1978B x 1957 and 15.2% in 1978B x 8915A.

b. Reciprocal translocations

Identification of translocation types

In *T. dicoccoides*, chromosome pairings of 131 hybrid combinations were observed at MI. Of these, 33 formed no multivalent indicating the structural homozygosity of the chromosomes. The other hybrids formed multivalents and were inferred to be heterozygous for one or more translocations. As mentioned in the previous parapraph, the translocations found in *T. dicoccoides* were classified into two groups, major ones and minor ones. In the present study, chromosome types differing with reciprocal translocations (translocation types) were identified by using major translocations except for one described later. That is, the two strains were grouped into the same translocation type when multivalents were not observed or observed at a low frequency in their hybrid.

Six translocation types were recognized in *T. dicoccoides* and they were named from E_1 to E_6. Of these, five (E_1 - E_5) were already reported by Kawahara and Tanaka (1978, 1981). The identification of the translocation type for each strain is described in the Appendix I. The results are shown in Fig. 2 and Table 4. They are briefly summarized as follows:

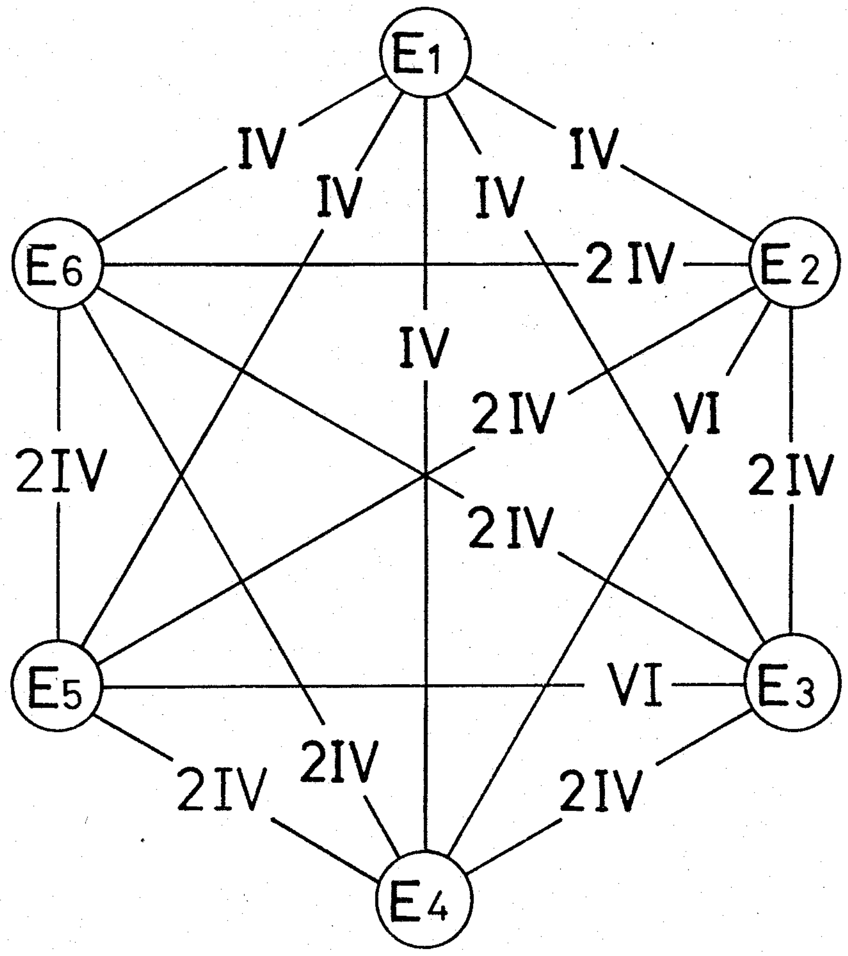

Fig. 2. Expected multivalent formations among six translocation types of *T. dicoccoides*.

Table 4. Translocation types found in strains of *T. dicoccoides*

Type	Stock No.
E1	108-1, 108-2, 108-3, 108-4, 108-5, 110, 198, 1921, 1947, 1948, 1951, 1953, 1955, 1959A, 1959B, 1972B, 1974, 1976B, 1978B, 1991, 8536, 8539, 8541, 8736A, 8736B, 8737, 8804, 8808, 8816A, 8816B, 8817, 8821A, 8821C, 8935, 8937B, 8941, 8942, 8943
E2	109
E3	195
E4	8915A, 8915B
E5	1945
E6	1952, 1957
unidentified	1949

Type E_1: Kawahara and Tanaka (1978) chose arbitrary a Syrian strain 108-3 as a tester and named its translocation type EA. Its naming was later changed from EA to E_1 (Kawahara and Tanaka 1981). This strain was also used as a tester in this study. Of 46 strains observed, 38 (82.6%) belonged to this type.

Type E_2: The EB type of Kawahara and Tanaka (1978) is now called the type E_2. The chromosome structure of E_2 differed from that of E_1 by one translocation. An Israeli strain, 109 belonged to this type.

Type E_3: This corresponds to the EC type of Kawahara and Tanaka (1978). A strain, 195 from Israel belonged to this type. A quadrivalent was formed in hybrids with type E_1 and two quadrivalents were observed in hybrids with E_2.

Type E_4: Two strains, 8915A and 8915B, produced a quadrivalent in hybrids with E_1, a sexivalent in those with E_2 and two quadrivalents in those with E_3. As the hybrid between these two strains showed normal meiosis with 14 bivalents, they were both called the type E_4.

Type E_5: A Turkish strain, 1945, belonged to this type. one quadrivalent was formed in hybrids E_5 x E_1, two quadrivalents in E_2 x E_5 and E_5 x E_4 and a sexivalent in E_3 x E_5.

Type E_6: Hybrids E_1 x E_6 produced one quadrivalent per cell at MI. Two quadrivalents were observed in the hybrids between E_6 and E_2, E_3, E_4 or E_5. Two strains from Turkey, 1952 and 1957 belonged to this type.

Unidentified: Translocation type of the strain 1949 remains unidentified because of the lack of data on chromosome pairings in hybrids with different translocation types. This strain belongs to neither E_1 nor E_2 (Appendix I).

Subtypes of E_1 differing with a minor translocation

As mentioned above, these six translocation types of *T. dicoccoides* were identified by using major translocations. Therefore, the present grouping does not necessarily mean that there are no minor translocations nor other types of chromosome differentiations (inversions *etc*.) among strains belonging to the same translocation type. In fact, multivalents were sometimes observed at a low frequency in hybrids between strains of the type E_1. Since E_1 was thus considered to be heterogeneous for minor translocations, an attempt was made to identify subtypes differing with minor translocations. Details of the identification are described in the Appendix I, and the results are shown in Table 5. One minor translocation was recognized between the two subtypes, E_{1a} and E_{1b}. In average, 0.16 quadrivalent per cell was observed in hybrids between E_{1a} and E_{1b}. Twelve strains from Turkey, Iraq and Iran were revealed to belong to type E_{1a}. Two strains from Syria belonged to type E_{1b}. Twenty-three strains of the type E_1 remain unidentified with regard to the minor translocation between E_{1a} and E_{1b}. There is the possibility of discovering more than the above two subtypes if more strains of E_1 are examined carefully.

The fundamental chromosome structure

In general, variations in chromosome structures in

Table 5. Subgrouping of strains of type E_1 by a minor reciprocal translocation

Type	Stock No.
E_{1a}	108-5, 1959B, 1976B, 1978B, 8536, 8541, 8736A, 8736B, 8817, 8821C, 8935, 8943
E_{1b}	108-2, 108-3
unidentified	108-1, 108-4, 110, 198, 1921, 1947, 1948, 1951, 1953, 1955, 1959A, 1972B, 1974, 1991, 8539, 8737, 8804, 8808, 8816A, 8816B, 8821A, 8837B, 8941, 8942

polyploid species are either due to the variations already present in their ancestral species or due to the sporadic occurrence of structural differentations after the establishment of the polyploid species. In *Trillium*, chromosomal differentiation found in some tetraploid or hexaploid species were attributed to those found in their ancestral species (Haga 1956; Watanabe and Kayano 1971). However, this would not be the case for *T. dicoccoides*. One of the two genomes, A, of *T. dicoccoides* is homologous to that carried by the diploid wheats while the other genome, B, is found only in the hexaploid wheats but not in diploid species of *Triticum* or its closely related genus *Aegilops* (Sect. II). Therefore, it is difficult to assume that structural differences found in *T. dicoccoides* are derived directly from its ancestral species. Instead, all the six translocation types would have originated from the fundamental chromosome structure. In *T. dicoccoides*, types E_2, E_3, E_4, E_5 and E_6 differ from E_1 by one translocation but differ from each other by two translocations. When E_1 was regarded as the fundamental chromosome structure, the present structural variations could be explained by the sporadic occurrence of five major translocations. However, when the other types were considered to be the fundamental type, more translocations are needed to explain the present variations; for example, nine translocations in the case of E_2. Consequently, E_1 was considered to have the fundamental chromosome structore of *T. dicoccoides* as was assumed by Kawahara and Tanaka (1981).

A high proportion of E_1 type strains among the strains of T. dicoccoides and their wide geographical distribution (see below) would also support this assumption. In the type E1, two subtypes, E1a and E1b, were recognized by the presence of a minor translocation. At present, it is impossible to determine the fundamental structure within the type E_1 by the number of minor translocations. However, the number of strains belonging to either E_{1a} or E_{1b} and their geopraphical distributions strongly suggest that the type E_{1a} is more fundamental than E_{1b}. The type E_{1b} would have differentiated from the fundamental E_{1a} by one minor translocation and E_2, E_3, E_4, E5 or E6 by one major translocation. These types might be so called "derived types"

Estimation of chromosomes involved in translocations

Chromosomes involved in each translocation were estimated from the occurrence of multivalents among six translocation types. At first, chromosomes involved in the translocation between E1 and E2 (E1 - E2) were arbitrarily numbered as 1 and 2. As two quadrivalents were found between E_2 and E_3, translocations between E1 and E_2 and between E1 and E3 do not located on the same chromosomes. Therefore, chromosomes involved in the translocation E1 - E3 were named 3 and 4. E_4 produced a sexivalent in hybrids with E_2 and two quadrivalents in those with E3. Thus, the chromosomes involved in the translocation E1 - E_4 would be either 1 and 5 or 2 and 5. Here, it was arbitrarily fixed as 1 and 5. Since one sexivalent per cell was formed in a hybrid E_3 x E_5, the translocation carried by E5 would involve a pair of chromosomes in common with that of E_3. So, the translocation E_1 - E5 might be expressed as 3 and 6. Since two quadrivalents were found in hybrids between E6 and E2, E_3, E_4 or E5, the chromosomes involved in the translocation E_1 - E6 differ from those involved in E_1 - E2, E_1 - E3, E_1 - - E_4 and E_1 - E5 and were named 7 and 8. Chromosomes involved in the minor translocation E_{1a} - E1b could not be identified because there was often no difference in the occurrence of multivalents between hybrids of these two types when crossed to types other than E_1. The chromosomes involved in five major translocations in <u>T. dicoccoides</u> are as follows;

Type	Chromosomes involved
E1 (E_{1a})	none (the fundamental chromosome structure)
E2	1 - 2
E_3	3 - 4
E_4	1 - 5
E5	3 - 6
E6	7 - 8

The genomes to which these chromosomes belong will be discussed in Section VI.

<u>Geographical distribution of translocation types</u>

Geographical distribution of each translocation type is summarized in Table 6 and shown in Fig. 3. As shown in Table 6, types other than E1 occur sporadically in a single locality in Israel or Turkey. E_2(109) and E3(195) were

Table 6. Geographical distribution of translocation types in *T. dicoccoides*

Country	Region	No. of strains observed	Translocation type						
			E_1	E_2	E_3	E_4	E_5	E_6	uniden-tified
Iran	Kermanshah	3	3	-	-	-	-	-	-
Iraq	Sulaymaniyah	3	3	-	-	-	-	-	-
	Rowanduz	3	3	-	-	-	-	-	-
	Jabal Sinjar	5	5	-	-	-	-	-	-
	Amadiyah	2	2	-	-	-	-	-	-
Turkey	Silvan	2	-	-	-	2	-	-	-
	Ergani	2	2	-	-	-	-	-	-
	Urfa	1	1	-	-	-	-	-	-
	Maras-Gaziantep	16	12	-	-	-	1	2	1
Syria	Sueida	2	2	-	-	-	-	-	-
Israel	Palestine	4	2	1	1	-	-	-	-
unknown		3	3	-	-	-	-	-	-
Total		46	38	1	1	2	1	2	1

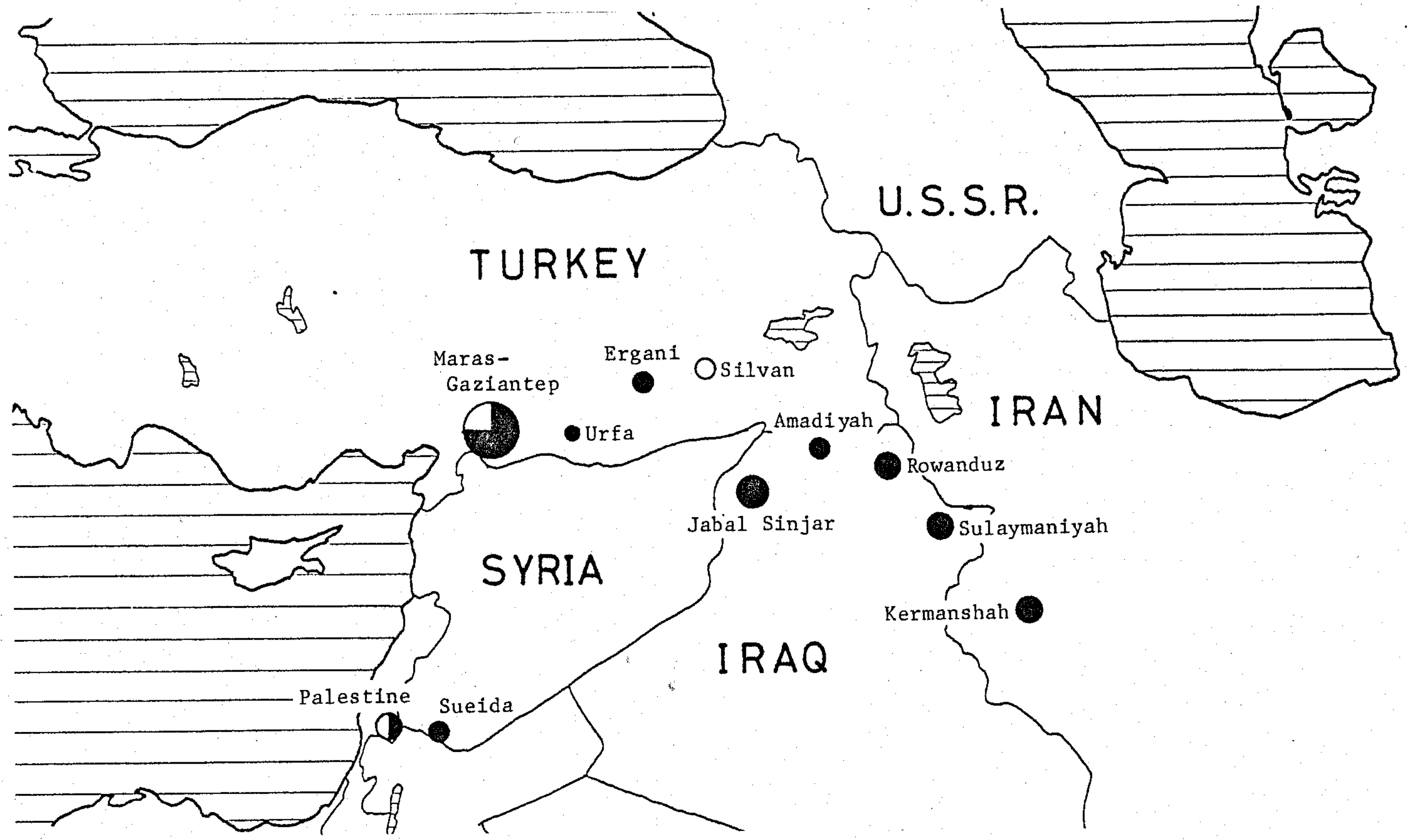

Fig. 3. Geographical distribution of T. dicoccoides having translocations between the fundamental type.

● : the fundamental type, ○ : strains with one translocation between the fundamental type.

found in Israel. Strains of E_4, E_5 and E_6 were collected in Turkey; E_4 (8915A and 8915B) were collected at a site near Silvan, E_5 (1945) and E_6 (1952 and 1957) at a site between Maras and Gaziantep. While, the geopraphical distribution of E_1 is wide. It is found in Syria, Israel, Turkey, Iraq and Iran (Table 6). In the present materials, types other than E_1 were not found in samples from Iraq and Iran. Of the two subtypes of E_1, E_{1b} was found in a single locality, Suedia in Syria, but E_{1a} in six localities. Strains 1959B, 1976B and 1978B were collected in a site between Maras and Gaziantep, Turkey. In Iraq, 8536 and 8541 were sampled in Sulaymaniyah, 8736A and 8736B in Rowanduz, 8817 in Jabal Sinjar and 8821C in Amadiyah. 8935 was collected in Ergani, Turkey and 8943 in Kermanshah, Iran.

In order to obtain information on the amount of differentiation within natural populations, as many strains as possible were examined from the samples collected in a site between Maras and Gaziantep. Of 16 strains examined, 12 were of the type E_1, one was E_5 and two were E_6. The translocation type of the remaining one could not be identified but it was not E_1. That is, this population contains at least three translocation types and 75 per cent of the strains had the fundamental chromosome structure whereas 25 per cent were of the derived types.

The data obtained in the present study show wide geographical distribution of the fundamental chromosome structure and the sporadic occurrence of the derived types.

This strongly suggests that these derived types were established independently in populations having the fundamental chromosome structure as was mentioned above. In Iraq and Iran, all the strains observed were of the type E_1 and three translocation types were found in Israel. While, at least four translocation types were found in Turkey (Table 6). Consequently, in regard to translocations, Turkey was considered to be the center of diversity.

c. Inversions

In hybrids among strains of _T._ _dicoccoides_, bridges and fragnemts were sometimes observed at AI of the PMCs. Eight hybrid combinations randomly chosen were observed in detail in regard to bridges and fragments at AI. As shown in Table 7, all these hybrids formed, at least, a bridge and a fragment in several cells. A cell with two bridges and two fragments were observed in two hybrids, 108-3 x 8808 and 1957 x 1952. These data show that all the hybrids listed in Table 7 are heterozygous for, at least, one or two paracentric inversions. The number of hybrids observed was rather small as compared to that of the hybrids in which chromosome pairings were observed at MI. However, the present results may suggest that the structural differences in the chromosomes caused by inversions are common in _T._ _dicoccoides_.

d. Seed fertilities

Seed fertilities were observed in 87 F_1 hybrids of _T._ _dicoccoides_ (Table IId). They ranged from 0.0 to 90.3

Table 7. Occurrence of bridges and fragments at AI in hybrids between strains of _T. dicoccoides_

Cross combination	No. of cells observed	No. of cells with			
		1 br.	1 br. + 1 frag.	2 br.	2 br. + 2 frag.
108-3 x 1957	157	5	1	1	-
108-3 x 1978B	137	-	3	-	-
108-3 x 8808	127	-	3	-	1
109 x 8808	204	1	1	1	-
195 x 1978B	242	8	5	1	-
195 x 8808	66	2	1	-	-
1957 x 195	139*	4	4	-	-
1957 x 1952	94	1	4	-	1

* Two plants were observed.

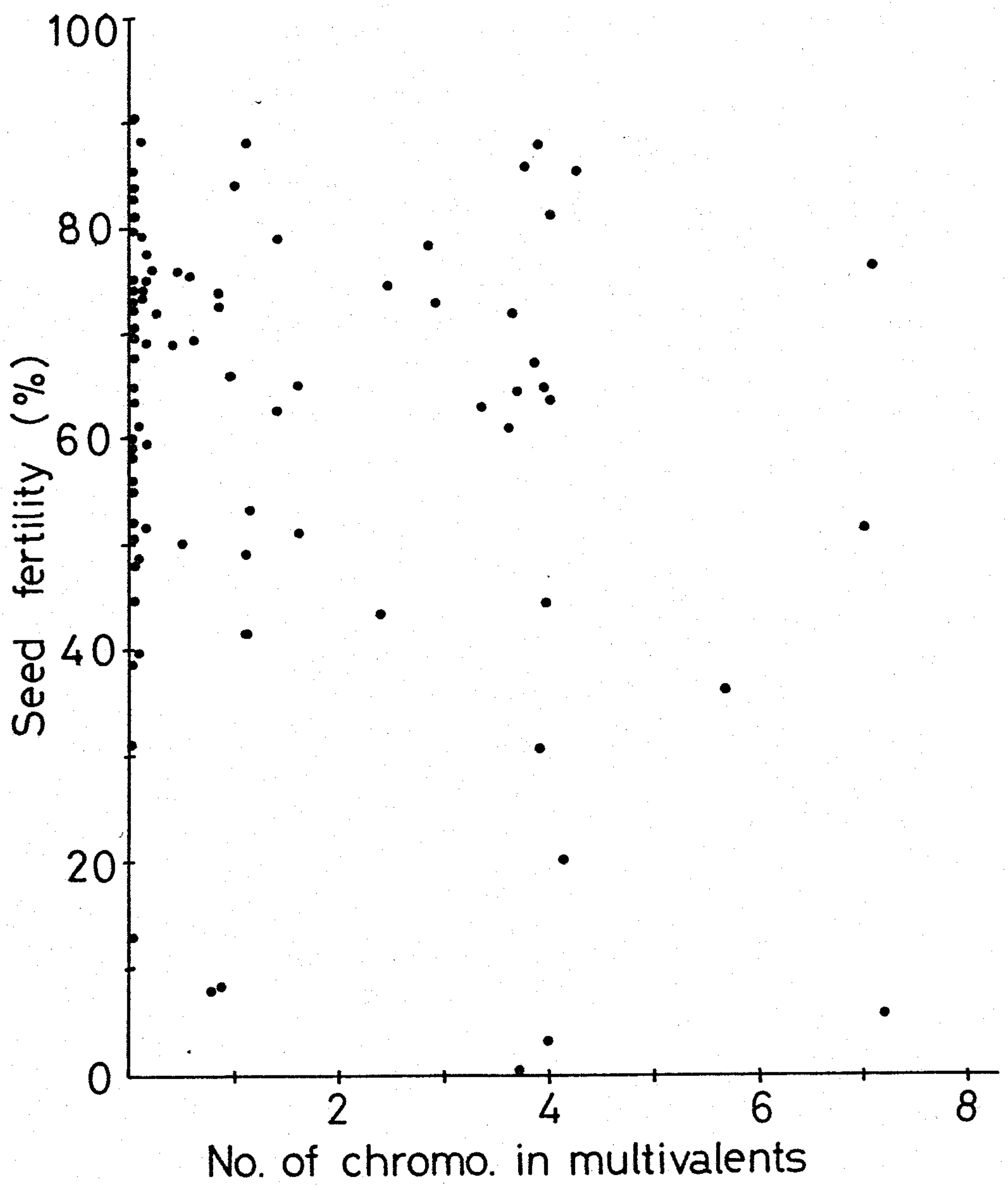

Fig. 4. Relationship between the seed fertility and the number of chromosomes involved in multivalents in intraspecific hybrids of _T. dicoccoides_.

per cent with an average of 60.7 per cent. To find out the effect of multivalent formations at meiosis on seed fertility, the latter was plotted against the number of chromosomes included in multivalents of the hybrid (Fig. 4). It was suggested that the multivalent formation *per se* does not greatly reduce the fertility in these hybrids. In a hybrid 1945 x 1978B, 0.97 quadrivalent was formed in the PMCs and the seed fertility was 87.9 per cent. In 1949 x 109, 0.18 trivalent and 1.64 quadrivalent were produced and the seed fertility was 76.9 per cent. This would be explained by the high proportion of zigzag or alternate arrangements as was observed in several hybrids.

Similarly in the diploid wheats, it is known that translocations do not cause great reduction in pollen fertility (Yamashita 1952; and see also Burnham 1956). However, many hybrids showed reduction in seed fertility even when little or no multivalents were recognized in the PMCs. There may be some other genetical factors that reduce the fertility in these hybrids. One of them might be structural hybridity of chromosomes due to inversions.

3. General discussion

As mentioned in the Section II, *T. dicoccoides* shows a disjunct pattern of distribution in the Palestine area and in the Zagros-Taurus area. Tanaka and Ishii (1973) and Tanaka *et al*. (1978, 1979a, b) suggested that this species had originated in Mesopotamia (Zagros-Taurus area) and then the distribution area was extended to Palestine. Similarly, evidences obtained from studies on host-parasite interaction (Saito and Ishida 1979) and on isozymes (Nakai 1978, 1979) suggested the dissemination of *T. dicoccoides* from the Zagros-Taurus Mountain area to the Palestine area.

On the contrary, Feldman (1979) assumed that *T. dicoccoides* had originated in the Palestine area and then distributed to the Zagros-Taurus area. He offered several lines of evidence supporting this theory. One of them was that *T. dicoccoides* occurs abundantly in the upper Jordan Valley and its adjacent regions but only sporadically in the Zagros-Taurus area. Since this species occupies the primary habitat in Palestine (Harlan and Zohary 1966; Zohary 1969), this area was regarded by Feldman (1979) as the birth-place of *T. dicoccoides*. However, Zohary and Brick (1961) has already stated concerning the massive stands of *T. dicoccoides* in the upper Jordan Valley that it was not until the nation of Israel was established and grazing was controlled that the abundance of these stands was recognized. Other kinds of evidence which may show that the abundance of *T. dicoccoides* in Palestine is the result of adaptation of this species is available. Harlan and Zohary (*loc. cit.*) described the Palestine race of the wild tetraploid wheats as large and robust with large seeds, heavy awns, wide leaves and thick stems. These morphological characteristics suggest that the Palestine race, *i. e.*, *T. dicoccoides* in Palestine, has weediness to some extent. While, they regarded the rather small Turkish-Iraqi race not weedy. Their Turkish-Iraqi race would involve both T. dicoccoides and T. araraticum since these two species are morphologically very similar (Sect. II). Recently, Sakamoto (1982) showed that the wild tetraploid wheats in the Zagros Mountain area are far less weedy than their putative ancestors, T. boeoticum and Ae. speltoides. From these reports, it may be assumed that T. dicoccoides had acquired some degree of weediness after the dessimination into Palestine. Consequently, the present abundance of T. dicoccoides in the Palestine area would not indicate that it had originated in this area.

The present results indicate that the variation in chromosome structures is the highest in Southern Turkey followed by Israel, while T. dicoccoides in Iraq and Iran showed no variation. A similar pattern of variation was also obtained by Saito and Ishida(1979) in the study of susceptibility to leaf rust. All the dicoccoides strains from Israel, Iraq and Iran were susceptible, but those from Turkey showed variations. These data may suggest that the distribution of T. dicoccoides in the Zagros-Taurus area was extended from Southern Turkey to Northern Iraq and Western Iran. Possibly, T. dicoccoides would have originated in the western part of the Zagros-Taurus area, Southern Turkey and its adjacent regions in Northern Iraq. Its distribution would have been first extended southward to Jordan, Syria and Israel and then to the southern part of the Zagros Mountains in Iraq and Iran.

V. DIFFERENTIATION OF CHROMOSOME STRUCTURES IN *TRITICUM ARARATICUM* JAKUBZ.

In *T. araraticum*, reciprocal translocations have been found between several strains but no systematic analysis have been made (Sect. II). Recently, Tanaka and Ichikawa (1972) reported that an *araraticum* strain from Transcaucasus differs from another strain by one reciprocal translocation. Further, Tanaka and Ishii (1975) found another strain from Transcaucasus that differs from the two strains of Tanaka and Ichikawa (1972) by one or two translocations. Based on these findings, Kawahara and Tanaka (1977) and Tanaka *et al*. (1979a) analyzed several strains from Turkey, Iraq and Iran and reported four new translocation types. In the presnet study, the translocation types in *T. araraticum* were analyzed and their geographical distribution are reported. Structural differentiations other than translocations found in this study are also described.

1. Materials

One hundred and thirty one strains of *T. araraticum* as listed in Table 8 were used in the present study. Of these, 77 strains were collected in 1970 by the members of BEM in Turkey, Iraq and Iran. Forty-three were collected in Turkey by KUET. Eight are from the collection of the Kyoto University Botanical Expedition to the Caucasus in 1966 (BEC) and two were obtained from the All Union Institute

Table 8. List of *T. araraticum* used

Stock No. (KU-)*	Source and locality**
196-1, 196-2	Collection of All Union Institute of Plant Industry, Leningrad, U.S.S.R.(1964), Armenia(31628)
1907A, 1907B, 1908A, 1908B, 1909A, 1909B, 1909C, 1911	BEC, 8 km W of Garni(Erevan-Garni), U.S.S.R.
1914	N. Jaaska(1975), 5-10 km SE of Erevan, Armenia, U.S.S.R.
1923, 1924, 1925, 1926A, 1927, 1928, 1929, 1931, 1932, 1933, 1934, 1935, 1936, 1937, 1938, 1939	KUET, 12 km E of Silvan(Diyarbakir-Malabadi), Turkey
1943, 1946, 1950, 1958, 1960, 1962, 1963, 1964, 1965, 1966, 1967, 1969, 1972A, 1978A, 1979A, 1979B, 1980A, 1980B, 1981A, 1981B, 1982, 1983, 1985, 1986, 1987, 1988, 1990	KUET, 45 km SE of Maras(Maras-Gaziantep), Turkey
8456, 8460, 8469, 8478, 8491, 8497, 8500, 8514A, 8521	BEM, 13.2 km S from Sulaymaniyah to Qara Dagh, Iraq (alt. 950 m)

* Stock No. of the Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University.

** The following abbreviations were used.

BEC: The Kyoto University Botanical Expedition to the Caucasus, 1966;

KUET: The Kyoto University Scientific Exploration to the Eastern Turkey, 1976;

BEM: The Kyoto University Botanical Expedition to the Northern Highlands of Mesopotamia, 1970.

Table 8. List of _T. araraticum_ used (continued)

Stock No. (KU-)*	Source and locality**
8528A, 8529	BEM, 22.1 km S from Sulaymaniyah to Qara Dagh, NE slope of Shakh i Baranan, Iraq (alt. 1090 m)
8543, 8544, 8551	BEM, 19.3 km S from Sulaymaniyah to Qara Dagh, NE slope of Shakh i Baranan, Iraq
8561, 8567, 8572	BEM, 14.0 km S from Sulaymaniyah to Qara Dagh, NE slope of Shakh i Baranan, Iraq
8593	BEM, 35.3 km NNE from Sulaymaniyah to Chuarta, Iraq (alt. 1140 m)
8597, 8601, 8616	BEM, 52.4 km NW from Sulaymaniyah, Iraq
8662, 8668, 8673, 8674	BEM, 58.3 km NW from Sulaymaniyah to Dukan Dam, Iraq (alt. 680 m)
8682	BEM, 53.0 km NW from Sulaymaniyah to Dukan Dam, Iraq (alt. 780 m)
8697, 8700	BEM, 5.5 km ENE from Koi Sanjaq to Ranya, Iraq (alt. 690 m)
8707	BEM, 11.4 km ENE from Koi Sanjaq to Ranya, Iraq (alt. 700 m)
8709, 8711, 8712	BEM, 10.6 km ENE from Koi Sanjaq to Ranya, Iraq (alt. 760 m)
8713, 8714A	BEM, 19.1 km W from Shaqlawa to Arbil, SW slope of Pirman Dagh, Iraq (alt. 880 m)
8715, 8718A, 8719	BEM, 17.9 km W from Shaqlawa to Arbil, NE slope of Pirman Dagh, Iraq (alt. 880 m)

Table 8. List of <u>T. araraticum</u> used (continued)

Stock No. (KU-)*	Source and locality**
8720, 8724	BEM, South of Shaqlawa, Iraq
8725, 8729, 8731, 8732	BEM, 7.1 km NE from Shaqlawa to Rowanduz, Iraq (alt. 680 m)
8733, 8734	BEM, 33.2 km W from Rowanduz to Shaqlawa, Iraq (alt. 580 m)
8735	BEM, SSW of Rowanduz, Iraq (alt. 850 m)
8742, 8761, 8770	BEM, ca. 2 km S from the position of 38.9 km E from Rowanduz to Rayat, Iraq (alt. 770 m)
8779, 8784	BEM, 4.8 km NNE from Shaqlawa to Rowanduz, Iraq
8797, 8799B, 8802	BEM, Shaqlawa, Iraq
8819, 8821B, 8822, 8824A, 8824B, 8827	BEM, 15.3 km ENE from Dohuk to Amadiyah, Iraq (alt. 780 m)
8831, 8866	BEM, 4.4 km NW from Amadiyah, Mazorka Gorge, Iraq (alt. 1120 m)
8880	BEM, 13.4 km W from Amadiyah to Bamarni, Iraq (alt. 940 m)
8884	BEM, 21.9 km W from Amadiyah to Dohuk, Iraq
8890, 8907	BEM, 22.4 km W from Amadiyah to Bamarni, Iraq (alt. 790 m)
8912, 8913	BEM, 26.3 km NE from Mardin to Midyat, Turkey (alt. 960 m)

Table 8. List of *T. araraticum* used (continued)

Stock No. (KU-)*	Source and Locality**
8924, 8926, 8928, 8933	BEM, 17.3 km E from Silvan to Bitlis, Turkey (alt. 660 m)
8940	BEM, 39.9 km N from Elazig to Hozat, Turkey (alt. 1000 m)
8944, 8945	BEM, 12.2 km NW from Karand to Qasri Shirin, Iran (alt. 1640 m)
8947, 8948	BEM, 15.1 km NW from Karand to Qasri Shirin, Iran (alt. 1540 m)

of Plant Industry, Leningrad, U.S.S.R. The remaining one was collected by N. Jaaska in Armenia, U.S.S.R. Further, a strain of *T. timopheevi* (KU-107-1, Zhukovsky, 1931) was used as a tester in crossings with *T. araraticum*.

The identification of the species of samples collected by BEC, BEM and KUET was made by Dr. M. Tanaka by morphological characteristics and was confirmed cytogenetically (Tanaka and Ishii 1973, 1975; Kawahara and Tanaka 1977; Tanaka *et al*. 1979b and the present study).

All these strains were established from a single plant of the original sample and maintained by selfing at the Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University. So, each strain was considered to be a structural homozygote.

In the hybridization, strains used in the earlier reports (Tanaka and Ichikawa 1972; Tanaka and Ishii 1975; Kawahara and Tanaka 1977) were used as testers (for details, see Appendix I).

2. Results and Discussions

a. Cytogenetical analysis at MI

Mean chromosome pairings in F_1 hybrids among strains of the timopheevi wheats are shown in Table IIe (Appendix II). A similar tendency was also recognized in these hybrids as in *T. dicoccoides*, that is, a low frequency of univalents and a high frequency of multivalents, especially those of even valencies. The average univalent frequency in *T.*

araraticum in hybrids without multivalents was 0.067 and that in hybrids with multivalents was 0.134 (Table 9). In hybrids between *T. araraticum* and *T. timopheevi*, the frequency for hybrids without multivalents was 0.044 and that for hybrids with multivalents was 0.079 (Table 10). The mean univalent frequencies were lower than 0.30 in 310 hybrids (94.2%). Thus, most of the irregularities observed at the MI in hybrids between strains of the timopheevi wheats could be explained by structural heterozygosities due to reciprocal translocations. Here also, higher univalent frequencies in hybrids with multivalents than in those without multivalents would be due to the breakdown of multivalents into smaller chromosome configurations.

Detailed data on the occurrence of multivalents in the hybrids between strains of *T. araraticum* or between *T. araraticum* and *T. timopheevi* are listed in Table Ic (Appendix I). The frequency distribution of quadrivalents in hybrids heterozygous for one translocation is shown in Fig. 5. As is observed in Fig. 5, the tendency that the frequency of a quadrivalent rarely takes an intermediate value around 0.5 is more prominent in hybrids between strains of the timopheevi wheats than those of *T. dicoccoides* (Fig. 1). Consequently, translocations found between strains of *T. araraticum* or between *T. araraticum* and *T. timopheevi* were classified into two groups, major translocations and minor ones, as was done in *T. dicoccoides*.

Chromosome arrangements in quadrivalents were observed in several hybrids and the results are shown in Table 11.

Table 9. Frequency of mean univalent per cell in F_1 hybrids between strains of *T. araraticum*

Mean univalent per cell	No. of hybrids without multivalent	No. of hybrids with multivalents
0.00	19	56
0.01 - 0.10	10	73
0.11 - 0.20	8	38
0.21 - 0.30	3	20
0.31 - 0.40	-	4
0.41 - 0.50	-	4
0.51 - 0.60	-	3
0.61 - 0.70	-	3
0.71 - 0.80	-	-
0.81 - 0.90	-	1
0.91 - 1.00	-	2
2.01 - 2.10	-	1
Total	40	205
Average	0.067(0.00-0.28)*	0.134(0.00-2.08)

* Range of means

Table 10. Frequency of mean univalent per cell in F_1 hybrids between T. araraticum and T. timopheevi

Mean univalent per cell	No. of hybrids	
	without multivalent	with multivalents
0.00	18	18
0.01 - 0.10	17	17
0.11 - 0.20	5	7
0.21 - 0.30	-	1
0.31 - 0.40	-	2
0.41 - 0.50	-	-
0.51 - 0.60	-	1
Total	40	46
Average	0.044(0.00-0.20)*	0.079(0.00-0.55)

* Range of means.

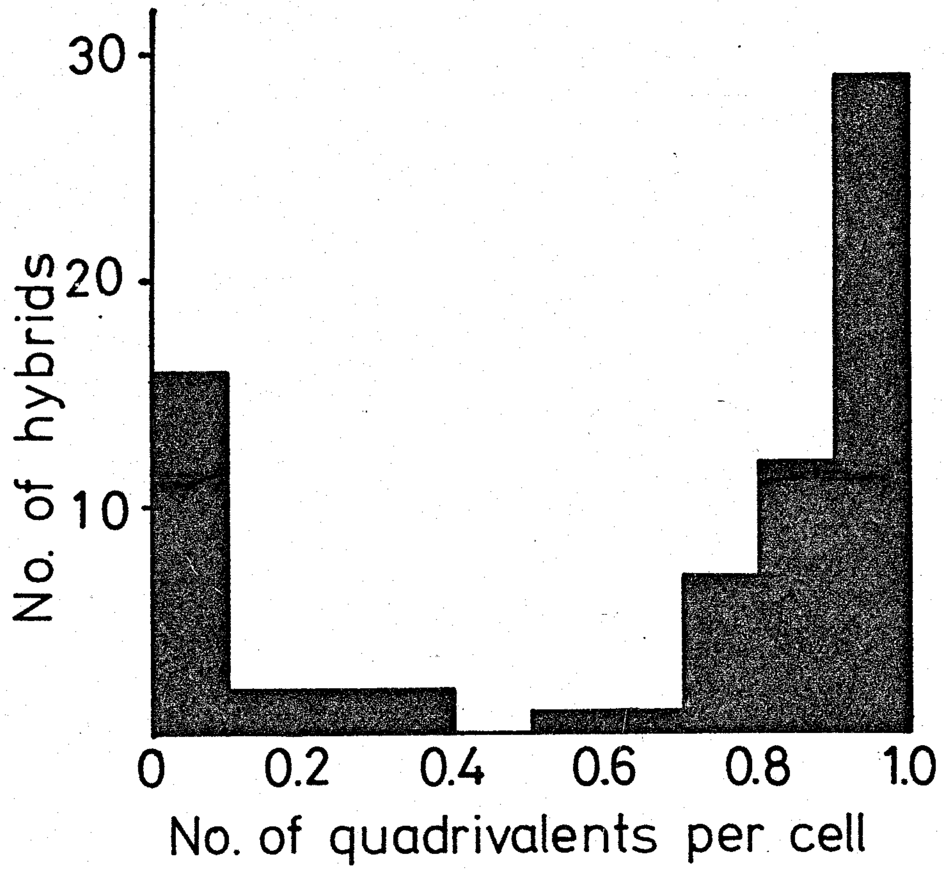

Fig. 5. Frequency distribution of quadrivalents in intraspecific hybrids of <u>T. araraticum</u>. (for details, see text)

Table 11. Type of quadrivalents in F_1 hybrids between strains of the timopheevi wheats

Cross combination	No. of cells observed	Mean frequency of quadrivalents	Per cent of ring quadrivalents	Per cent of zigzag arrangements
8733 x 8593	50	0.24	75.0	-
8733 x 8912	50	0.26	69.2	-
8733 x 8674	23	0.35	50.0	-
8733 x 8467	50	0.36	83.3	-
8784 x 8824A	33	0.88	55.2	51.7
1979B x 107-1	33	0.94	35.5	87.1
1908A x 8732	54	1.56	60.7	48.8
1909C x 8732	33	1.79	66.1	59.3
8567 x 8674	33	1.97	44.1	-
8725 x 1908A	33	2.45	59.3	77.8
8732 x 8725	33	2.45	76.5	-
1911 x 8714A	33	2.79	75.0	72.8
8460 x 8725	66*	3.59	79.7	-
1909C x 8725	33	3.61	66.4	67.2

* Two plants were observed.

These hybrids were chosen at random in those which produce only quadrivalents or trivalents, as in *T. dicoccoides*. The mean frequency of quadrivalents were from 0.24 to 3.61 per cell. In these hybrids, the proportion of ring quadrivalents ranged from 35.5 to 83.3 per cent with the average of 64.0 per cent. There observed no clear correlation between the mean frequency of quadrivalents and that of ring quadrivalents in hybrids between the timopheevi wheats as in *T. dicoccoides*. In seven hybrids where the arrangement of quadrivalents were recorded, frequencies of zigzag arrangement were from 48.8 to 87.1 with the average of 66.3 per cent.

b. Reciprocal translocations

Identification of translocation types

In total, 318 hybrid combinations were examined in *T. araraticum* and *T. timopheevi*. As in *T. dicoccoides*, translocation types were identified by the occurrence of multivalents in hybrids between strains.

Fifteen translocation types were recognized in *T. araraticum* and were named as T1 to T_{15}. Of these, seven were the types reported by Kawahara and Tanaka (1977), Tanaka *et al*. (1979a) and Kawahara and Tanaka (1981), but the designation was changed as follows;

Kawahara and Tanaka (1977) Tanaka *et al*. (1979a) Kawahara and Tanaka (1981)	Present study
A	T_2

Kawahara and Tanaka (1977) Tanaka *et al.* (1979a) Kawahara and Tanaka (1981)	Present study
B	T_1
C	T_3
D	T_6
E	T_4
F	T_8
G	T_{14}

The other eight types, T_5, T_7, T_9, T_{10}, T_{11}, T_{12}, T_{13} and T_{15} were newly identified in the present study.

The method of identifying the translocation type for each strain is described in Appendix I and the results are summarized in Table 13. Expected multivalent formations among 15 translocation types are shown in Table 12. In these tables, the results obtained by earlier works (Tanaka and Ichikawa 1972; Tanaka and Ishii 1975) are also included.

Type T_1: In the course of the present study, a *timopheevi* strain, 107-1, was used as a primary tester and then several other *araraticum* strains of the type T_1 were also used as testers. Those strains which formed no multivalents or multivalents at a low frequency in hybrids with testers of the type T_1 were grouped into this type. Of 139 *araraticum* strains examined, 79 (56.8%) belonged to this type.

Type T_2: The chromosome structure of this type differs from that of T_1 by one translocation. A strain, 196-1, from Transcaucasus belonged to this type.

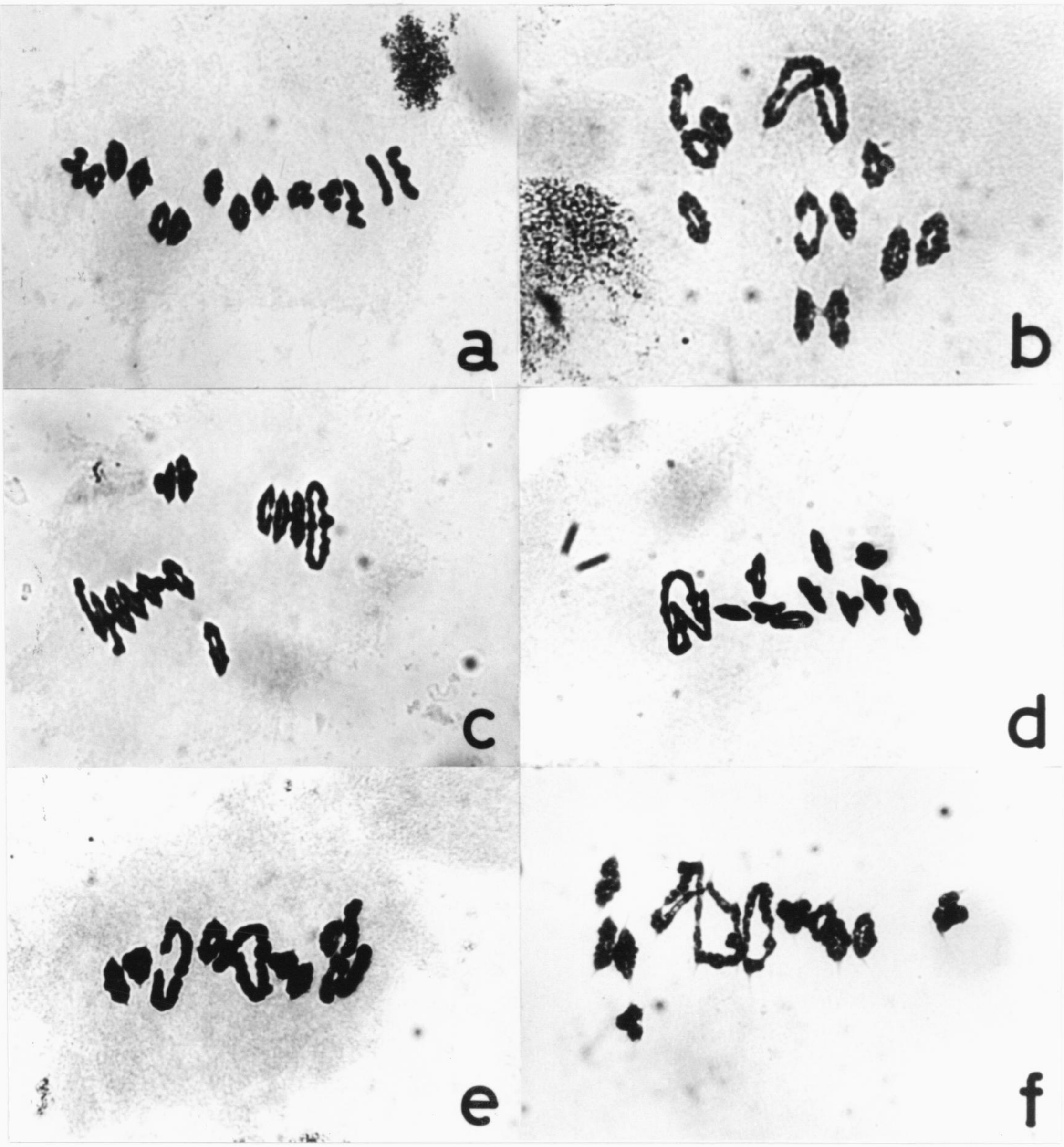

Fig. 6. Chromosome pairings at MI in F_1 hybrids among translocation types of the timopheevi wheats. (x750)

a; 14II in 8731 x 107-1 (T_1 x T_1),
b; 11II + 1VI in 8824A x 8719 (T7 x T_6),
c; 10II + 2IV in 8572 x 196-1 (T_4 x T_2),
d; 10II + 1VIII in 1908A x 8784 (T_3 x T_8),
e: 7II + 2IV + 1VI in 8866 x 8725 (T_{14} x T_{13}),
f; 9II + 1X in 8732 x 8713 (T_4 x T_{15}).

Table 12. Expected multivalent formations among 15 translocation types of *T. araraticum*

	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9	T_{10}	T_{11}	T_{12}	T_{13}	T_{14}	T_{15}
T_1	IV	IV	IV	IV	IV	IV	VI	2 IV	2 IV	2 IV	2 IV	2 IV	2 IV	IV+VI
T_2		VI	2 IV	-	2 IV*	-	IV+VI*	IV+VI	3IV or IV+VI	3 IV	3 IV	3 IV	IV+VI	2VI
T_3			2 IV	VI	2 IV	VI	VIII	-	3 IV	IV+VI	-	3 IV	3 IV	2IV+VI
T_4				VI	VI	VI	VI	2 IV	IV+VI	VIII	-	3 IV	IV+VI	X
T_5					2 IV	-	VIII	-	-	IV+VI	-	-	-	-
T_6						VI	VIII	IV+VI	3 IV	IV+VI	2 IV	3 IV	IV+VI	IV+VI
T_7							IV	-	-	-	-	-	3 IV	-
T_8								-	IV+VIII	VI	X	2IV+VI	IV+VIII	XII
T_9									2IV+VI	-	-	4 IV	2IV+VI	-
T_{10}										2IV+VI	-	2IV+VI	2IV+VI	-
T_{11}											-	4 IV	2IV+VI	VI+VIII
T_{12}												-	2 VI	VIII
T_{13}													2IV+VI	2IV+ VIII
T_{14}														VIII

* Data obtained by Tanaka and Ishii(1973), cited by Kawahara and Tanaka(1977).

Table 13. Translocation types found in strains of *T. araraticum**

Type	Stock No.
T_1	196-2, 1901, 1902, 1903, 1904, 1905, 1906, 1914, 1923, 1924, 1925, 1926A, 1927, 1928, 1929, 1931, 1932, 1933, 1934, 1935, 1936, 1937, 1939, 1960, 1963, 1964, 1965, 1969, 1978A, 8456, 8469, 8478, 8491, 8528A, 8529, 8543, 8551, 8561, 8593, 8597, 8616, 8673, 8697, 8700, 8707, 8709, 8711, 8712, 8718A, 8724, 8731, 8735, 8742, 8761, 8770, 8779, 8797, 8799B, 8802, 8819, 8821B, 8822, 8827 8831, 8873, 8880, 8882, 8884, 8890, 8907, 8912, 8913, 8924, 8926, 8928, 8933, 8940, 8947, 8948
T_2	196-1
T_3	1907A, 1908A, 1909A, 1909B
T_4	8567, 8572, 8732
T_5	8674
T_6	8714A, 8719
T_7	8824A, 8824B
T_8	8784
T_9	1909C
T_{10}	1911
T_{11}	8460
T_{12}	8715
T_{13}	8725
T_{14}	8866
T_{15}	8713
unidentified	1907B, 1908B, 1938, 1943, 1946, 1950, 1958, 1962, 1966, 1967, 1972A, 1979A, 1979B, 1980A, 1980B, 1981A, 1981B, 1982, 1983, 1985, 1986, 1987, 1988, 1990, 8497, 8500, 8514A, 8521, 8544, 8601, 8662, 8668, 8720, 8729, 8733, 8734, 8944, 8945

* Chromosome types of 1901, 1902, 1903, 1904, 1905 and 1906 were identified based on the data by Tanaka and Ishii(1975) and those of 8873 and 8882 based on the unpublished data by Tanaka and Ishii(1973) which were cited by Kawahara and Tanaka(1977).

Type T_3: A quadrivalent was formed in hybrids with type T_1 and a sexivalent was formed in hybrids with T_2. Four strains, 1907A, 1908A, 1909A and 1909B, from Transcaucasus belonged to this type.

Type T_4: A quadrivalent was formed in hybrids with T_1 and two quadrivalents were recognized in hybrids with T2 (Fig. 6c) or T_3. Three strains, 8567, 8572 and 8732, from Iraq belonged to this type.

Type T_5: The chromosome structure of this type differs from that of T_1 by one translocation. A sexivalent was observed in hybrids with T_3 or T_4. Strain 8674 from Iraq belonged to this type.

Type T_6: A quadrivalent was formed in hybrids with T_1, two quadrivalents per cell were recognized in hybrids with T_2, T_3 or T_5 and a sexivalent was observed in hybrids with T_4. Two strains, 8714A and 8719, from Iraq belonged to this type.

Type T_7: A quadrivalent was formed in hybrids T_7 x T_1. A sexivalent was formed in hybrids with T_3, T4 and T6 (Fig. 6b). Two strains, 8824A and 8824B, from Iraq belonged to this type.

Type T_8: A sexivalent was observed in hybrids with T_1 indicating the presence of two translocations involving three pairs of chromosomes. A quadrivalent and a sexivalent were formed in hybrids with T_2, an octavalent in hybrids with T_3 (Fig. 6d), T_5 or T_6, a sexivalent in T_4 x T_8 and a quadrivalent in T_7 x T_8. Strain 8784 from Iraq belonged to this type.

Type T_9: A strain, 1909C, from Transcaucasus belonged to this type. Two quadrivalents were observed in hybrids with T_1 or T_4. A quadrivalent and a sexivalent were formed in hybrids with T_2 or T_6.

Type T_{10}: Strain 1911 from Transcaucasus belonged to this type. Two quadrivalents were formed in T_{10} x T_1. Three quadrivalents or a quadrivalent and a sexivalent were expected to occur in hybrid T_2 x T_{10}. Three quadrivalents were formed in hybrids with T_3 or T_6. A quadrivalent and a sexivalent, a quadrivalent and an octavalent or two quadrivalents and a sexivalent were recognized in hybrids with T_4, T_8 or T_9, respectively.

Type T_{11}: Two quadrivalents were recognized in hybrids with T_1. Three quadrivalents were observed in T_{11} x T_2, and a quadrivalent and a sexivalent in hybrids with T_3, T_5 or T_6. An octavalent was formed in T_4 x T_{11}, a sexivalent in T_{11} x T_8 and two quadrivalents and a sexivalent in T_{10} x T_{11}. Strain 8460 from Iraq belonged to this type.

Type T_{12}: Two quadrivalents were formed in hybrids T_{12} x T_1 and T_{12} x T_6. Three quadrivalents were formed in a hybrid with T_2 and a decavalent was observed in T_{12} x T_8. Strain 8725 from Iraq belonged to this type.

Type T_{13}: Strain 8715 fron Iraq was of this type. Two quadrivalents were formed in hybrids with T_1 and three quadrivalents in those with T_2, T_3, T_4 and T_6. Two quadrivalents and a sexivalent in hybrids with T_8 and T_{13}. Four quadrivalents were recognized in hybrids with T_9 and T_{11}.

Type T_{14}: Two quadrivalents were formed in hybrids with T_1. A quadrivalent and a sexivalent were expected in hybrids between T_2 and T_{14}. In hybrids with the other types, the following multivalents were observed; three quadrivalents with T_3 or T_7, a quadrivalent and a sexivalent with T_4 or T_6, a quadrivalent and an octavalent with T_8, two quadrivalents and a sexivalent with T_9, T_{10}, T_{11} or T_{13} (Fig. 6e) and two sexivalents with T_{12}. Strain 8866 from Iraq belonged to this type.

Type T_{15}: The chromosome structure of strain 8713 differs from that of T_1 by three translocations and was named the type T_{15}. A quadrivalent and a sexivalent was formed in T_{15} x T_1. The following multivalents were recognized in hybrids with the types other than T_1; two sexivalents in T_{15} x T_2, two quadrivalents and a sexivalent in T_3 x T_{15}, a decavalent in T_4 x T_{15} (Fig. 6f), a quadrivalent and a sexivalent in T_{15} x T_6, a duodecavalent in T_{15} x T_8, a sexivalent and an octavalent in T_{11} x T_{15}, an octavalent in T_{15} x T_{12} or T_{14} x T_{15} and two quadrivalents and an octavalent in T_{15} x T_{13}.

Unidentified: In the present study, the translocation types of 39 strains remain unidentified because the data obtained so far are insufficient to determine whether each strain belongs to the types described above or whether they have chromosome structures other than those reported so far. Of 39 unidentified strains, 37 differ from T_1 by one translocation and two differ by two translocations. Occurrences of multivalents in hybrids involving these unidentified strains are described in the Appendix I.

The fundamental chromosome structure

Similar to the case of *T. dicoccoides*, one of the two genomes (A) of *T. araraticum* is homologous to that of the diploid wheats but the other genome (G) is not homologous to that of the supposed ancestral species (Sect. II). Therefore, the structural differences revealed here would have occurred spontaneously after the formation of this tetraploid species, *T. araraticum*. Among 15 translocation types in *T. araraticum*, the number of translocations were fewer in hybrids between T_1 and the other 14 types than those between types other than T_1. Thus the type T_1 was considered to be the fundamental chromosome structure in respect to translocations. Types other than T_1 would have differentiated from this fundamental type by spontaneous reciprocal translocations. Types T_2, T_3, T_4, T_5, T_6 and T_7 differ from T_1 by one translocation, T_8, T_9, T_{10}, T_{11}, T_{12}, T_{13} and T_{14} by two and T_{15} by three translocations. These may be called the derived types. Those types which have two or three translocations between T_1 would have originated either from the hybridization between derived types or through spontaneous reciprocal translocation in strains of the derived types. Examples of the accumulation of translocations were observed in the present materials. As is described in the next paragraph, one of the two translocations carried by T_8 and by T_{11} is the same as that found in T_7. T_{12} and T_{15} share a translocation and T_{14} and T_{15} share another translocation in common. At present, these types were not found to grow sympatrically. However, there is the possibility of discovering two types having a common translocation in a single locality, because some of the derived types are found in two localities (see later).

Estimation of chromosomes involved in translocations

As in the case for *T. dicoccoides*, chromosomes involved in translocations of *T. araraticum* were identified from the occurrence of multivalents among 15 translocation types. Since the type T_1 is the fundamental chromosome structure of *T. araraticum*, this was taken as a standard. Of 14 derived types, translocations involved in six types, T_9, T_{10}, T_{11}, T_{12}, T_{13} and T_{15} were not fully identified because all the hybrid combinations between the derived types were not observed.

The chromosomes involved in the translocations of T_2, T_3, T_4, T_5, T_6, T_7, T_8 and T_{14} were identified as follows;

T_2: 1 - 2 Arbitrarily numbered.

T_3: 1 - 3 A sexivalent was formed in the hybrid with T_2. Therefore, the translocation would be located on chromosomes 1 and 3 or 2 and 3. Here they were arbitrarily taken to be on 1 and 3.

T_4: 4 - 5a Two quadrivalents were recognized in hybrids with T_2 and T_3. Because a translocation involving the same pair of chromosomes was found in the other types (T_8 and T_9, see below), this was named as 4 - 5a.

T_5: 1 - 5 As a sexivalent was formed in hybrids of T_5 with T_3 or T_4, the translocation of T_5 might be located between chromosomes 1 or 3 and 4 or 5. Chromosome 4 is excluded because two quadrivalents were formed in hybrid T_6 x T_5. Since an octavalent was produced in a hybrid with T_8, the translocation would not be on 3 - 5 but on 1 - 5.

T_6: 4 - 6a Two quadrivalents were recognized in hybrids with T_2 or T_3 and a sexivalent was formed in a hybrid with T_4. So the chromosomes would be either 4 and 6 or 5 and 6 and were arbitrarily taken to be on 4 and 6.

T_7: 3 - 4 Since a quadrivalent was observed in hybrids

T_8: 3 - 4 and 4 - 5b between T_7 and T_8, one of the two translocations of T_8 would be the same as that carried by T_7. Another translocation would be 4 - 5b since a sexivalent was formed in a hybrid T_4 x T_8. Because a sexivalent was formed in hybrids T_3 x T_7 and in T_4 x T_7, the translocation in T_7 would be 3 - 4 or 3 - 5 and here it was arbitrarily taken to be on 3 - 4.

T_{14}: 2 - 5 and 6 - 7 Since three quadrivalents were recognized in hybrids between T_{14} and T_3 or T_7, chromosomes 1, 3 and 4 would not be involved in the two translocations of T_{14}. While the occurrence of a sexivalent and a quadrivalent in hybrids of T_{14} with T_2, T_4 and T_6 indicated that chromosomes 1 or 2, 4 or 5 and 4 or 6 are involved in them. Thus, the two translocations of T_{14} would be located on four chromosomes, 2, 5, 6 and 7. They would be either 2 - 5 and 6 - 7, 2 - 6 and 5 - 7 or 2 - 7 and 5 - 6 and were arbitrarily taken to be on 2 - 5 and 6 - 7.

Based on a similar rationale, translocations involved in types T_9, T_{10}, T_{11}, T_{12}, T_{13} and T_{15} were tantatively identified as follows;

T_9: 1 - 3 and 4 - 5b or c / 1 - 8 and 4 - 5b or c
T_{10}: 5 - 8 and 9 - 10 / 5 - 9 and 10 - 11
T_{11}: 3 - 4 and 5 - 11 / 3 - 4 and 5 - 8 / 3 - 4 and 5 - 12
T_{12}: 4 - 6b and 5 - X / 4 - 6b and 5 - X / 4 - 6b and 5 - X
T_{13}: 7 - X and 12 - 13 / 7 - X and 12 - 13/ 7 - X and 13 - 14
T_{15}: 2 - 5, 4 - 6b and / 2 - 5, 4 - 6b and/ 2 - 5, 4 - 6b and
4 or 6 - X / 4 or 6 - X / 4 or 6 - X
(X = 8, 9, or 10) / (X = 9, 10 or 11) / (X = 9, 10 or 11)

As shown above, the translocation carried by T_7 would be the same as one of the two translocations of T_8 and one of those of T_{11}. Types T_{12} and T_{15} would share a translocation (4 - 6b) and types T_{14} and T_{15} another translocation (2 - 5) in common. Consequently, at least 17 different translocations were recognized. When T_9 was assumed to have the two translocations 1 - 3 and 4 - 5b, that is, 1 - 2, 1 - 3, 1 - 5, 2 - 5, 3 - 4, 4 - 5a, 4 - 5b, 4 - 6a, 4 - 6b, 4 or 6 - X, 5 - 8, 5 - 11, 5 - X, 6 - 7, 7 - X, 9 - 10 and 12 - 13 (X = 8, 9 or 10). Sometimes, two or three translocations involved in different translocation types were located on the same pair of chromosomes but on different arms. They were 4 - 5a of T_4, 4 - 5b of T_8 and 4 - 5 b or c of T_9 and 4 - 6a of T_6 and 4 - 6b of T_{12} and T_{15}.

These reults clearly showed the concentration of break-points of translocations on particular chromosomes. Chromosome 5 was involved in seven different translocations, 4 in five or six translocaitons and X (8, 9 or 10) in four translocations. While, chromosomes 11, 12, 13 and two out of 8, 9 and 10 were involved in only one translocation.

Geographical distribution of translocation types

Geographical distribution of each translocation type is summarized in Table 14 and is shown in Fig. 7. As shown in Table 14, T_1 occurs in all the regions where T. araraticum was sampled. While, the derived types except for T_4 and T_6, were restricted to a single locality. The T_2 type strain was collected in Armenia, but the precise locality is not known (Table 8). Types T_3, T_9 and T_{10} were found in a site west of Garni, Armenia, U.S.S.R. The remaining ten types, T_4, T_5, T_6, T_7, T_8, T_{11}, T_{12}, T_{13}, T_{14} and T_{15} were found in Iraq. The type T_5 was found at 58.5 km NW from Sulaymaniyah to Qara Dagh. T_7 was collected at 15.3 km ENE from Dohuk to Amadiyah. T_8 was sampled in a site 4.8 km

NNE from Shaqlawa to Rowanduz and T_{11} at 13.2 km S from Sulaymaniyah to Qara Dagh. T_{12} and T_{15} were collected on the NE and SW slope of Pirman Dagh, respectively. T_{13} was found at 7.1 km NE from Shaqlawa to Rowanduz. The type T_{14} was collected in a site 4.4 km NW from Amadiyah. Both of the two strains of T_6, 8714A and 8719, were collected in Rowanduz region in Iraq but at the different sites. The two collection sites were separated about 1.2 km apart (Table 8). The two strains of T_4, 8567 and 8572, were collected at the same site; 14 km S from Sulaymaniyah to Qara Dagh, NE slope of Shakh i Baranan, Iraq. But the other strain of T_4, 8732, was collected in a different region, 7.1 km NE from Shaqlawa to Rowanduz, Iraq, the same site as the type T_{13}. This suggests the possibility that derived types other than T_4 and T_6 might also be found in two or more localities if more strains of T. araraticum are examined. The wide geographical distribution of the fundamental type and the sporadic occurrence of the derived types would support the earlier assumption that the derived types were differentiated from the fundamental one by spontaneous reciprocal translocations.

In T. araraticum, three populations were examined intensively. One is a population located 8 km W of Garni, Armenia, U.S.S.R. In total, 14 strains have been examined. Tanaka and Ishii (1975) found six strains, 1901, 1902, 1903, 1904, 1905 and 1906, from this site to have the same chromosome structure as timopheevi 107-1, the T_1 type. They also found that strain 1908A differs from 107-1 by one transloca-

Table 14. Geographical distribution of translocation types in <u>T. araraticum</u>

Country	Region	No. of strains observed	Translocation type															
			T_1	T_2	T_3	T_4	T_5	T_6	T_7	T_8	T_9	T_{10}	T_{11}	T_{12}	T_{13}	T_{14}	T_{15}	uniden- tified
U.S.S.R.	Armenia	17	8	1	4	-	-	-	-	-	1	1	-	-	-	-	-	2
Turkey	Hozat	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Silvan	20	19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
	Mardin-Midyat	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Maras-Gaziantep	27	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21
Iraq	Amadiyah	14	11	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-
	Rowanduz	22	11	-	-	1	-	2	-	1	-	-	-	1	1	-	1	4
	Koi Sanjaq	6	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Sulaymaniyah	26	13	-	-	2	1	-	-	-	-	-	1	-	-	-	-	9
Iran	Ravansir	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Total		139	79	1	4	3	1	2	2	1	1	1	1	1	1	1	1	39

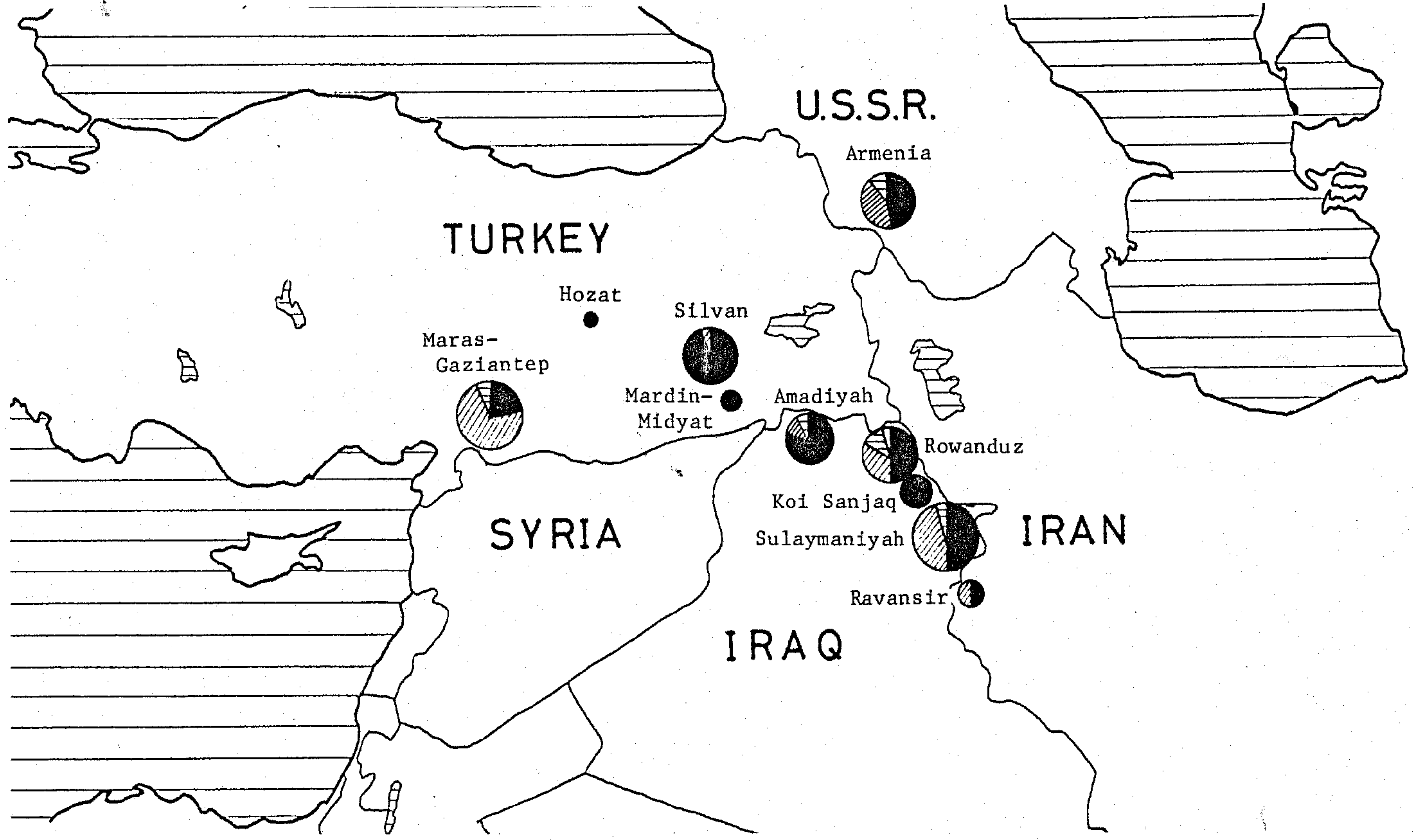

Fig. 7. Geographical distribution of T. *araraticum* having translocations between the fundamental type.

●: the fundamental type, ▨:strains with one translocation between the fundamental type, ⊜ : those with two translocations, ○ : those with three translocations.

tion. Translocation type of 1908A was T_3. In the present study, other seven strains were examined. Of these, three, 1907A, 1909A and 1909B, belonged to the type T3 (Table 11). 1909C belonged to T9 and 1911 was of T_{10}. Translocation types of the remaining two strains, 1907B and 1908B, have not been identified. Thus, samples from this site consist of, at least, four translocation types; six strains (42.9%) of the type T1, four of T3, one each of T9 and T_{10} and two unidentified strains.

In a site 12 km E of Silvan, Turkey, 16 strains were examined. Of these, 15 (93.8%) belonged to the type T_1 and one differed from T_1 by one translocation (unidentified).

Twenty-seven strains were observed from another site in Turkey, 45 km SE of Maras. Only six strains (22.2%) belonged to T_1. 19 strains differed from T_1 by one translocation and the other two, 1967 and 1972A, by two translocations. In hybrids with 107-1 of T. timopheevi, 1967 formed a sexivalent and 1972A produced two quadrivalents (Appendix I). Because chromosome structures of these two strains differ from each other, at least four translocation types are expected in this site.

It is clear from the present data that structural differentiations in chromosomes occur in all the distribution area of T. araraticum. Wagenaar (1966) suggested that chromosome differentiation in the timopheevi wheats is restricted to the northern regions of the distribution area (the Transcaucasus and northern tip of Turkey). Similarly, Ishii (1970) considered that the translocations found in several strains of T. araraticum occurred secondarily in Transcaucasus. But the present data show that chromosome differentiation in T. araraticum is more abundant in the center of its distribution area as was shown by Kawahara and Tanaka (1977). As shown in Table 14, five types were found in Transcaucasus, while seven types were recognized in Rowanduz region, Iraq. But the number of translocation types found in one region may not be a good indicator of the amount of diversity because translocation types of a number of strains (39, 28.1%) remain unidentified. Therefore, the maximum number of translocations carried by each strain, namely the amount of structural deviations from T_1, was compared between the regions. In Rowanduz region, the T_{15} type has three translocations relative to T_1. Strains having two translocations were found in Armenia, Maras-Gaziantep, Amadiyah and Sulaymaniyah (Fig. 7). Samples from Silvan and Ravansir contain strains that differ from T_1 by one translocation. All the samples from Hozat, Mardin-Midyat and Koi Sanjaq belonged to type T_1. These data also show that the Rowanduz region is the center of diversity in regard to translocations in T. araraticum.

The present data further show that the frequency of strains of the fundamental type or of the derived types vary greatly from population to population. As described above, a population in Armenia consists of, at least, four translocation types and 42.9 per cent of the strains were of the type T_1. Quite contrasting results were obtained from two populations in Turkey; 93.8 per cent of the strains from Silvian were of T_1, while only 22.2 per cent at a site 45 Km SE of Maras belonged to this type. The latter population consists of, at least, four translocation types. The high frequency of derived types at a site SE of Maras suggests that the spontaneous structural differentiation by translocation is now still under way.

c. Inversions

In hybrids between strains of the timopheevi wheats, bridges with fragments were sometimes observed at the AI of PMCs. Of these, the chromosome behavior of the following three hybrids was recorded in detail; 1908A x 1911, 8940 x 107-1 and 8947 x 107-1. In 1908A x 1911, one cell had a bridge with a fragment in 74 cells observed. Of a total of 137 cells observed in 8940 x 107-1, eight formed a bridge and a fragment and a cell had two bridges and two fragments. Fifty-nine PMCs were observed in 8947 x 107-1 and four had a bridge with a fragment and three had two bridges and two fragments. The number of hybrids observed is quite small at present. But these data may suggest that structural differentiation in chromosomes by inversions is rather common in *T. araraticum* as was observed in *T. dicoccoides*

d. Seed fertilities

Seed fertilities were observed in 77 hybrids between strains of *T. araraticum* and in 29 hybrids between *T. araraticum* and *T. timopheevi* (Table IIe). They ranged from 7.0 to 100

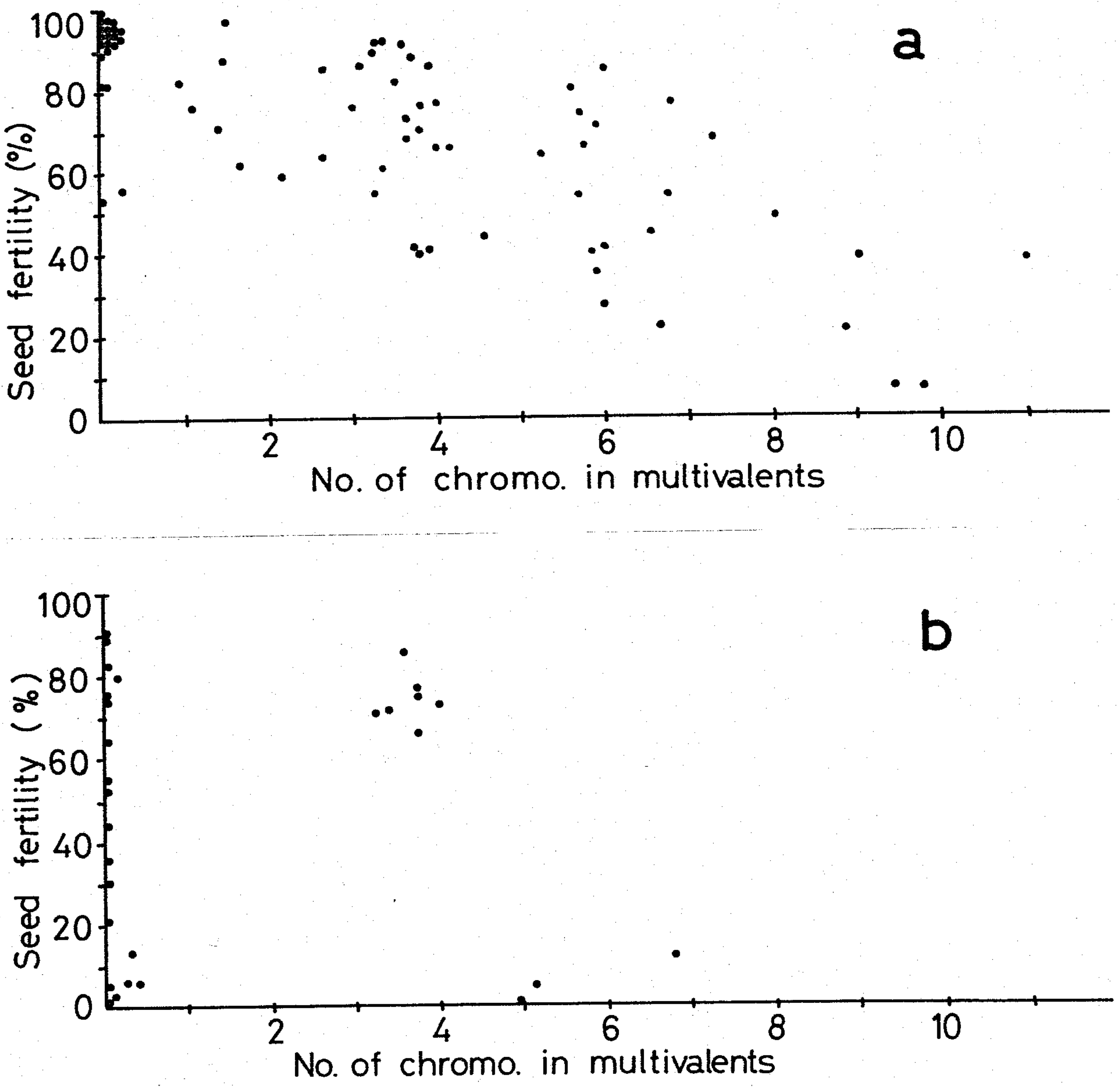

Fig. 8. Relationship between the seed fertility and the number of chromosomes involved in multivalents.
a, intraspecific hybrids of T. araraticum;
b, hybrids between T. araraticum and T. timopheevi.

per cent with an average of 69.4 per cent in the former and from 0.0 to 90.4 per cent with an average of 46.0 per cent in the latter. In *T. araraticum*, translocations do not seem to reduce greatly the seed fertility (Fig. 8a) as was the case in *T. dicoccoides*. In 8567 x 8561, 3.32 chromosomes were involved in multivalents but the seed fertility was 91.9 per cent. In 8725 x 8561, the values were 6.04 and 85.1 per cent, and in 8866 x 1908A, 10.90 and 38.4 per cent, respectively. However, the seed fertilities of most of the hybrids were much lower than that expected from these values. Probably, there may be some other genetical factors that reduce the fertility in intraspecific hybrids of *T. araraticum* as in those of *T. dicoccoides*.

In hybrids between *T. araraticum* and *T. timopheevi*, no correlation was recognized between the number of chromosomes and the seed fertility (Fig. 8b). As was reported by Tanaka and Ishii (1973) and by Kawahara and Tanaka (1977), hybrids between *T. araraticum* and *T. timopheevi* showed continuous variation in seed fertility from almost sterile to fully fertile even when no multivalent was recognized in them. In combinations that produced no multivalent, the lowest seed fertility was observed in 8890 x 107-1 (1.3%) and the highest was recorded in 1931 x 107-1 (90.4%). It was also high in 1927 x 107-1 (89.2%). The present finding of fertile hybrids between *T. araraticum* and *T. timopheevi* confirms the earlier finding of a fertile hybrid combination between them (Kawahara and Tanaka 1977). These data clearly indicate that reproductive barriers between the two species of the timopheevi group are incomplete and confirm the generally accepted theory that cultivated T. timopheevi was originated from wild T. araraticum. The wide range of seed fertility seen in hybrids between the T1 type strains of T. araraticum and T. timopheevi 107-1 may be partly due to the difference in cryptic structural hybridity in the chromosomes as was suggested by Sachs (1953).

3. General discussion

T. araraticum is found in the two distinct areas, Transcaucasus, U.S.S.R., and the Zagros-Taurus area in Turkey, Iraq and Iran (Sect. II). In Armenia, Transcaucasus, this species is found in segetal or ruderal habitats (Troitzky 1932). Zohary (1969) reported that T. araraticum grows in what seemed to be a genuine primary habitat (Quercus brantii forest belt) in Southeastern Turkey, Northern Iraq and Western Iran but that it is restricted to places highly disturbed by man's activity in Transcaucasus. The occurrence of T. araraticum in the oak park-forest belt of this area was further confirmed by Dagan and Zohary (1970) and by Tanaka and Ishii (1973). So, it is evident that T. araraticum occupies primary habitats in this area but secondary habitats in Transcaucasus. The shift from primary to secondary habitats suggests its dispersal from this area northward to Transcaucasus. Similar to T. dicoccoides, T. araraticum would have acquired some degree of weediness after its dispersal into Transcaucasus.

The dissemination of _T. araraticum_ from the Zagros-Taurus area to Transcaucasus was further confirmed by the present results that intraspecific structural differentiation in chromosomes is more abundant in the former than in the latter area. Studies on the intraspecific variation in _T. araraticum_ by Nakai (1978, 1979) and Saito and Ishida (1979) also support the above conclusion. The present study further revealed that the center of diversity in chromosomal differentiation lies in the northern tip of Iraq, the same region as proposed by Tanaka and Sakamoto (1979) in the study on several morphological characteristics. Therefore, _T. araraticum_ is likely to have originated somewhere in Northeastern Iraq and its adjacent regions in Southeastern Turkey and then disseminated westward to South-central Turkey, northward to Transcaucasus and southward to Western Iran.

VI. IDENTIFICATION OF GENOMES INVOLVED IN THE RECIPROCAL TRANSLOCATIONS OF THE WILD TETRAPLOID WHEATS

As described in the previous sections, several reciprocal translocations have been found between strains of the wild tetraploid wheats, T. dicoccoides and T. araraticum. In order to compare the degree of structural differentiation of chromosomes belonging to the different genomes, chromosomes involved in these translocations were identified through hybridization experiments with the diploid wheats, T. boeoticum Boiss. and T. monococcum L. This section describes other two kinds of hybrids which were produced and their meiosis observed. They are hybrids between strains of the diploid wheats, which were made to obtain the cytogenetic backgrounds of the strains used in the hybridization with the tetraploid wheats, and those between T. aestivum L. cv. Chinese Spring and T. dicoccoides which were made to clarify the cytogenetic position of Chinese Spring in the hexaploid wheats since most of the translocations in the hexaploid wheats have been identified by using Chinese Spring as a standard.

1. Materials

The strains of the diploid wheats used are listed in Table 15. Ten strains were of wild T. boeoticum and two were of cultivated T. monococcum. Eight of these strains

Table 15. List of the diploid wheats used

Stock No.* (KU-)	Species**	Source and locality***
101-1	b	Collection of College of Agric. Hokkaido Univ. Japan(1927)
101-2	b	Vavilov(1930), Balaklaua, Crimea, U.S.S.R.
101-3	b	Agr. Exp. Station, Teheran(1955), (KUSE 3365)
102	b	Vavilov(1930), Balaklaua, Crimea, U.S.S.R.
103	b	Agr. Exp. Station, Teheran(1955), (KUSE 3336)
104-1	m	Collection of College of Agric. Hokkaido Univ. Japan(1927)
1501	b	BEC, 20 km E of Erevan(Erevan-Garni), U.S.S.R.
1519	b	BEC, 8 km W of Garni(Erevan-Garni), U.S.S.R.
3621	b	BMUK, 58 km S of Ankara(Ankara-Adana), Turkey
3636	m	BMUK, 36 km W of Bursa(Bursa-Boudirma), Turkey

Table 15. List of the diploid wheats used (continued)

Stock No.* (KU-)	Species**	Source and locality***
8082	b	BEM, 19.3 km S from Sulaymaniyah to Qara Dagh, NE slope of Shakh i Baranan, Iraq
8143	b	BEM, 7.1 km NE from Shaqlawa to Rowanduz, Iraq

* Stock No. of the Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University.

** b: *Triticum boeoticum*, m: *T. monococcum*.

*** The following abbreviations were used.

KUSE: The Kyoto University Scientific Expedition to Karakoram and Hindukush, 1955;

BMUK: The Botanical Mission of the University of Kyoto to the Eastern Mediterranean Countries, 1959;

BEC: The Kyoto University Botanical Expedition to the Caucasus, 1966;

BEM: The Kyoto University Botanical Expedition to the Northern Highlands of Mesopotamia, 1970.

were collected in U.S.S.R., Turkey or Iraq but the origin of the remimaining four strains is not known. All these strains were maintained at the Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University by selfing and therefore were considered to be structural homozygotes.

Tetraploid wheats used in the crossings with diploid wheats were nine strains of *T. dicoccoides*, one of *T. timopheevi* and 14 of *T. araraticum*. Stock numbers and their translocation types are as follows;

T. dicoccoides; 1978B and 8935 of the type E1a, 108-2 and 108-3 of the E1b, 109(E2), 195(E_3), 8915A(E_4), 1945(E_5) and 1957(E_6).

T. timopheevi; 107-1(T_1).

T. araraticum; 196-2, 8700, 8821B and 8822 of the type T_1, 196-1(T_2), 1908A(T_3), 8732(T_4), 8674(T_5), 8784(T_8), 1909C(T_9), 1911(T_{10}), 8460(T_{11}), 8725(T_{13}) and 8866(T_{14}).

Sources and localities of these strains and their cytogenetical relationships are described in the respective chapters in the previous sections.

Chinese Spring is maintained by selfing as three lines under the separate stock numbers of 184-1, 184-2 and 910 at the Plant Germ-plasm Institute, Faculty of Agriculture, Kyoto University. Strain 184-1 was obtained from Sando (1948, P 218) and 184-2 from Sears (1949). Strain 910 is a disomic line in monosomic series of Chinese Spring by Sears. These were crossed with eight strains of *T.*

dicoccoides and chromosome pairings were observed at MI (and AI in some hybrids) of the PMCs in F_1 hybrids. Strains of *T. dicoccoides* used in the hybridization with Chinese Spring were as follows, 108-5(E_{1a}), 8935(E_{1a}), 108-2(E_{1b}), 108-3(E_{1b}), 109(E_2), 195(E_3), 8915A(E_4) and 1957(E_6).

2. Results and Discussions

a. The fundamental chromosome structure in the diploid wheats in regard to translocations

Table 16 shows the occurrence of multivalents in hybrids between strain 103 of *T. boeoticum* and nine other strains of the diploid wheats. Of nine hybrids observed, quadrivalents were formed in two hybrids involving 1501 and 1519. In both hybrids, 92.0 per cent of the PMCs had a quadrivalent (Fig. 9b). In 1501 x 103, 60.9 per cent of the quadrivalents were ring shaped and 78.3 per cent were rings in 1519 x 103. While, no multivalent was formed in the remaining seven hybrids and their meiosis was normal with seven bivalents (Fig. 9a).

The present data show that the chromosome structures of strains 1501 and 1519 differ from that of 103 by one reciprocal translocation but those of the other strains, 101-1, 101-2, 102, 3621, 3636, 8082 and 8143, do not. Therefore, the above eight strains except for 1501 and 1519 can be grouped into one translocation type which was tentatively named as type I. Strains 1501 and 1519 belonged to type II. Eight strains of type I were collected from

Table 16. Occurrence of multivalents in F_1 hybrids between strains of the diploid wheats

Cross combination	No. of cells observed	Cells with multivalents(%)
101-1 x 103	50	none
101-2 x "	"	"
102 x "	"	"
1501 x "	"	1 IV 92.0
1509 x "	"	1 IV 92.0
3621 x "	"	none
3636 x "	"	"
8082 x "	"	"
8143 x "	"	"

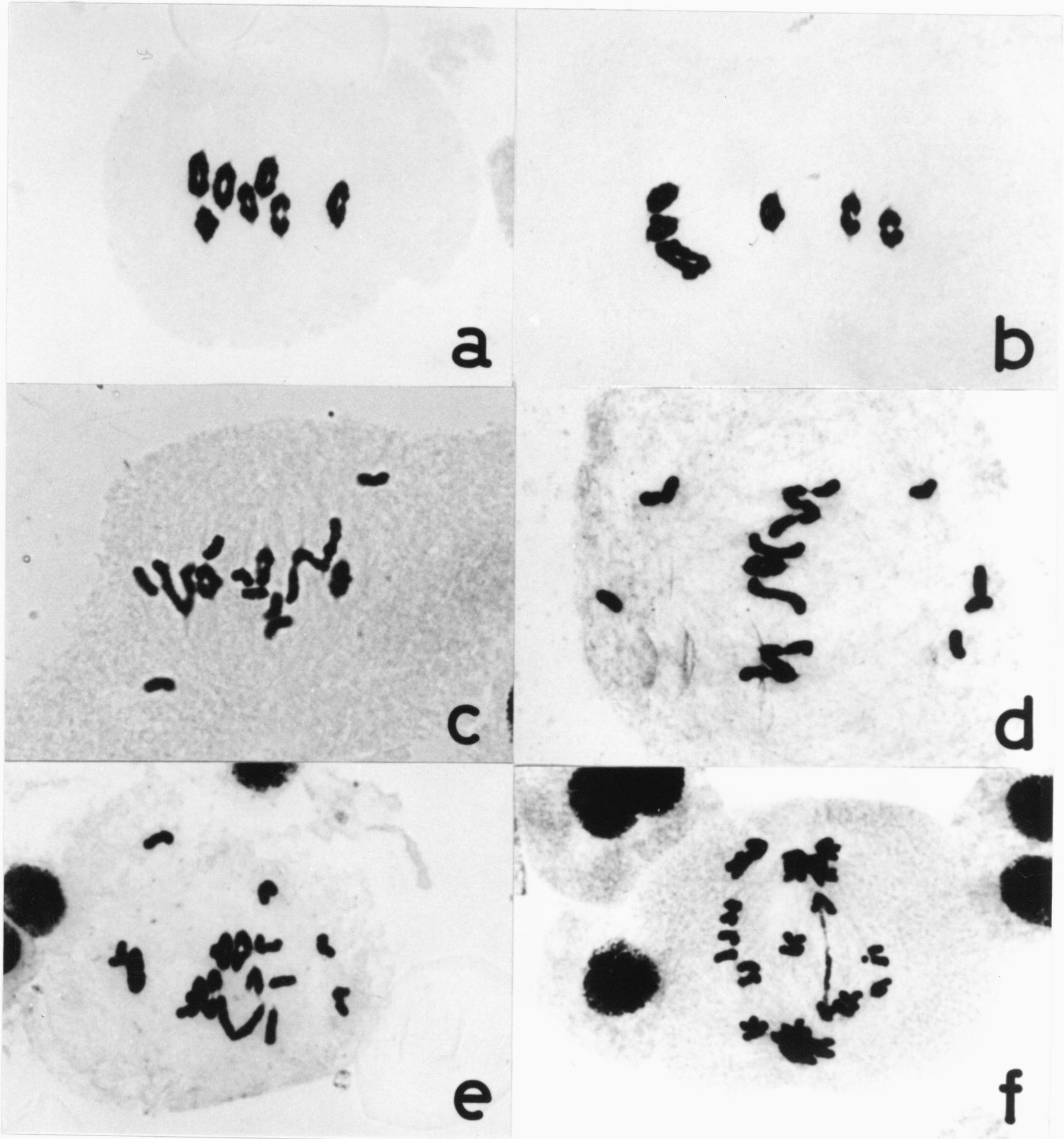

Fig. 9. Chromosome pairings at MI or AI in F_1 hybirds involving the diploid and tetraploid wheats. (x750)

a; 7II in 101-1 x 103 (with AA genome),
b; 5II + 1IV in 1501 x 103 (AA),
c; 8I + 3II + 1Ⅲ + 1IV in 1957 x 103 (AAB),
d; 7I + 3II + 2IV in 8725 x 103 (AAG),
e; 7I + 3II + 1VⅢ in 1911 x 103 (AAG),
f; A bridge with a fragment in 1978B x 103 (AAB).

various regions. Strains 101-2 and 102 were collected in Crimea, U.S.S.R., 3621 and 3636 in Turkey and 8082 and 8413 in Iraq. The collection site of the remaining two strains, 101-1 and 103, is not known. On the other hand, 1501 and 1519 were sampled from adjacent localities in Armenia, U.S.S.R. (Table 15). Further, type I was found in both wild and cultivated species; in seven strains of wild *T. boeoticum* and one of cultivated *T. monococcum*. Based on these data, chromosome structures of the eight strains, 101-1, 101-2, 102, 103, 3621, 3636, 8082 and 8413, were considered to be fundamental in regard to translocations in the diploid wheats. Chromosomes of 1501 and 1519 would have structurally differentiated from this fundamental structure by one spontaneous translocation.

In a hybrid 101-2 x 103, PMCs at AI were also observed. Of 58 cells, one had a bridge with a fragment indicating heterozygosity for a paracentric inversion. Thus, 101-2 and 103 differ from each other by, at least, one paracentric inversion though they have the same translocation type. At present, data on the chromosome behavior at AI was obtained from this hybrid only, but it is evident that the other kinds of structural differentiation than translocations are present between strains of the diploid wheats.

b. Identification of genomes involved in the reciprocal translocations in *T. dicoccoides*

Average multivalent and chiasma frequencies in hybrids between T. dicoccoides and the diploid wheats (AAB hybrids) are summarized in Table 17.

In the present experiment, most of the data were obtained from plants growing either in the experimental fields or in an unheated glasshouse. But in two hybrid combinations, 108-2 x 103 and 108-3 x 103, the PMCs were sampled from two plants growing under both of these two different environmental conditions. Differences in the average multivalent and chiasma frequencies due to the two environmental factors were likely to have little effect in the interpretation of the present data as shown in Table 17.

Since all the dicoccoides strains were crossed to, at least, boeoticum 103, effects of structural differentiations in the diploid wheats on chromosome pairings in these hybrids is negligible. In a hybrid 1957 x 103, a quadrivalent was observed in the PMCs (Fig. 9c). The mean frequency of quadrivalents was 0.45 per cell in this hybrid (Table 17). In the remaining 10 hybrid combinations, a trivalent or two trivalents were formed at a various frequency but no quadrivalent was observed. The mean frequency of trivalents ranged from 0.12 to 0.79. The value was low in hybrids involving 109, 195, 1945, 1978B and 8935 (0.04 - 0.36), while, hybrids of 108-2, 108-3 and 8915A showed high frequencies of trivalents (0.50 - 0.79).

Two causes could be offered to explain the occurrence of trivalents in these hybrids, i. e., they are due to the homoeologous pairings of the A and B genomes or due to trans-

Table 17. Mean multivalent and chiasma frequencies and occurrence of multivalents in F_1 hybrids between <u>T. dicoccoides</u> and the diploid wheats

Cross combination	Type*	Envir. cond.**	No. of cells	Freq. of mult.		Xta/ cell	Per cent of cells with multivalents
				III	IV		
1978B x 103	E_{1a}	G	33	0.21	-	9.70	1III 15.2, 2III 3.0
8935 x 103	"	F	50	0.22	-	10.68	1III 18.0, 2III 3.0
108-2 x 103	E_{1b}	G	33	0.55	-	10.24	1III 54.5
" x "	"	F	"	0.61	-	9.79	1III 48.5, 2III 6.1
108-3 x 101-3	"	G	50	0.50	-	8.46	1III 50.0
" x 103	"	G	33	0.79	-	10.27	1III 51.5, 2III 15.2
" x "	"	F	"	0.61	-	10.15	1III 36.4, 2III 12.1
109 x 101-3	E_2	G	60	0.22	-	10.06	1III 21.7
" x 103	"	G	33	0.36	-	10.55	1III 30.3, 2III 3.0
195 x 103	E_3	F	"	0.12	-	9.73	1III 12.2
8915A x 103	E_4	F	50	0.54	-	10.48	1III 46.0, 2III 4.0
1945 x 103	E_5	G	50	0.04	-	7.64	1III 4.0
1957 x 103	E_6	F	33	0.30	0.45	9.15	1IV 36.4, 1III 21.2, 1III+1IV 9.1

* Translocation type of the female parent.

** Environmental conditions: F=Field, G=Glasshouse.

locations between the A and B genome chromosomes of *T. dicoccoides*. In haploid plants (AB) of *T. durum*, bivalents have been observed 0.183 (Kihara 1936) or 0.37 (Lacadena and Ramos 1968) per cell on the average as shown in Table 18. Mean trivalent frequencies in hybrids of 109, 195, 1945, 1978B and 8935 did not exceed the frequency of bivalents in haploid plants with the AB genome. Therefore, the occurrence of trivalents in these hybrids was inferred to be caused by homoeologous pairings between the A and B genomes. These five strains had different chromosome structures; 109 belonged to E_2, 195 to E_3, 1945 to E_5 and 1978B and 8935 to the type E_{1a}. Therefore, one major translocation found between E_2, E_3 or E_5 and E_{1a} is probably located on chromosomes belonging to the B genome. Those strains which formed trivalents at a high frequency in hybrids with diploid wheats have chromosome types different from E_{1a}; 108-2 and 108-3 belong to E_{1b} and 8915A to E_4. Since there was little difference in mean chiasma frequency between hybrids of 108-2, 108-3 or 8915A and those of 109, 195, 1945, 1978B or 8935 (Table 17), the difference in the trivalent frequency between the two groups would not be caused by a genic factor(s) controlling the amount of homoeologous pairing. Instead, it would be due to translocations between the A and B genomes of *T. dicoccoides*. Thus, the minor translocation between E_{1a} and E_{1b} and the major translocation between E_{1a} and E_4 might be located on chromosomes of the A and B genomes. Quadrivalents were found only in a hybrid 1957 x 103. Since

Table 18. Chromosome pairings at MI in haploid plants of *T. durum* or *T. timopheevi*

Species	No. of cells observed	Chromosome pairings*			Reference
		I	II	III	
T. durum	1262	13.63 (8-14)	0.183 (0-3)	-	Kihara, 1936
"	94	13.26 (10-14)	0.37 (0-2)	-	Lacadena and Ramos, 1968
T. timopheevi	100	13.35 (10-14)	0.31 (0-2)	0.01 (0-1)	Simonet and Chesneaux, 1954
"	60	13.45	0.25	0.02	Riley and Chapman, 1957

* Means and ranges(in parentheses).

no quadrivalent was observed in hybrids of the type $E1_a$ with the diploid wheats, this shows that the translocation between $E1_a$ and E6 is located on two different chromosomes belonging to the A genome.

Based on the above results, the chromosomes tentatively identified in Section IV were allocated into the A or B genome as follows;

Numbering in Section IV	Present designation
1 - 2	B_1 - B_2
3 - 4	B_3 - B_4
1 - 5	B_1 - A_1
3 - 6	B_3 - B_5
7 - 8	A_2 - A_3

The present designation is also summarized in Table 21. As shown above, major translocations identified in <u>T. dicoccoides</u> consist of three between the B genome chromosomes, one between the A and B genomes and one between the A genome chromosomes. In addition to these, one minor translocation is found between the A and B genomes.

The present results also showed that the A genome of the type $E1_a$ have the same chromosomal arrangement as that of the fundamental type of the diploid wheats in regard to translocations. Therefore, type $E1_a$ was regarded to have the primitive chromosome structure of <u>T. dicoccoides</u> and, further, of the tetraploid emmer wheats.

c. Identification of genomes involved in the reciprocal translocations in <u>T. araraticum</u>

Average multivalent and chiasma frequencies in hybrids of T. araraticum or T. timopheevi with the diploid wheats (AAG hybrids) are summarized in Tables 19 and 20. As shown in these tables, more multivalents were formed in these AAG hybrids than in AAB hybrids (Table 17). AAG hybrids formed 0.40 - 0.95 trivalent, 0.03 - 0.52 quadrivalent, 0.0 - 0.27 quinquevalent, 0.0 - 0.11 sexivalent and 0.0 - 0.08 octavalnet with an average of 0.59, 0.30, 0.06, 0.005 and 0.003, respectively. The average chiasma frequency was 9.53 with the range of 7.84 - 10.66. While, AAB hybrids produced 0.04 - 0.70 trivalent and 0.0 - 0.45 quadrivalent with the average of 0.34 and 0.04, respectively, and the average chiasma frequency was 9.69 (7.64 - 10.68). To avoid effects of translocations on multivalent formation, further comparisons were made between AAG hybrids of the type T_1 (8700, 8821B and 8822) and AAB hybrids of the type E_{1a} (1978B and 8935). Hybrids involving 107-1 or 196-2 were excluded because of their apparently high values of multivalents and will be discussed later. Hybrids of 8700, 8821B and 8822 with diploid wheats formed 0.46 - 0.62 trivalent, 0.12 - 0.35 quadrivalent and 0.0 - 0.08 quinquevalent per cell with the average of 0.51, 0.24 and 0.03 respectively, while, hybrids of 1978B and 8935 with boeoticum 103 formed only trivalents, the frequency being 0.21 and 0.22, respectively. The average chiasma frequency of the former hybrids were 9.27 (8.40 - 10.21) and that of the latter was 10.19 (9.70 - 10.68). Thus, the chiasma frequency was lower in the former than the latter but more multivalents were formed in the former than the latter. This tendency was also recognized when all the AAG hybrids were compared to all the AAB hybrids as described above. This indicates that higher frequencies of multivalents in AAG hybrids than AAB are not due to the difference in genic factor(s) controlling the amount of homoeologous pairing. Instead, it would indicate structural differentiation between the A genome in *T. araraticum* or *T. timopheevi* and that of the diploid wheats as was shown in *T. timopheevi* by Lilienfeld and Kihara (1934) and by Matsumura (1950). Choromosome parings of haploid plants of *T. timopheevi* (AG) were similar to those reported in haploid *T. durum* except for the occurrence of trivalents at a low frequency (Table 18). This would further be an evidence that the multivalent formations in AAG hybrids are mostly due to structural heterozygosity between the two A genomes in these hybrids.

In AAG hybrids, four strains, 101-1, 101-3, 103, 104-1 were used in the hybridization as diploid parents. Two strains, 101-1 and 103, have the fundamental chromosome structure of the diploid wheats in regard to translocations. Of 17 tetraploid strains, 14 were crossed to, at least, 103 and the remaining three, 107-1, 8732 and 8866 were crossed to, at least, 101-1. Therefore, chromosome pairings in hybrids involving 101-1 and 103 were mainly used in the analysis of the data. There was little difference in the frequencies of multivalents or chiasmata and in the occur-

Table 19. Mean multivalent and chiasma frequencies in F_1 hybrids between *T. timopheevi* or *T. araraticum* and the diploid wheats

Cross combination	Type*	Envir. cond.**	No. of cells	Frequency of multivalent per cell				Xta/ cell
				III	IV	V	VI-VIII	
107-1 x 101-1	T_1	G	50	0.70	0.50	0.04	-	10.66
" x 104-1	"	G	62	0.40	0.44	0.05	-	10.66
196-2 x 101-1	"	G	64	0.86	0.33	0.03	-	9.37
" x 101-3	"	G	59	0.78	0.22	0.14	-	10.25
" x 103	"	G	33	0.85	0.33	0.09	-	10.12
8700 x 103	"	F	50	0.62	0.12	-	-	8.40
8821B x 101-1	"	G	54	0.46	0.35	0.04	-	10.21
" x 103	"	F	50	0.46	0.32	-	-	9.36
8822 x 103	"	F	"	0.50	0.18	0.08	-	9.12
196-1 x 101-1	T_2	G	"	0.44	0.40	0.06	-	9.14
" x 103	"	F	33	0.58	0.21	0.15	-	8.85
1908A x 101-1	T_3	G	60	0.40	0.38	0.12	-	10.27
" x 101-3	"	G	42	0.69	0.45	-	-	9.87
" x 103	"	G	33	0.64	0.24	0.09	-	10.09

Table 19. Mean multivalent and chiasma frequencies in F_1 hybrids between *T. timopheevi* or *T. araraticum* and the diploid wheats (continued)

Cross combination	Type*	Envir. cond.**	No. of cells	Frequency of multivalent per cell III	IV	V	VI-VIII	Xta/ cell
8732 x 101-1	T_4	G	46	0.46	0.28	0.04	-	9.94
8674 x 103	T_5	G	50	0.44	0.22	0.04	-	8.66
8784 x 101-1	T_8	G	44	0.48	0.16	-	-	8.85
" x 103	"	F	50	0.48	0.24	0.08	-	9.68
1909C x 103	T_9	G	"	0.68	0.42	0.10	-	10.06
1911 x 103	T_{10}	G	37	0.95	0.27	0.27	0.11VI 0.08VIII	10.27
8460 x 103	T_{11}	G	50	0.58	0.02	0.02	-	8.42
" x "	"	F	33	0.79	0.03	-	-	9.03
8725 x 103	T_{13}	G	50	0.68	0.52	-	-	7.84
8866 x 101-1	T_{14}	G	45	0.42	0.27	-	-	8.78

* Translocation type of the female parent.

** Environmental conditions: F=Field, G=Glasshouse.

Table 20. Occurrence of multivalents in F_1 hybrids between *T. timopheevi* or *T. araraticum* and the diploid wheats

Cross combination*	No. of cells	Per cent of cells with multivalents
107-1 x 101-1	50	1IV 26.0, 1III 22.0, 1III+1IV 18.0, 2III 8.0, 1V 4.0, 3III 2.0, 2III+1IV 2.0, 2III+2IV 2.0
" x 104-1	62	1IV 32.2, 1III 27.4, 1III+1IV 6.5, 2III 3.2, 1V 3.2, 2IV 1.6, 1IV+1V 1.6
196-2 x 101-1	64	1IV 23.4, 2III 21.9, 1III 20.3, 1III+1IV 7.8, 3III 3.1, 2III+1IV 1.6, 1V 1.6, 1III+1V 1.6
" x 101-3	59	1III 30.5, 2III 20.3, 1IV 18.6, 1V 10.2, 1III+1IV 3.4, 1III+1V 3.4
" x 103	33	1III 33.3, 1III+1IV 15.2, 1IV 12.1, 2III 12.1, 1V 9.1, 2III+1IV 6.1
8700 x 103	50	1III 46.0, 1IV 12.0, 2III 8.0
8821B x 101-1	54	1III 44.4, 1IV 33.3, 1V 3.7, 1III+1IV 1.9
" x 103	50	1III 40.0, 1IV 30.0, 2III 2.0, 1III+1IV 2.0
8822 x 103	50	1III 30.0, 1IV 14.0, 2III 8.0, 1V 8.0, 1III+1IV 4.0
196-1 x 101-1	50	1III 30.0, 1IV 30.0, 1III+1IV 6.0, 1V 6.0, 2III 4.0, 2IV 2.0
" x 103	33	1III 48.5, 1IV 18.2, 1V 9.1, 1III+1V 6.1, 1III+1IV 3.0

* Same as Table 19.

Table 20. Occurrence of multivalents in F_1 hybrids between *T. timopheevi* or *T. araraticum* and the diploid wheats (continued)

Cross combination*	No. of cells	Per cent of cells with multivalents
1908A x 101-1	60	1IV 35.0, 1III 21.7, 1V 8.3, 2III 3.3, 1III+1IV 3.3, 1III+1V 3.3, 3III 1.7
" x 101-3	42	1IV 35.7, 1III 31.0, 1III+1IV 9.5, 2III 7.1, 3III 4.8
" x 103	33	1III 48.5, 1IV 15.2, 1V 9.1, 1III+1IV 9.1, 2III 3.0
8732 x 101-1	46	1III 37.0, 1IV 28.3, 1V 4.3, 2III 4.3
8674 x 103	50	1III 42.0, 1IV 20.0, 1V 4.0, 1III+1IV 2.0
8784 x 101-1	44	1III 29.5, 1IV 15.9, 2III 9.1
" x 103	50	1III 40.0, 1IV 24.0, 2III 4.0, 1V 2.0
1909C x 103	50	1IV 30.0, 1III 24.0, 1III+1IV 12.0, 1V 8.0, 2III 8.0, 1III+1 V 2.0, 3III 2.0, 4III 2.0
1911 x 103	37	1V 18.9, 2III 13.5, 1III+1IV 13.5, 1III 10.8, 1VIII 8.1, 1III+1V 8.1, 1IV 5.4, 1VI 5.4, 1III+1VI 5.4, 3III 2.7, 4III 2.7, 2IV 2.7, 2III+1IV 2.7
8460 x 103	50	1III 54.0, 2III 3.0, 1IV 2.0, 1V 2.0
" x "	33	1III 66.7, 2III 3.0, 1IV 3.0

Table 20. Occurrence of multivalents in F_1 hybrids between *T. timopheevi* or *T. araraticum* and the diploid wheats (continued)

Cross combination*	No. of cells	Per cent of cells with multivalents
8725 x 103	50	1III 24.0, 1IV 24.0, 1III+1IV 14.0, 2III 10.0, 2IV 6.0, 3III 2.0, 2III+1IV 2.0
8866 x 101-1	45	1III 35.6, 1IV 24.4, 2III 2.2, 1III+1IV 2.2

rence of multivalents between hybrids of 101-1 and 103 with a common tetraploid parent (Tables 19 and 20).

The identification of chromosomes involved in the translocations in T. araraticum was made by comparing multivalent formations in hybrids of each translocation type to those in hybrids of three T_1 strains, 8700, 8821B and 8822. The results and dicussion will be arranged according to the tetraploid parents used in the hybridization.

8700, 8821B and 8822 (T_1): As described earlier, four hybrids involving these three strains produced 0.46 - 0.62 trivalent, 0.12 - 0.35 quadrivalent and 0.0 - 0.08 quinquevalent per cell. The frequency of cells with a trivalent, a quadrivalent, two trivalents, a quinquevalent or a trivalent and a quadrivalent ranged from 30.0 to 46.0 per cent, from 12.0 to 33.3 per cent, from 0.0 to 8.0 per cent or from 0.0 to 4.0 per cent, respectively. For the sake of brevity, hybrids involving these three strains will be expressed as "standards" in the following descriptions. From the occurrence of a quadrivalent in several cells, it was inferred that at least one translocation exists between the A genome of the type T1 of T. araraticum and that of the fundamental chromosome structure of the diploid wheats as was observed in T. timopheevi by Matsumura (1950). The formation of trivalents is possibly due to the result of breakdown of a quadrivalent into an uni- and a trivalent, or due to to translocations between the A and G genomes.

107-1 (T_1); Because this timopheevi strain was used as a T_1 type tester in many hybrids (see Appendix I), chromosome parings in hybrids of this strain with the diploid wehats were observed. Two hybrids with 101-1 and 104-1 were observed. In a hybrid with 101-1, the frequencies of trivalents and quadrivalents were a little higher than those involving 8700, 8821B and 8822 and cells with many multivalents (three trivalents, two trivalents and a quadrivalent or two trivalents and two quadrivalents) were observed (Tables 19 and 20). In hybrids with 104-1, cells with many multivalents (two quadrivalents or a quadrivalent and a quinquevalent) were also observed. Chiasma frequencies of these two hybrids were the highest of AAG hybrids. This may suggest some difference in genic factor(s) controlling the amount of homoeologous pairing between timopheevi 107-1 and 8700, 8821B and 8822 of T. araraticum.

196-2 (T_1): In three hybrids of 196-2, the frequency of trivalents was high (0.78 - 0.86) and the frequency of cells with two trivalents was also high (12.1 - 21.9%). Chiasma frequencies were similar to those of the standards (Table 19). Though 196-2 belonged to the same translocation type as 8700, 8821B and 8822, it may have a minor translocation between the A and G genomes.

196-1(T_2) and 1908A(T_3): Hybrids involving these two strains showed a slightly high value in trivalent and/or quadrivalent frequencies (Table 19). But the difference from those of the standards was not large. In three hybrids, 196-1 x 101-1, 196-1 x 103 and 1908A x 101-1, cells with two quadrivalents, three trivalents or a trivalent and a quinquevalent were found but at a low frequency (Table 20). Consequently, translocations between T_1 and T_2 or T_3 were assumed to involve no A genome chromosome.

8732 (T_4), 8674 (T_5), 8784 (T_8) and 8866 (T_{14}): Mean multivalent frequencies and the occurrence of multivalents in hybrids involving these strains were similar to those in the standards. Mean frequencies of trivalents, quadrivalents or quinquevalents were within the range of 0.42 - 0.48, 0.16 - 0.28 or 0.0 - 0.08 per cell, respectively (Table 20). Therefore, translocations T_1 - T_4, T_1 - T_5, T_1 - T_8 and T_1 - T_{14} would involve no chromosome of the A genome. Chromosomes involved in these translocations are 1, 2, 3, 4, 5, 6 and 7 (Sect. V). These might be G_1, G_2, G_3, G_4, G_5, G_6 and G_7, respectively.

1909C (T_9): The frequencies of tri-, quadri- and quinquevalents were higher than the standards (Table 19) and cells with three or four trivalents were recognized (Table 20). But the difference from the standards was not large enough to indicate that at least one A genome chromosome is involved in the two major translocations of T_9. The two translocations of T_9 were 4 - 5c and 1 - 3 or 8 (Sect. V). Since this strain was established from one original sample along with 1909A and 1909B with T_3 (1 - 3 translocation), it is highly possible that the second translocation is not 1 - 8 (between the A and the G genomes) but 1 - 3 (between G genome chromosomes).

1911 (T_{10}): In 1911 x 103, the frequency of trivalents was high (0.95 per cell) and sexivalents or octavalents were observed (Tables 19 and 20). Of 37 PMCs observed, three had an octavalent (Fig. 9e) and four had, at least, a sexivalent. Possibly, the A genome of this strain differs from that of the fundamental chromosome structure of the diploid wheats by three translocations. Since at least one translocation is inferred between the A genome of 8700, 8821B and 8822 and that of the diploid wheats, both of the two translocations between T_1 and T_{10} may be among the A genome chromosomes. Or else, one of them may be that between the A and G genomes because the frequency of trivalents was high. Since one of the four chromosomes is assumed to belong to the G genome (Sect. V and above discussions), the latter seems to be more adequate. This strain produced a quadrivalent and a sexivalent at a low frequency in a hybrid with 107-1 (see Appendix I). Therefore, the presence of three translocations between the A genome of this strain and that of the diploid wheats may be explained by a minor translocation other than the two major ones between T_1 and T_{10}.

8460 (T_{11}): In 8460 x 103, two plants grown in the experimental field and in a glasshouse were observed but there was little difference in both multivalent and chiasma frequencies between them (Table 19). As compared to the standards, an extremely low frequency of quadrivalents was obtained. Of a total of 83 cells, one cell had a quinquevalent, two had a quadrivalent and the other two had two trivalents. The remaining cells with multivalents had a trivalent (Table 20). In spite of the relatively low frequency of chiasmata (8.73 in the average), the frequency of trivalents was higher than the standard (0.68 in the average). Two translocations between T_1 and T_{11} were located on chromosomes G3 and G4 and on G5 and an unidentified chromosome (8, 11 or 12. Sect. V and above discussions). Probably, this unidentified chromosome would belong to the A genome.

8725 (T_{13}): Though the chiasma frequency is the lowest among AAG hybrids, the trivalent and the quadrivalent frequencies were a little high in hybrids involving this strain (Table 19). Of 50 cells observed, three had two quadrivalents (Fig. 9d), six had, at least, two trivalents and one had three trivalents (Table 20). Therefore, one of the two translocations between T_1 and T_{13} would be that within the A genome chromosomes and another one might be that between the A and G genomes.

Based on these data, chromosomes tentatively identified in Section V were allocated into the A or G genomes (Table 21). As shown in Table 21, chromosomes 8 to 14 tentatively identified in Section V would, most probably, belong to the A genome. However, the chromosomes belonging to the A genome were not numbered because they were not fully identified. The present estimation shows that 10 of 17 different translocations found in *T. araraticum* (Sect. V) were between the G genome chromosomes, 5 were between the A and G genomes and two were between the A genome chromosomes.

Table 21. An estimation of major reciprocal translocations in the wild tetraploid wheats

Species	Type	Chromosomes involved*
T. dicoccoides	$E_1(E_{1a})$	none
	E2	B1 - B2
	E3	B3 - B4
	E4	B1 - A1
	E5	B3 - B5
	E6	A2 - A3
T. araraticum	T1	none
	T2	G1 - G2
	T3	G1 - G3
	T4	G4 - G5 a
	T5	G1 - G5
	T6	G4 - G6 a
	T7	G3 - G4
	T8	G3 - G4 and G4 - G5 b
	T9	G1 - G3 and G4 - G5 b or c
	T10	G5 - A and A - A
	T11	G3 - G4 and G5 - A
	T12	G4 - G6 b and G5 - A
	T13	G7 - A and A - A
	T14	G2 - G5 and G6 - G7
	T15	G2 - G5, G4 - G6 b and G4 or G6 - A

* The numbering of chromosomes is arbitrary, and does not refer to any other conventional denomination.

In *T. araraticum*, it is impossible to determine the primitive chromosome structure if primitiveness means the absence of structural differentiation in chromosomes between the amphidiploid and its parental species: All the translocation types have the A genome chromosomes structurally more or less differentiated from those of the diploid wheats. Of course, there still remains some possibility that a translocation type whose A genome has the same chromosomal arrangement as the fundamental type of the diploid wheats will be discovered. Nevertheless, the type T_1 is the most probable candidate to have the primitive chromosome structure because all the other types are likely to have differentiated from this type (Sect. V).

d. Inversions found in triploid hybrids involving *T. dicoccoides* and *T. araraticum*

In several triploid hybrids involving *T. dicoccoides*, *T. araraticum* and *boeoticum* 103, bridges and fragments were observed at AI and the results are shown in Tables 22 and 23.

As shown in these tables, seven AAB hybrids and ten AAG hybrids were observed and at least one bridge with a fragment per cell (Fig. 9f) was recognized in all of these. In the hybrid 1978B x 103 (AAB) and in that of 1908A x 103 (AAG), two bridges with two fragments were observed in one cell. Therefore, it is clear that, at least, one or two paracentric inversions exist between the A genome of these strains and that of 103.

In *T. dicoccoides*, two strains, 1978B and 8935, have

Table 22. Occurrence of bridges and fragments at AI in F_1 hybrids between *T. dicoccoides* and *T. boeoticum*

Cross combination	No. of cells observed	No. of cells with:				
		1 br.	1 br. + 1 frag.	2 br.	2 br. + 1 frag.	2 br. + 2 frag.
108-2 x 103	278*	8	18	1	-	-
108-3 x "	267*	14	1	-	1	-
109 x "	77	2	3	-	-	-
195 x "	59	5	2	2	1	-
1957 x "	104	4	4	-	-	-
1978B x "	250	10	7	-	-	1
8935 x "	284	12	5	-	-	-

* Two plants were observed.

Table 23. Occurrence of bridges and fragments at AI in F_1 hybrids between _T. araraticum_ and _T. boeoticum_

Cross combination	No. of cells observed	No. of cells with:				
		1 br.	1 br.+ 1 frag.	2 br.+ 1 frag.	2 br.+ 2 frag.	3 br.
196-1 x 103	173	5	5	-	-	-
1908A x "	123	2	3	-	1	-
1909C x "	73	1	1	-	-	-
1911 x "	163	4	4	-	-	-
1979B x "	191	4	8	1	-	-
8460 x "	68	-	5	-	-	-
8674 x "	187	5	3	-	-	1
8784 x "	53	3	3	-	-	-
8821B x "	121	4	2	-	-	-
8822 x "	127	5	1	-	-	-

the primitive chromosome structure ($E_{1}a$). As mentioned above, there were observed no structural differentiation by translocations between the A genome of type $E_{1}a$ and that of the fundamental chromosome structure of the diploid wheats. However, the present data show that structural differentiations by inversions are found between them. In *T. araraticum*, 8821B and 8822 have the fundamental chromosome structure. As in *T. dicoccoides*, structural differentiations by inversions exist between the A genome of the fundamental type of *T. araraticum* and that of the diploid wheats. Inversions in the diploid wheats have not been analyzed extensively; the chromosome structure of 103 may or may not be typical in regard to inversions. However, the present data would suggest that structural differentiations in chromosomes by inversions had occurred in the process of the evolution of the tetraploid wheats, *T. dicoccoides* and *T. araraticum*.

e. Confirmation of the primitive chromosome structure in the hexaploid wheats

Mean multivalent and chiasma frequencies and occurrence of multivalents in F_1 hybrids between Chinese Spring and *T. dicoccoides* of six translocation types are listed in Table 25. In 910 x 8935, no multivalent was recognized. While, multivalents were observed in all the other hybrid combinations. Trivalents were recognized at a low frequency (0.06 per cell) in a hybrid with 108-5. In 184-1 x 108-2, no quadrivalent was formed but in another combination involving 108-2, 184-2 x 108-2, a quadrivalent was produced in one PMC. Quadrivalents were recognized at a low frequency (0.03 - 0.10) in 184-2 x 108-1, 184-1 x 108-3 and 184-2 x 108-3. While, they were formed at a high frequency (0.46 - 0.74) in hybrids with 109, 195, 1957 and 8915A. As mentioned in Section IV, a minor translocation exists between E1a and E_{1b} and major ones exist between E1a and E2, E3, E4 or E_6. Since no quadrivalent is formed in hybrids of Chinese Spring with E_{1a}, quadrivalents observed in hybrids other than E1a would be due to translocations carried by the derived types of *T. dicoccoides*. In haploid plants of Chinese Spring, bivalents are formed at meiosis and the average frequency ranged from 0.10 to 0.52 (Table 25). Therefore, trivalents formed in 184-1 x 108-5(E_{1a}) are, most probably, due to the homoeologous pairing but not due to translocations between D and A or B genomes of Chinese Spring.

It is clear from the present data that chromosomes of the A and B genomes of Chinese Spring have the same structure as those of the primitive type of *T. dicoccoides* in regard to translocations. This indicates that the chromosome structure of the primitive type of T. *dicoccoides* has been retained unchanged through the evolotional process of the hexaploid wheats and would provide cytogenetical evidence to the primitiveness of the chromosome structure of Chinese Spring. However, in regard to other kind of differentiation, chromosomes of Chinese Spring may not have the primitive hexaploid structure. In two hybrids with E_{1a}, 910 x 8935

Table 24. Mean multivalent and chiasma frequencies and occurrence of multivalents in F_1 hybrids between T. aestivum cv. Chinese Spring and T. dicoccoides

Cross combination	Type*	No.of cells	Freq. of mult.		Xta/ cell	Per cent of cells with multivalents
			III	IV		
184-1 x 108-5	E_{1a}	50	0.06	-	23.86	1III 6.0
910 x 8935	"	100**	-	-	24.13	none
184-1 x 108-2	E_{1b}	30	0.13	-	-	1III 13.3
184-2 x "	"	35	0.29	0.03	-	1III 28.6, 1IV 2.9
184-1 x 108-3	E_{1b}	50	0.04	0.10	-	1IV 8.0, 1III 2.0, 1III+1IV 2.0
184-2 x "	"	50	0.14	0.06	-	1III 14.0, 1IV 6.0
184-1 x 109	E_2	50	0.14	0.46	-	1IV 46.0, 1III 14.0
" x 195	E_3	50	0.06	0.72	-	1IV 68.0, 1III 6.0, 2IV 2.0
910 x 8915A	E_4	47	0.17	0.74	22.74	1IV 63.8, 1III 10.6, 2IV 4.3, 1III+1IV 2.1, 2III 2.1
" x 1957	E_6	50	0.22	0.50	22.14	1IV 50.0, 1III 22.0

* Translocation type of the male parent.

** Two plants were observed.

Table 25. Chromosome pairings at MI in haploid plants of *T. aestivum* cv. Chinese Spring

No. of plants observed	No. of cells per plant	Chromosome pairings		Reference
		I	II	
8	30	20.52 (17-21)*	0.24 (0-2)	Miller and Chapman, 1976
9	ca. 50	20.46 (19.97-20.97)**	0.27 (0.10-0.52)	McGuire and Dvořák, 1982

* Range.

** Range of means.

and 184-1 x 108-5, cells at AI were also observed. Of 260 cells examined in the former, six had a bridge and a fragment. In the latter combination, a bridge with a fragment was observed in six of the 105 cells examined. These hybrids are inferred to be heterozygous for, at least, one paracentric inversion. Because of the lack of the extensive analysis on inversion, the fundamental chromosome structure concerning inversions is not yet determined in *T. dicoccoides*. Nevertheless, these data may show that chromosomes of Chinese Spring have changed structurally by inversion(s) during the process of evolution.

As mentioned in Section II, some controversy exists about the primitiveness of chromosome structure of Chinese Spring. Riley *et al*. (1967) concluded that Chinese Spring has the primitive chromosome structure of the hexaploid wheats. Later, Larsen (1973) suggested that the chromosome structure of Chinese Spring is not so primitive as generally assumed. In these studies, only one strain of *Ae*. *squarrosa*, *T. dicoccoides* or synthetic hexaploid wheat was used without examining the cytogenetical relationthips to other strains.

In the present experiment, however, the chromosome structures of the *dicoccoides* strains used are well clarified through intraspecific hybridization experiments (Sect. IV). As to the structure of the D genome chromosomes, no experiment was made in the present study. However, studies by Kihara *et al*. (1965) clearly show that structural differeniations in chromosomes are very rare in *Ae*. *squarrosa*.

So, it may be concluded that the strain of *Ae. squarrosa* used by Riley and Chapman (1960), most probably, had the fundamental chromosome structure of *Ae. squarrosa*. Therefore, there would be little doubt that Chinese Spring has the primitive chromosome structure of the hexaploid wheats in respect to translocations as concluded by Riley *et al.* (1967). Nullisomic-tetrasomic compensation tests by Sears (1954) also support this conclusion.

3. General discussion

The data obtained in this section show that the chromosomes of the B or G genome of the two wild tetraploid wheats, *T. araraticum* and *T. dicoccoides*, are more frequently involved in translocations than the A genome chromosomes (Table 21).

The tendency that the B genome chromosomes are more frequently involved in translocations was also recognized in the hexaploid wheats (Larsen 1973 and Table 26). Translocations listed in Table 26 had been identified by means of crosses to monosomic or other aneuploid lines of Chinese Spring which have the primitive chromosome structure of the hexaploid wheats. Because these data were collected from many sources, it can not be confirmed whether translocations located on the same chromosome pair are identical or not. Larsen (1973) treated all the identified translocations as equally different even when they were located on the same chromosome set. But this would not be adequate. It is

Table 26. Summary of identified translocations in the hexaploid wheats*

Variety/Stock	Chromosomes involved	No. of translocations	Reference
Indian	3B - 7B	1	Sears, 1953
Thatcher	4A - 6B	1	"
Poso	5B - 7B	1	"
S 615	2B - 3B, 4A - 6B	2	Larson, 1954 (cited by Riley *et al.*, 1967)
Sonora	3A - 7B	1	Baker and McIntosh, 1966
S 2303	4A - 1B	1	"
Eligulate	4A - 6A - 7B	2	"
Holdfast	3B - 3D	1	Riley *et al.*, 1967
Cappelle-Desprez	3B - 3D, 5B - 7B	2	"
Wachtel	1D - 6D	1	Röbbelen, 1968
Poros	7B - 2D	1	Mettin, 1969 (cited by Baier *et al.*, 1974)
Vilmorin 27	5B - 7B	1	The and Baker, 1970 (")
Bersee	5B - 7B	1	Law, 1971 (")
Hybride du Joncqois	3B - 3D, 5B - 7B	2	" (")
Maris Ensign	7B - 2D	1	Larsen, 1973
Synthetic hexaploid	6B - 7D	1	"
Solo	2A-4D, 5B-7B, 7A-7D	3	Baier *et al.*, 1974
Canaleja	4A - 3D, 5B - 7B	2	Vega and Lacadena, 1981 (cited by Vega and Lacadena, 1982)

* Added after Baier *et al.* (1974)

possible that some of the cultivars listed in Table 26 have recieved the same translocation from a common ancestral strain. But translocations involving the different set of chromosomes are, of course, different ones. It is clear from Table 26 that at least 15 different translocations have been recognized in the hexaploid wheats. They are as follows, 2A - 4D, 3A - 7B, 4A - 6A, 4A - 1B, 4A - 6B, 4A - 3D, 6A - 7B, 7A - 7D, 2B - 3B, 3B - 7B, 3B - 3D, 5B - 7B, 6B - 7D, 7B - 2D and 1D - 6D. Of these, ten translocations involve the B genome chromosomes; four between the A and B genomes, three within the B genome, three between the B and D genomes. Three were between the A and D genomes. The remaining two were within the A genome and within the D genome. The chromosome most frequently involved in the translocations is 7B (5 translocations), followed by 4A (4), 3B (3), and 6A, 6B, 3D and 7D (2). Chromosomes that are involved in only one translocation are 2A, 3A, 7A, 1B, 2B, 5B, 1D, 2D, 4D and 6D. It is clear from these data that the B genome chromosomes are most frequently involved in translocations in the hexaploid wheats, followed by the A genome chromosomes and the D genome chromosomes least. It is also clear that translocations are more frequently located on several chromosomes, especially, 7B, 4A and 3B, than the others as was recognized in *T. araraticum*.

In the present study, structural differentiations due to reciprocal translocations were examined systematically. Translocation results from the breakage of chromosomes.

But it is not the only result of chromosomal breakage. Other kinds of chromosomal mutations (inversion, insertion, deficiency and duplication) also occur as the result of chromosomal breakage. The high frequency of the B and G genomes involved in translocations means that the breakpoints are more frequently distributed on chromosomes of these two genomes than on those of the A genome. This strongly suggests that other kinds of structural rearrangements occur more frequently in the B or G genome than in the A (or D) genome. Evidently, inversions were observed in all the intraspecific hybrids of *T. dicoccoides* or *T. araraticum* in which chromosomal behavior was recorded at AI (Sect. IV and V). They were also recognized between the tetraploid and the diploid or hexaploid wheats.

Thus, it was strongly suggested that the B and G genomes are structurally more variable than the A genome and that the D genome is more stable than the A genome. The basis for such a differential structural variability of the genomes would be better sought in the structure of the chromosomes. In several plant species, the breakage of chromosome was often associated with heterochromatic regions. Whittingham and Stebbins (1969) examined chromosomal rearrangements induced by gamma rays in *Plantago insularis* Eastw. and found that breakage positions were usually (72.6% of all breaks) located within heterochromatic segments or at the ends of heterochromatic regions. Such a tendency has been also reported in tomato, *Lycopersicon esculentum* Mill. (Gottschalk

1951; Barton 1954; Rick and Khush 1961; Khush and Rick 1968) and in maize, *Zea mays* L. (Longley 1961). In *Oenothera*, Cleland (1956) reported that natural translocations always involve whole arms, and threfore breaks in or near heterochromatic regions adjacent to the centromere.

By using the Giemsa C-banding technique, Gill and Kimber (1974) compared individual chromosomes of Chinese Spring to those of the diploid species, *T. monococcum*, *Ae. speltoides* and *Ae. squarrosa*. They reported that, "In terms of total heterochromatin per genome in wheat, the B genome was the most heterochromatic, the D genome the least and the A genome slightly more heterochromatic than the D genome." Similar data were obtained by Natarajan and Sarma (1974). This is in parallel to the frequency of breakpoints of translocations in the hexaploid and, also, the tetraploid emmer wheats. In diploid species observed by Gill and Kimber (1974), Iordansky *et al*. (1978) and Teoh and Hutchinson (1983), chromosomes of *Ae. squarrosa* and *T. monococcum* had faint terminal or interstitial bands or both. While, most of the *Ae. speltoides*, the most probable donor of the B and G genomes, chromosomes are characterized by large terminal bands and centric heterochromatin was always present. The C-banding pattern of *T. timopheevi* and *T. araraticum* was observed by Zurabishvili *et al*.(1978). They assumed that the chromosomes rich in heterochromatin belonged to the G genome since chromosomes of *T. monococcum* were poor in heterochromatin. Thus, it is likely that the structural basis for the high frequency of the B and G genomes involved in translocations lies in the abundance of the heterochromatic regions. The high frequency of 4A chromosome involved in translocations in the hexaploid wheats might be explained by this hypothesis because 4A is the only chromosome in the A genome with conspicuous interstitial C-bands (Gill and Kimber 1974).

Another characteristic of the genomes that would be worth mentioning here is the amount of the DNA. From the measurements of the DNA content of the genomes, Furuta (1975) found in *Aegilops* that the unstable genomes referred to by Zohary and Feldman (1962) or modified genomes by Kihara (1954), had a higher DNA content while stable genomes had a lower DNA content than the modified ones. Recently, heterochromatic regions have been shown to contain the repeated DNAs (John and Miklos 1979; Flavell 1980; Hutchinson and Lonsdale 1982). Therefore, genomes rich in heterochromatin, *i. e.*, repeated DNAs are likely to have a higher DNA content. Consequently, the three different characteristics of the genomes assembled here, the amount of heterochromatin, the amount of total DNA and the structural variability, are probably closely related to each other.

VII. GENERAL DISCUSSION

Based on their hypothesis that modified genomes had been established from the introgressive hybridization of the raw amphidiploids, Zohary and Feldman (1962) and Zohary (1966) predicted the presence of intraspecific variation in chromosome structures in tetraploid species of the genera Aegilops and Triticum. They further presumed that such a variation is concentrated in the modified genomes. The present study revealed extensive intraspecific structural differentiations in chromosomes due to translocations in the two wild tetraploid wheats, T. dicoccoides and T. araraticum. It also showed that the B and G genome chromosomes were more frequently involved in these translocations than the A genome chromosomes.

These results may be interpretted to give cytogenetical evidence to their hypothesis. But, such an interpretation would not be valid. According to them, modified genomes had resulted from the introduction of chromosome segments into a genome from another genome, i. e., segmental replacements of a genome with another genome. If this process is also responsible for the intraspecific differentiations of chromosomes, the results would be the segmental asynapsis of chromosomes and consequently univalents would be observed at the MI of intraspecific hybrids. In the present study, however, meiotic irregularities observed at MI were the formation of multivalents and the frequency of univalents was very low. The formation of multivalents was explained by spontaneous reciprocal translocations which had occurred in the fundamental or primitive chromosome structure. Feldman (1963) observed the concentration of structural variation in the S^v genome in *Ae*. *variabilis*. But the structural variations in chromosomes he observed were also reciprocal translocations. Furuta (1981a, b) cuncluded in his studies on intraspecific variation in *Ae*. *ovata*, *Ae*. *variabilis* and *Ae*. *kotschyi* that the main factor of variation in chromosome structures was reciprocal translocations. Therefore, extensive intraspecific variation in chromosome structures so far observed in *Triticum* and *Aegilops* would not give a cytogenetical evidence to the hypothesis by Zohary and Feldman (1962) and Zohary (1966). Consequently, an alternative hypothesis is needed to explain the origin of modified genomes and the formation of species clusters in *Triticum* and *Aegilops*.

Tanaka (1963 and personal communication) classified the diploid species of *Triticum* and *Aegilops* into two groups, those with stable genomes and with unstable genomes, based on the geographical distribution, intraspecific variation and the stability of artificially produced amphidiploids. According to his classification, the A and D genomes are stable but the S genome of section Sitopsis and M and M^u genome of section Comopyrum are unstable. Tanaka (*loc*. *cit*.) concluded that amphidiploids consisting of two stable genomes had remained unchanged but various tetraploid species had differentiated from amphidiploids with a stable and an unstable genomes. In this study, the difference in structural variability was recognized between the B or G genome and the A genome chromosomes. Data on translocations in the hexaploid wheats showed that the D genome is less variable than the A genome. The variability of a genome was assumed to have a close relationship to the structure of the chromosomes, the amount of heterochromatin. So, the present results might give cytogenetical evidence to the stable and unstable genome hypothesis by Tanaka.

The present finding of the different degree of variability of genomes would have some implications in the evolution of the genomes in *Triticum* and *Aegilops*. When a variable and a stable genome are combined in an amphidiploid, structural rearrangements of chromosomes would occur more frequently in the former. Consequently, one of the two genomes of a tetraploid may become more differentiated from its ancestral genome while the other remains relatively unchanged. Thus, a stable genome served as a genetic buffer in the process of the modification of genomes in an amphidiploid. The formation of many modified genomes in *Triticum* and *Aegilops* including the loss of homology of the B and G genomes to the supposed ancestral genome would be explained by the high structural variability of their ancestral genomes.

Many lines of evidence (Sect. II) indicate that *Ae. speltoides* (SS) is the most probable donor of the B and G genomes. The present conclusion that the wild tetraploid wheats had originated in Southern Turkey and Northern Iraq is also in accord with this theory. Of the species belonging to section Sitopsis of *Aegilops*, only *Ae. speltoides* occurs in the Zagros Taurus area in Turkey, Iraq and Iran. Other species of this section, *longissima*, *sharonensis*, *searsii* and *bicornis* are distributed in Egypt, Palestine and Transjordan along eastern coast of the Mediterranean Sea. Probably, the two wild tetraploid wheats had originated from amphidiploids between *Ae. speltoides* and *T. boeoticum* through structural rearrangements of chromosomes belonging to the S genome as was suggested by Tanaka *et al.* (1978, 1979a, b).

According to the present hypothesis, major structural differentiations (translocations and inversions) would be observed more frequently between the B and G genomes than between the A genomes of *T. dicoccoides* and *T. araraticum*. Because of the lack of cytological markers such as telosomes, however, pairing behavior of individual chromosomes of these two species can not be traced, at present. Instead, Dvořák and Appels (1982) observed structural differentiation in hybrids between *T. araraticum* and *T. aestivum* cv. Chinese Spring. They found that the numbers of translocation and inversion differences between chromosomes of the two species were not substantially greater in the B and G genomes than in the A genome. Consequently, they considered the hypothesis of uneven genome differentiation in polyploids by differential accumulation of major structural changes to be very unlikely. However, the numbers of translocations and inversions between the B and G genomes obtained by them would be underestimated: The amount of pairings between the B genome telosomes and the corresponding chromosomes of the G genome was much lower than that between the A genome chromosomes. They crossed two lines of *T. araraticum* to ditelosomics of Chinese Spring. In hybrids involving one line of *T. araraticum*, 73.0 per cent of the A genome telosomes paired while only 23.7 per cent of the B genome telosomes paired with corresponding chromosomes of *T. araraticum*. In hybrids involving the other *araraticum* line, these values were 60.2 per cent and 14.3 per cent, respectively. Feldman (1966) obtained similar data for *T. timopheevi*. Therefore, when the pairing frequencies of the A and B genome telosomes were taken into account more precisely, the numbers of translocations and inversions between the B and G genomes will be in great excess of those between the A genomes. Consequently, the data obtained by Dvořák and Appels (1982) do not seem to be inconsistent with the present hypothesis.

It is also expected that translocations and inversions would rarely occur in diploid species with stable genomes, A, D and C^u, while they would be found frequently in those with variable genomes, S, S^1, Sb, M and M^u. In the wild diploid wheat, *T. boeoticum* (AA), translocations are found only in strains collected in Transcaucasus (sect. VI). Translocations are also rare in *Ae. squarrosa* (DD) (Kihara *et al*. 1965). Species of sections Sitopsis and Comopyrum were assumed to have variable genomes. In these two sections, intravarietal chromosome differentiation due to translocation has been reported in spite of the small number of strains examined (Kihara 1937, 1954; Tanaka 1955; see Sect. II). Studies on intraspecific structural variation in chromosomes of the diploid species is quite limited in the number of species and the number of strains examined. Nevertheless, the data obtained so far are likely to support the present hypothesis.

Consequently, it was concluded that a varying degree of differentiation between ancestral genomes of diploid species and corresponding genomes in polyploid species observed in *Triticum* and *Aegilops* resulted from differential structural variability of the ancestral genomes.

VIII. SUMMARY

1) Intraspecific differentiation in chromosome structures in the two wild tetraploid wheats, Triticum dicoccoides (Körn.)Schweinf. and T. araraticum Jakubz. was analyzed through hybridization experiments to obtain information concerning the place of origin and the course of dissemination of these species.

In both T. dicoccoides and T. araraticum, the main factor of variation was a reciprocal translocation. Inversions were also observed but they were not analyzed extensively.

In T. dicoccoides, six translocation types, E_1 - E_6, differing with major reciprocal translocations were recognized. Of 46 dicoccoides strains observed, 38 belonged to the type E_1. Seven were of the other five types. One had chromosome structures other than E_1, but its translocation type remains unidentified. The type E_1 was further divided into two subtypes, E_{1a} and E_{1b}, by a minor reciprocal translocation. Of 38 E_1 strains, 12 were E_{1a}, two were E_{1b} and 24 remained unclassified. The number of translocations between E_{1a} and the other types was smaller than that found between the types other than E_1. So, the type E_1 was assumed to have the fundamental chromosome structure of T. dicoccoides. Further, the geographical distribution of E_{1a} and E_{1b} suggested that the type E_{1a} is the fundamental type of E_1.

Four translocation types were found in Turkey and three in Israel but the types other than E_1 were not recognized in Iraq and Iran. This and other evidence suggested that *T. dicoccoides* had originated in Southern Turkey and its adjacent region in Northern Iraq and that its distribution area was first extended to the Palestine area and then to the southern part of the Zagros Mountains.

In *T. araraticum*, 15 translocation types, T1 - T15, differing with major reciprocal translocations were recognized. Of 139 strains observed, 79 were of type T_1, and 21 strains were of the other 14 types. The remaining 39 strains had chromosome structures other than T_1, but their translocation types remain unidentified. The number of translocations between T_1 and the other 14 types was smaller than that observed among the types other than T_1. The type T_1 was found in all the regions where samples were collected. From these observations, it was concluded that the type T_1 is the fundamental chromosome structure of *T. araraticum* and that the other 14 types were derived from T_1 by one to three reciprocal translocations.

Strains of the derived types were found in the whole distribution area. In Southeastern Turkey, most strains were of the fundamental type. While, a population in South-central Turkey was marked by its very low frequency of the fundamental type. The greatest variation was found in Rowanduz region in Northern Iraq suggesting that *T. araraticum* might have originated in Northern Iraq.

Possibly, *T. dicoccoides* and *T. araraticum* would have originated from amphidiploid between *T. boeoticum* and *Ae*.

speltoides in the center of the Fertile Crescent, Southeastern Turkey and Northern Iraq.

2) In order to compare the degree of structural differentiation of chromosomes belonging to the different genomes, chromosomes involved in translocations in the two wild tetraploid wheats were identified through crossing experiments with the diploid wheats, *T. boeoticum* Boiss. and *T. monococcum* L. Concurrently, structural differentiations of chromosomes in the diploid wheats and those between *T. dicoccoides* and *T. aestivum* L. cv. Chinese Spring were examined.

In the diploid wheats, ten strains were examined and two *boeoticum* strains from Transcaucasus had a translocation relative to other eight strains of *T. boeoticum* and *T. monococcum* from various regions. Most of the hybridizations with the tetraploid wheats were made by using the strains having the fundamental chromosome structure of the diploid wheats.

Of five major translocations in *T. dicoccoides*, three were among the B genome chromosomes, one was between the A and B genomes and one was among the A genome chromosomes. Minor translocation between $E1_a$ and $E1_b$ was assumed to be that between the A and B genomes. In *T. araraticum*, chromosomes involved in translocations were not identified completely. However, the results showed that 10 translocations were among the G genome chromosomes, 5 were between the A and G genomes and two were among the A genome chromosomes.

From the hybridization experiments between Chinese Spring and T. dicoccoides of six translocation types, it was revealed that Chinese Spring had no translocation between the original E_{1a} type of T. dicoccoides. This confirmed that Chinese Spring has the primitive chromosome structure of the hexaploid wheats. Thus, it was possible to compare the present data to the identified translocations in the hexaploid wheats reported so far.

The present results and the data obtained in the hexaploid wheats clearly showed that the B and G genome chromosomes are more frequently involved in translocations than those of the A and D genomes. This would indicate that the former two genomes are structurally more variable than the latter. The differential variability of the genomes revealed here would have some implications in the evolution of the genomes. In many tetraploid species of Triticum and Aegilops, one of the two genomes are more differentiated from its ancestral genome while the other genome remains relatively unchanged. This is likely to be caused by the differential structural variability of the genomes.

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APPENDIX I.

Identification of the translocation type for each strain of _T._ _dicoccoides_ and _T._ _araraticum_

APPENDIX I.

Identification of the translocation type for each strain of T. dicoccoides and T. araraticum

In this appendix, detailed data on the occrrence of multivalents in hybrids between strains of T. dicoccoides or between strains of T. araraticum (or between T. araraticum and T. timopheevi) are presented and the method of identifying the chromosome type differing with reciprocal translocations (translocation type) is described.

As mentioned in Sections IV and V, the translocations found in the strains of T. dicoccoides or T. araraticum can be classified into major and minor translocations by the frequency with which multivalents are observed at the MI of hybrids between strains, i.e., the hybrid with a frequency of quadrivalents larger than 0.5 per cell was regarded to be heterozygous for one major translocation, and that with a frequency smaller than 0.5 was regarded to have minor translocation. When the hybrid between two strains has two or more translocations, the frequency of cells with a certain chromosome configuration may become less than 0.5. For example, if the hybrid between strains A and B has two translocations on different chromosome pairs, two quadrivalents are expected to be found at the meiosis in hybrid A x B. If each translocation produces a quadrivalent at a probability of 0.5, the expected number of cells with two quadrivalents will be $0.25(=0.5^2)$. Therefore the formation of several quadrivalents and/or higher valency of chromosome associations (sexivalent, octavelent etc.) were, in some cases, inferred to indicate the presence of several major translocations even when the number of cells with two or more quadrivalents was small. Because of the limited kinds of hybrids, the present grouping of translocation types is based mainly on major translocations. Namely, two strains were grouped into one translocation type when they had no major translocation between them. Therefore, the present grouping does not necessarily mean that the chromosome structures of strains belonging to the same group are identical in every respect. There may be structural differences in the chromosomes caused by minor reciprocal translocations, inversions, deficiencies, duplications, etc., within one translocation type.

For the sake of brevity, III, 2IV and IV + VI, and so on are used in this appendix to represent a trivalent, two quadrivalents and a quadrivalent plus a sexivalents, and so on, respectively.

1. *T. dicoccoides*

Kawahara and Tanaka (1978) analyzed translocations in *T. dicoccoides* and reported the following three translocation types.

EA, 108-1, 108-2, 108-5, 110, 198, 8536, 8541, 8736A, 8736B, 8737, 8804, 8816B, 8817, 8821A, 8935, 8937B, 8941, 8943;

EB, 109;

EC, 195.

They concluded that the type EA was the standard chromosome structure in this species because many strains belonged to this type. The name of the translocation types was then changed from EA to E_1, EB to E_2 and EC to E_3 (Kawahara and Tanaka 1981). In the present study, further analysis was made using several strains reported by Kawahara and Tanaka (1978) as testers.

Per cent of cells with the indicated multivalents in F_1 hybrids between strains of *T. dicoccoides* are summarized in Table Ia. Data obtained by Kawahara and Tanaka (1978) are included for comparison. The asterisk(*) attached to the stock number indicates that its translocation type was already reported.

a. Type E_1

Those strains which have no major translocation between 108-3, 108-5 or other strains of the type E_1 were classified into this type. Stock numbers and the occurrence of multivalents in some of the hybrids are described below.

108-1* IV was observed at a very low frequency (4.0%) in 108-1 x 108-3.

108-2* No multivalent was observed in 108-2 x 108-3.

108-3* A tester strain (Kawahara and Tanaka 1978).

108-4 IV or III was observed at a low frequency (10.5% each) in 108-4

	x 108-3.
108-5*	A tester strain. IV was observed at a very low frequency (1.6%) in 108-5 x 108-3.
110*	Only 2.4% of the PMCs had IV in 110 x 108-3.
198*	IV was observed at a low frequency (17.4%) in 198 x 108-2.
1921	IV or III was observed at a low frequency in hybrids with E_1; 21.2% in 1959B x 1921 and 12.1% in 1921 x 8817.
1947	No multivalent was observed in 1947 x 8935(E_1).
1948	23.0% of the PMCs had IV in 1948 x 108-3. This indicates that 1948 has no major translocation between 108-3.
1951	No multivalent was observed in 1951 x 108-3.
1953	No multivalent was observed in 1953 x 8935(E_1).
1955	No multivalent was observed in 1955 x 1991(E_1).
1959A	Only one cell (3.0%) in 1959A x 8937B(E_1) had IV.
1959B	No multivalent was observed in 1959B x 8536(E_1).
1972B	17.6% of the PMCs in 1972B x 108-3 had III or IV.
1974	No multivalent was observed in 1974 x 1991(E_1).
1976B	In 1976B x 108-3, 7.1% of the cells had IV.
1978B	III or IV was observed in 30.0% of the cells in 1978 x 108-3 and in 11.2% of the PMCs in the reciprocal cross. No multivalent was formed in 1978B x 1959B(E_1).
1991	8.8% of the PMCs in 1991 x 108-3 had III or IV.
8528A	Only one cell (2.0%) in 8528A x 108-3 had IV.
8536*	IV was observed at a very low frequency (2.0%) or no multivalent was observed in 8536 x 108-5.
8539*	2.0% of the cells in 8539 x 108-3 had IV.
8541*	36.1% of the PMCs in 8531 x 108-3 had III or IV. No multivalent

was observed in 8541 x 108-5.

8736A* 2.0% of the PMCs in 8736A x 108-5 had IV.

8736B* III was observed at a very low frequency (6.0%) in 8736B x 108-5.

8737* 40.0% of the PMCs had IV in 8737 x 108-3. In 8737 x 108-5 III or IV was observed at a low frequency (12.2%) or no multivalent was observed.

8804* No multivalent was observed in 8804 x 108-3.

8808 IV was observed in 19.7% of the PMCs in 108-3 x 8808.

8816A III or IV was observed in 32.1% of the PMCs in 8816A x 108-2.

8816B* IV was observed at a very low frequency (4.0%) in 8816B x 108-3.

8817* IV was observed at a low frequency (10.3%) in 8817 x 108-2, but in 8817 x 108-5, no multivalent was observed.

8821A* IV was observed in 6.0% of the PMCs in 8821A x 108-3.

8821C 15.2% of the PMCs had IV in 8821C x 108-3 and 4.0% of the cells in 8821 x 8943(E_1) had IV.

8935* No multivalent was observed in 8935 x 108-5 but III or IV was produced in 14.9% of the PMCs in 8935 x 108-3.

8937B* No multivalent was observed in hybrids with 108-3 or 108-5.

8941* 4.0% of the PMCs of 8941 x 108-5 had IV.

8942 III or IV was observed at a low frequency (22.2%) in 8942 x 108-3.

8943* No multivalent was observed in 8943 x 108-5 though III or IV was observed in 36.4% of the PMCs in 8943 x 108-3.

b. Subgrouping of the type E_1 by minor translocation

In the course of this study, I noticed that when 108-2, 108-3 or 108-5 were crossed to a common female parent of the type E_1, multivalents (III or IV) were produced or the frequency of multivalents was higher in the hybrids between 108-2 or 108-3 and the E_1 type strains but not in those between 108-5 and the E_1 type strains (Table Ib). Among the above three strains, no multivalent was observed in 108-2 x 108-3 but in 108-5 x 108-3, IV was observed at a very low frequency (1.6%). These observations would indicate that there is a minor translocation between 108-2 or 108-3 and several other E_1 type strains including 108-5. In Section VI, I mentioned that this minor translocation could be located on a chromosome of the A genome and that of the B genome. Since the type E_1 was thus considered to be heterogeneous for minor translocations, an attempt was made to identify chromosome types differing with minor translocations. As shown in Table Ib, no multivalents were found in the hybrids between 108-5 and 8541, 8736B, 8817, 8935, 8937B or 8943. But the frequency of multivalents varied greatly (0.0% - 36.4%) in the hybrids between 108-3 and these strains. That is, the frequency of quadrivalents produced by the estimated minor translocation varied greatly in different hybrid combinations. Therefore, for the sake of accuracy, each strain was classified into a subgroup only when two or more hybrids were available.

First, 108-5 and 108-3 were chosen as the standard E_{1a} and E_{1b} strain, respectively, based on the observations descrived above. Strains were included into each type when either of the following criteria was fullfilled:

1) No multivalent was observed in hybrids with E_{1a} but multivalents were observed at a low frequency in hybrids with E_{1b} (8541, 8736B, 8935 and 8943);
2) No multivalent was observed in two or more hybrids with E_{1a} (8536, 8736A, 8817 and 8821C).

Three strains (within which no multivalent was observed) that fulfil the above criteria were also included in the type E_{1a}. They were 1959B, 1976B and 1978B. Based on a similar rationale, 108-2 was included into E_{1b}. The average frequency of cells with multivalents in 11 hybrids between E_{1a} and E_{1b} was 16.2% (1.6 - 36.4%). Among the strains of the E_{1a} type thus identified, IV was sometimes observed at a very low frequency (2.4 - 4.0%). This may suggest some other minor translocations within the type E_{1a}, but they were not analyzed.

c. Type E_2

109*: Kawahara and Tanaka (1978) observed IV in 65% of the cells in 109 x 108-3 and recognized this to have a chromosome structure different from that of 108-3. In hybrids with E_{1a} strains, IV was observed at a high frequency; 78.8% in 1976B x 109, 87.9% in 1978B x 109 and 82.6% in 8536 x 109. In these hybrids, VI was also observed at a low frequency, 3.0%, 3.0% and 8.7%, respectively. VI was also observed (8.4%) in 109 x 108-3(E_{1b}). The chromosome structure of strain 109 thus differs from that of E_{1a} or E_{1b} by two translocations, a major one and a minor one, having a pair of chromosomes in common.

d. Type E_3

195*: The chromosome structure of this strain differs from that of 108-3 by one translocation and from that of 109 by two translocations (Kawahara and Tanaka 1978). In hybrids with E_{1a}, 195 x 1978B, 93.9% of the PMCs had IV and 6.1% had 2IV, indicating the presence of a major and a minor translocation on different chromosome pairs. In 109(E_2) x 195, 2IV was observed in 76.3% of the cells and 60.0% of the PMCs had 2IV in the reciprocal cross.

e. Type E_4

8915A and 8915B: These two strains were establised by selfing from two different plants belonging to a single original sample. Meiosis was normal with 14 bivalents in a hybrid between them. IV was observed in about 60% of the cells in hybrids with 108-3 or 108-5. Most of the cells had VI in hybrids with 109; 87.9% in 8915A x 109 and 78.8% in 8915B x 109. 2IV was observed at a high frequency in hybrids with 195; 75.8% in 8915A x 195 and 60.6% in 8915B x 195. The frequency of IV was smaller than 0.5 in hybrids with several strains of E_{1a} type such as 8536, 8736A, 8817, 8821C, 8935 and 8943. However, all the PMCs had IV in hybrids with another strain of E_{1a}, 1978B. Therefore, it was inferred that the hybrid between E_1 and 8915A or 8915B has one major translocation. The high frequency of VI in hybrids with 109 and of 2IV in hybrids with 195 would support this assumption. Since chromosome structures of these two strains differ from E_1, E_2 and E_3, they were classified into the type E_4.

f. Type E_5

1945: IV was observed in all or most of the PMCs in hybrids with the E_{1a} type; 100% in 1945 x 1959B, 93.9% in 1945 x 1976B and 97.0% in 1945 x 1978B. 2IV was observed at a high frequency in hybrids with E_2, 109 x 1045 (84.8%), and E_4, 1945 x 8915A (68.2%). In 195(E_3) x 1945, 56.0% of the cells had VI and 24.0% had 2 III. Thus, the chromosome structure of this strain is different from that of type E_1, E_2, E_3 or E_4 by one or two translocations and was named type E_5.

g. Type E_6

1952 and 1957: IV was observed in two cells (6.1%) in 1957 x 1952. Because of the absence of a mojor translocation, these two strains were grouped into one type. IV was observed in 69.7% of the cells in 1952 x 108-3 and in 90.9% in 1957 x 8536(E_{1a}). 2IV was observed at a high frequency in hybrids with E_2 (77.1% in 1952 x 109 and 72.7% in 1957 x 109), with E_3 (83.6% in 1957 x 195) or with E_4 (72.7% in 1952 x 8915A). Most PMCs (90.0%) in 1957 x 1945(E_5) had 2IV. Thus, the chromosome structure of these two strains is different from that of type E_1, E_2, E_3, E_4 or E_5 and was named the type E_6.

h. Unidentified

1949: (neither E_1 nor E_2): IV was observed at a high frequency (76.3%) in 1949 x 108-3. All the PMCs showed IV in 1959B(E_{1a}) x 1949 and most of the cells (90.0%) in 1976B(E_{1a}) x 1949 had IV. 2IV was observed in a hybrid with 109 (69.7%). It is clear from these data that this strain has a chromosome structure different from that of type E_1 and E_2, but the translocation type is unknown.

Table Ia. Occurrence of multivalemts in F_1 hybrids between strains of *T. dicoccoides*

Cross combination	No. of cells observed	Per cent of cells with multivalents
108-1 x 108-3	50	1IV 4.0
108-2 x 108-3	"	none
108-3 x 195	38	1IV 89.5, 2IV 5.2, 1III 2.6
" x 1957	33	1IV 54.5, 2IV 27.3, 1III 3.3, 1III+1IV 3.3
" x 1978B	54*	1IV 9.3, 1III 1.9
" x 8808	66*	1IV 19.7
108-4 x 108-3	38	1IV 10.5, 1III 10.5
108-5 x 108-3	64	1IV 1.6
109 x 108-3	83	1IV 65.1, 1VI 8.4, 1III 3.6, 2III 2.4
" x 195	38	2IV 76.3, 1IV 15.8, 1III+1IV 5.3, 1III 2.6
109 x 1945	33	2IV 84.8, 1III+1IV 9.1, 1IV+1VI 6.1
" x 8808	33	1IV 78.8, 1III 15.2, 1 V 3.0, 1VI 3.0
110 x 108-3	83	1IV 2.4
195 x 108-3	25	1IV 100
" x 109	33	2IV 60.6, 1IV 27.3, 1III+1IV 6.1, 1VI 3.0
" x 1978B	"	1IV 93.9, 2IV 6.1
" x 1945	25	1VI 56.0, 2III 24.0, 1IV 12.0, 1V 4.0, 1IV+1VI 4.0
" x 8808	66*	1IV 65.2, 2IV 15.2, 1III 10.6, 1III+1IV 6.1, 1VI 1.5
198 x 108-2	23	1IV 17.4
1921 x 108-2	33	1IV 54.5, 1III 9.1
" x 109	30	2IV 73.3, 1VI+1VI 13.3, 1IV 10.0, 1III+1IV 3.3
" x 195	66*	1IV 95.5, 1III 3.0
" x 8817	33	1IV 9.1, 1III 3.0
" x 8915A	33	1IV 87.9, 2IV 9.1
1945 x 1921	33	1IV 97.0, 2IV 3.0
" x 1959B	"	1IV 100
" x 1976B	"	1IV 93.9, 1III+1IV 3.0
" x 1978B	"	1IV 97.0
" x 8915A	66*	2IV 68.2, 1IV 27.3, 1III+1IV 3.0, 1III 1.5

* Two plants were observed.

Table Ia. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
1947 x 8935	33	none
1948 x 108-3	74**	1IV 23.0
" x 109	33	1IV 90.9
" x 1921	33	1IV 3.0
1949 x108-3	38	1IV 76.3, 1III 10.5
" x 109	33	2IV 69.7. 1IV 15.2, 1III+1IV 9.1, 1Ⅲ 3.0, 2Ⅲ 3.0
" x 1921	"	1IV 90.9, 1III+1IV 3.0
1951 x 108-3	"	none
" x 109	66*	1IV 89.4, 1III 3.0, 2III 1.5
1952 x 108-3	33	1IV 69.7
" x 109	35	2IV 77.1, 1IV 17.1, 1VI 2.9, 1VⅢ 2.9
" x 1921	33	1IV 81.8, 2IV 15.2
" x 8915A	33	2IV 72.7, 1IV 21.2, 1III+1IV 6.1
1953 x 8935	"	none
1955 x 1991	"	"
1957 x 109	"	2IV 72.7, 1IV 18.2, 1VI 3.0, 1III+1IV 3.0
" x 195	55*	2IV 83.6, 3IV 9.1, 1IV 3.6, 1III+2IV 3.6
" x 1945	33	2IV 90.9, 1IV 9.1
" x 1952	"	1IV 6.1
" x 8536	"	1IV 90.9
1959A x 109	"	1IV 87.9, 1VI 12.1
" x 8937B	"	1IV 3.0
1959B x 1921	"	1IV 21.2
" x 1949	"	1IV 100
" x 8536	"	none
1972B x 108-3	34	1IV 14.7, 1III 2.9
" x 8915A	33	1IV 90.9, 1III 3.0
1974 x 1991	"	none
" x 8915A	"	1IV 93.9
1976B x 108-3	28	1IV 7.1
" x 109	33	1IV 78.8, 1III 15.2, 1VI 3.0
" x 1949	"	1IV 90.9, 1III 3.0
" x 1959B	"	none
" x 1978B	"	"

Table Ia. (continued)

Cross combinations	No. of cells observed	Per cent of cells with multivalents
1978B x 108-3	50	1IV 28.0, 1III 2.0
" x 109	33	1IV 87.9, 1VI 3.0
" x 1957	"	1IV 63.6
" x 1959B	"	none
" x 8915A	"	1IV 100
1991 x 108-3	34	1IV 5.9, 1III 2.9
" x 109	33	1IV 87.9, 1III 6.1
8528A x 108-3	51	1IV 2.0
8536 x 108-2	58*	1IV 10.3
" x 108-5	50	1IV 2.0
" x " **	27	none
" x 109	23	1IV 82.6, 1VI 8.7, 1III 4.3
" x 8821C	34	1IV 2.9
" x 8915B	50	1IV 38.0, 1VI 2.0
" x 8943	25	none
8539 x 108-3	50	1IV 2.0
8541 x 108-3	33	1IV 30.3, 1III 6.1
" x 108-5	50	none
8736A x 108-5	"	1IV 2.0
" x 8536	22	none
" x 8817	50	1IV 4.0
" x 8821C	"	1IV 2.0
" x 8915B	"	1IV 28.0
" x 8943	37	none
8736B x 108-3	50	1III 6.0
" x 108-5	"	none
8737 x 108-3	25	1IV 40.0
" x 108-5	100*	none
" x " **	74	1IV 10.8, 1III 1.4
8804 x 108-3	50	none

** Observed in different years.

Table Ia. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
8816A x 108-2	28	1IV 21.4, 1III 10.7
" x 109	48	1IV 81.3, 1VI 10.4, 2IV 4.2
8816B x 108-3	50	1IV 4.0
8817 x 108-2	29	1IV 10.3
" x 108-5	50	none
" x 8536	"	"
" x 8821C	"	"
" x 8915B	"	1IV 22.0
" x 8935	23	none
" x 8943	50	"
8821A x 108-3	"	1IV 6.0
8821C x 108-3	66*	1IV 15.2
" x 8943	50	1IV 4.0
8915A x 108-3	67	1IV 62.7, 1III 9.0, 2IV 1.5
" x 109	33	1VI 87.9, 1IV 12.1
" x 195	"	2IV 75.8, 1IV 18.2, 1III+1IV 6.1
" x 1921	33	1IV 75.8, 2IV 21.1, 1III 3.0
" x 8915B	66*	none
8915B x 108-3	38	1IV 60.5, 1III 18.4, 1III+1IV 2.6
" x 108-5	61	1IV 57.4, 1III 3.3
" x 109	33	1VI 78.8, 1IV 12.1, 2III 6.1, 1 III 3.0
" x 195	"	2IV 60.6, 1IV 36.4
" x 8821C	50	1IV 28.0
8935 x 108-3	54*	1IV 13.0, 1III 1.9
" x 108-5	50	none
" x 8536	"	"
" x 8736A	"	"
" x 8821C	"	"
" x 8915B	"	1IV 28.0
" x 8943	"	none

Table Ia. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
8937B x 108-3	50	none
" x 108-5	"	"
8941 x 108-2	55*	1IV 54.5, 1III 3.6
" x 108-5	50	1IV 4.0
8942 x 108-2	24*	1IV 20.8, 1III 4.2
" x 108-3	50	1IV 20.0, 1III 2.0
" x 195	33	1IV 90.9, 2IV 3.0
8943 x 108-3	"	1IV 30.3, 1III 6.1
" x 108-5	50	none
" x 8536	"	"
" x 8915A	"	1IV 24.0

Table Ib. Occurrence of multivalents in F_1 hybrids of <u>T. dicoccoides</u> involving 108-2 or 108-3 and 108-5 *

Cross combination	No. of cells observed	Cells with multivalents (%)
8536 x 108-2	58	1IV 10.3
" x 108-5	50	1IV 2.0
" x "	27	none
8541 x 108-3	33	1IV 30.0, 1III 6.1
" x 108-5	50	none
8736B x 108-3	"	1III 6.0
" x 108-5	"	none
8737 x 108-3	25	1IV 40.0
" x 108-5	100	none
" x "	74	1IV 10.8, 1III 1.4
8817 x 108-2	29	1IV 10.3
" x 108-5	50	none
8935 x 108-3	54	1IV 13.0, 1III 1.9
" x 108-5	50	none
8937B x 108-3	"	"
" x 108-5	"	"
8941 x 108-2	55	1IV 54.5, 1III 3.6
" x 108-5	50	1IV 4.0
8943 x 108-3	33	1IV 30.3, 1III 6.1
" x 108-5	50	none

* Extracted from Table Ia.

2. *T. araraticum*

Various degree of structural differentiation in chromosomes involving several translocations have been reported in hybrids involving *T. araraticum* and *T. timopheevi* (see Sect. II). In *T. araraticum*, Tanaka and Ichikawa (1972) reported intraspecific differentiation of chromosome structures by a reciprocal translocation. Further, Tanaka and Ishii (1975) analyzed translocations in *T. timopheevi* and *T. araraticum* from Transcaucasus and reported three chromosome types differing with reciprocal translocations. Using the three strains reported by Tanaka and Ichikawa (1972) and by Tanaka and Ishii (1975) as testers, Kawahara and Tanaka (1977) examined cytogenetical differentiations in *T. araraticum* from Turkey and Iraq and reported six chromosome types differing with reciprocal translocations. The six chromosome types and the stock numbers belonging to these types are as follows (Kawahara and Tanaka 1977, Table 3):

A,	196-1
B,	196-2, 1901, 1902, 1903, 1904, 1905, 1906, 8718A, 8797, 8827, 8940
C,	1908A
D,	8714A, 8719
E,	8732
F,	8784.

Later, some other strains were reported to belong to the type B (Tanaka *et al.* 1979b). They are 8819, 8821B, 8822, 8827, 8873, 8882, 8912, 8924, 8928 and 8948.

In the present study, a further analysis was made using as testers several strains used in the earlier studies. Per cent of cells with the indicated multivalents in F_1 hybrids between strains of *T. araraticum* or between *T. araraticum* and *T. timopheevi* are summarized in Table Ic. Data obrained by Kawahara and Tanaka (1977), Tanaka *et al*. (1979b) and Kawahara and Tanaka (1981) were included in this table. The asterisk(*) attached to the stock number indicates that its translocation type was already reported by Kawahara and Tanaka (1977) and Tanaka *et al*. (1979b).

In the present study, the name of the translocation types was changed as follows;

Kawahara and Tanaka (1977) Tanaka *et al*. (1979a) Kawahara and Tanaka (1981)	Present study
A	T_2
B	T_1
C	T_3
D	T_6
E	T_4
F	T_8
G	T_{14}

Types T_5, T_7, T_9, T_{10}, T_{11}, T_{12}, T_{13} and T_{15} were newly identified in the present study.

a. Type T_1

Those strains which have no major translocation between 107-1 of *T. timopheevi* or several T_1 type strains of *T. araraticum* reported so far were classified into this type. The stock numbers and the occurrence of multivalents in some of the hybrids are described below.

196-2* As was reported by the earlier works (Tanaka and Ichikawa 1972; Tanaka and Ishii 1975), no multivalent was observed in 196-2 x 107-1.

1914 No multivalent was observed in 1914 x 107-1.

1923	No multivalent was observed in a hybrid with 107-1.
1924	" "
1925	" "
1926A	" "
1927	" "
1928	" "
1929	" "
1931	" "
1932	" "
1933	Only one cell (1.6%) in 1933 x 107-1 had IV.
1934	IV was observed in one PMC (3.0%) in 1934 x 107-1.
1935	No multivalent was observed in a hybrid with 107-1
1936	" "
1937	" "
1939	" "
1960	IV was observed at a low frequency (12.9%) in 1960 x 107-1.
1963	No multivalent was observed in a hybrid with 107-1.
1964	" "
1965	" "
1969	" "
1978A	" "
8456	No multivalent was observed in a hybrid with 8561(T_1).
8469	" "
8478	" "
8491	" "
8528A	IV was observed at a very low frequency (2.6%) in 8528A x 107-1.
8529	No multivalent was observed in 8529 x 107-1.

8543	No multivalent was observed in 8543 x 8561(T_1).
8551	Only 2.8% of the PMCs in 8551 x 8561 had IV.
8561	No multivalent was observed in 8761(T_1) x 8561 and 8924(T_1) x 8561.
8593	IV was observed at a very low frequency (2.0%) in 8593 x 107-1.
8597	Only 3.8% of the cells in 8597 x 8561(T_1) had IV.
8616	No multivalent was observed in a hybrid with 8561.
8673	" "
8697	" "
8700	No multivalent was observed in 8731(T_1) x 8700.
8707	IV was observed at a very low frequency (3.3%) in 8707 x 8700(T_1).
8709	No multivalent was observed in 8709 x 8700(T_1).
8711	No multivalent was observed in a hybrid with 8561.
8712	" "
8718A*	According to the unpublished raw data obtained by Tanaka and Ishii (1973) cited by Kawahara and Tanaka (1977), no multivalent was observed in a hybrid with 107-1. Similarly, no multivalent was observed in 8561(T_1) x 8718A in the present study.
8724	IV was observed at a very low frequency (4.2%) in 8724 x 8718A(T_1).
8731	No multivalent was observed in 8731 x 107-1.
8735	III or IV was observed at a very low frequency (3.0% or 6.1%) in hybrids with 107-1.
8742	No multivalent was observed in 8742 x 8718A(T_1).
8761	No multivalent was observed in 8761 x 107-1.
8770	No multivalent was observed in 8770 x 8761(T_1).
8779	No multivalent was observed in 8779 x 8561(T_1).
8797*	III or IV was observed at a very low frequency (13.1%) in 8797 x 107-1.

8799B	No multivalent was observed in 8799B x 107-1.
8802	Only 2.9% of the PMCs had IV in 8802 x 8761(T_1).
8819*	No multivalent was observed in 8819 x 8827(T_1).
8821B*	No multivalent was observed in 8821B x 107-1.
8822*	No multivalent was observed in 8822 x 8827(T_1).
8827*	No multivalent was observed in a hybrid with 107-1.
8831	" "
8873*	No multivalent was observed in a hybrid with 107-1 (unpublished data obtained by Tanaka and Ishii (1973) cited by Tanaka *et al.* (1979b)).
8880	No multivalent was observed in a hybrid with 107-1.
8882*	2.0% of the cells had IV in 8882 x 107-1 (unpublished data obtained by Tanaka and Ishii (1973) cited by Tanaka *et al.* (1979b)).
8884	3.0% of the cells had IV in 8884 x 107-1.
8890	No multivalent was observed in 8890 x 107-1.
8907	III or IV was observed at a low frequency (8,0%) in 8907 x 107-1.
8912*	No multivalent was formed in 8912 x 8709(T_1) nor 8924(T_1) x 8912.
8913	No multivalent was observed in a hybrid with 107-1.
8924*	" "
8926	" "
8928*	" "
8933	" "
8940*	" "
8947	" "
8948*	No multivalent was observed in hybrids with 8718A(T_1) nor with 8947(T_1).

b. Type T_2

196-1*: The presence of a reciprocal translocation in the hybrid between 196-1 and 107-1 or 196-2 which was reported by Tanaka and Ichikawa (1972) and by Tanaka and Ishii (1975), was further confirmed in this study on the basis of the meiotic behavior in the hybrids with the T_1 type strains, 1914, 1969, 8851, 8770, 8802, 8819 and 8913. Forty per cent to 64.7% of the PMCs had IV in these hybrids. Cells with 2IV were also observed, i. e., in 3.3% of the hybrids with 1914, 11.8% of those with 1969, 3.0% of those with 8551, 14.8% of those with 8802, 3.1% of those with 8819 and 21.2% of those with 8913. Two cells (6.7%) with VI were observed in 1914 x 196-1. Therefore, it is probable that this strain is different from the T_1 type strains in that it has two translocations, a major one and a minor one. Consequently, type T_2 was assigned for this strain.

c. Type T_3

1907A, 1908A*, 1909A and 1909B: Hybrids among these four strains formed no multivalents (1908A x 1909B, 1909A x 1907A, 1909A x 1908A and 1909B x 1907A). Most of the PMCs (88.0 - 97.0%) had IV in hybrids with strains of T_1, 1907A x 107-1, 1909A x 107-1, 1909B x 107-1, 1933 x 1908A, 1963 x 1908A and 8926 x 1908A. Neither VI nor 2IV was observed. Hybrids with 196-1(T_2) had VI as reported by Tanaka and Ishii (1975) (66.7% in 1907A x 196-1, 58.0% in 1908A x 196-1 and 58.6% in 1909B x 196-1). In these hybrids, IV + VI and/or Ⅲ + VI, probably caused by the minor translocation carried by 196-1, were also observed. Thus, the chromosome structure of these four strains differs from that of T_1 and T_2 and they were classified into type T_3.

d. Type T_4

8567, 8572 and 8732*: No multivalent was observed in the hybrids between these strains (8567 x 8572, 8567 x 8732, 8732 x 8572). The hybrids between any of these strains and a T_1 type strain were suggested to have one major translocation because thay had IV at a high frequency. IV was observed in 79.2% of the PMCs in 8567 x 8561, 97.0% of those in 8831 x 8732 and 98.0% of those in 8884 x 8732. A cell (1.4%) with VI was observed in 8567 x 8561 but not in any of the other crosses. In 8572 x 196-1(T2), 2IV was observed in 67.3% of the PMCs followed by IV (23.6%) and 3IV (9.1%), indicating the presence of two major translocations. In hybrids with T_3, 2IV was observed at a high frequency; 92.4% in 1908A x 8567, 55.6% and 72.7% in 1908A x 8732 (observations in different years) and 76.8% in 8732 x 1908A. The chromosome structure of these three strains was thus different from that of the T_1 strains in that they had one major translocation and from that of the T_2 or T_3 in that they had two major translocations and was named the type T_4.

e. Type T_5

8674: In hybrids with the type T_1, IV was observed in 37.3% of the PMCs in 8674 x 8593, 92.5% in 8718A x 8674 and 76.5% in 8827 x 8674. A cell (1.5%) with VI was observed in 8718A x 8674. Though the frequency of IV was rather low in 8674 x 8593, it is highly probable that one major translocation exists between strains of T_1 and 8674. Most PMCs (93.9%) in 8674 x 1908A(T_3) had VI. 2III or VI was observed at a high frequency in hybrids with T_4; 78.8% in 8572 x 8674 and 85.9% or 87.8% in 8732 x 8674 (two hybrids were observed in different years). Hybrids with type T_2 were not observed. T_2 produces 2IV in hybrids with T_4 but this strain formed VI when crossed to T_4. Therefore, the translocation between T_1 and T_4 would differ from that between T_1 and T_2. Based on these observations, the translocation type of this strain was classified into type T_5.

f. Type T_6

8714* and 8719*: No multivalent was formed in 8719 x 8714A, indicating the absence of translocation. Most of or all the PMCs (79.3 - 100%) in F_1 hybrids between 8714A or 8719 and strains of the T_1 type, 8528A, 8529, 8551, 8718A, 8724, 8827, 8880, 8884, 8933 and 8940 had IV. Cells with 2IV or VI were not observed in these hybrids. According to the unpublished raw data obtained by Tanaka and Ishii (1973), 2IV was formed in 42% and 3IV was observed in 30% of the PMCs in 8714A x 196-1 (cited by Kawahara and Tanaka 1977). The formation of 3IV is possibly due to a minor translocation in chromosomes of 196-1. In 8714A x 1908 (T_3), IV was observed in 58.3% of the PMCs and the frequency of the cells with 2IV was low (20.0%). The formation of 2IV indicates that the two translocations between T_1 and T_3 or T_6 are located on different sets of chromosomes. Most of the cells had VI in hybrids with T_4; 85.2% in 8567 x 8714A, 86.7% in 8572 x 8714A, 92.5% in 8732 x 8714A and 82.5% in 8732 x 8719. In 8719 x 8674(T_5), 2IV was formed at a high frequency (75.9%). Thus, these two strains have a translocation type other than T_1, T_2, T_3, T_4 and T_5 and were classified into type T_6.

g. Type T_7

8824A and 8824B: These two strains were established as two single plant derivaties from one sample. No multivalent was formed in hybrids between them. IV was observed at a high frequency in hybrids with T_1, 8824A x 107-1 (87.9%) and 8824B x 8561 (64.0%). A few cells with III were also observed in these hybrids. VI was observed at a high frequency in hybrids with T_3 (78.8% in 1908A x 8824A and 84.8% in 1908A x 8824B) and with T_4 (93.9% in 8824A x 8732 and 95.5% in 8824B x 8732). Most or all of the PMCs in hybrids with T_6 (100 % in 8824A x 8719, 97.0% in 8824A x 8714A) had VI. Thus, the chromosome structure of these two strains differs from T_1 by one and from T_3, T_4 or T_6 by two translocations. The difference in chromosome structure between these two strains and the T_2 or T_5 was recognized in their hybrids with T_8 and T_{14} (see later). Therefore, these two strains were classified into type T_7.

h. Type T_8

8784*: In 8784 x 107-1, the frequency of cells with VI was not high (30.0%) but many cells with 2 III were observed (38.0%). In the other hybrids with T_1, most PMCs had VI (96.0% in 8784 x 8718A and 92.0% in 8784 x 8827). Therefore, the chromosome structure of this strain would differ from that of T_1 by two major translocations which involve a pair of chromosomes in common. Since translocation types from T_2 to T_7 differ from T_1 by one major translocation, this strain has a different translocation type from those described above and was classified into type T_8. According to the unpublished data obtained by Tanaka and Ishii (1973), IV was formed in 34%, IV + VI in 16% and VI in 10% of the PMCs observed in 8784 x 196-1 (Kawahara and Tanaka 1977). 1908A(T_3) x 8784 produced VIII in 48.0% of the cells followed by VII (18.0%) and 2IV (12.0%). In hybrids with T_4, VI was formed at a high frequency (93.9% in 8574 x 8784 and 98.0% in 8784 x 8732). VIII was observed in 57.6% of the cells in 8674(T_5) x 8784. In 8714A(T_6) x 8784, VIII and VI was observed at the same frequency, 37.5%. In another hybrid with T_6, 8719 x 8784, VIII was observed in 26.3% of the cells and VI in 44.7%. In hybrids with T_7, IV was observed in most PMCs (87.9% in 8784 x 8824A and 93.9% in

8824B x 8784, indicating the presence of one major translocation between T_7 and T_8. As described above, two translocations exist between T_1 and T_8 and one translocation is found between T_1 and T_7. Probably, one of the two translocations between T_1 and T_8 is the same as that between T_1 and T_7.

i. Type T_9

1909C: 57.6% of the cells had 2IV and 39.4% had IV in 1909C x 107-1. These observations show that the chromosome structure of this strain differs from that of T_1 in two independent translocations, i. e., these two translocations are located on two different sets of chromosomes. The translocation type of this strain was named type T_9. In 1909C x 196-1(T_2), 71.2% of the cells had IV + VI. The occurrence of 2IV + VI in some cells (4.5%) is probably due to a minor translocation carried by 196-1. 2IV was observed in 78.8% of the PMCs in 1909C x 8732(T_4). Cells with III + IV or with IV were also observed in this hybrid. In 1909C x 8714A(T_6), IV + VI was observed at a high frequency (84.8%).

j. Type T_{10}

1911: 2IV was observed in two hybrids with 107-1 at a high frequency (81.1% and 81.8%) and IV was formed at a low frequency (16.2% and 15.2%). A cell (2.7%) with IV + VI was also observed in a hybrid with 107-1. In 1911 x 196-2(T_2), 24.0% of the PMCs had IV + VI and other 24.0% had 3IV and 2IV + VI was observed in 20.0% of the PMCs. 1911 has two major translocations and 196-1 has one major and one minor ones relative to the chromosome structure of the type T_1. Concerning the major translocations, 196-1 and 1911 are expected to differ from each other by three translocations. From the present data, it could not be determined whether the three translocations form 3IV or IV + VI. In a hybrid with

T_3, 1908 x 1911, 3IV was observed in 66.7% of the cells and the remaining cells had 2IV. Most PMCs (93.9%) had IV + VI in 1911 x 8732(T_4). In 1911 x 8714A(T_6), 78.8% of the PMCs had 3IV. Seventeen cells were observed in 1911 x 8784(T_8). Of these, four cells had IV + VIII, three had III + IV + V and the other theree had IV + VI. It is likely that III + V is the result of breakdown of VII initially formed in the PMCs of this hybrid combination. In 1909C x 1911 (T_9 x T_{10}), 2IV + VI was formed at a high frequency (79.3%). 1909C(T9) and 1911 differ from T_1 by two translocations and the latter differs from the former by four translocations. Therefore, the translocation type of 1911 was named type T_{10}.

k. Type T_{11}

8460: 2IV was observed in 70.2% of the PMCs in 8460 x 8561(T_1) followed by IV (22.8%). Cells with VI or IV + VI were observed at a low frequency (3.5% or 1.8%, respectively). In 8460 x 196-1(T_2), 57.7% of the PMCs had 2IV and 38.5% had 3IV. In a hybrid with T_3, 1908A x 8460, IV + VI was observed at a high frequency (87.9%). Most of the PMCs in three hybrids with T_4 had VIII ; 90.9% in 8460 x 8567 or in 8460 x 8572 and 76.9% in 8460 x 8732. In 8460 x 8674(T_5), about half of the PMCs (52.5%) had IV + VI followed by 2IV (16.9%) and VI (10.2%). IV + VI was observed in 83.3% of the PMCs in 8460 x 8719(T_6) and the remaining cells had VI. VI was observed at a high frequency (78.8%) in 8460 x 8784(T_8). In 1911(T_{10}) x 8460, most PMCs (90.9%) had 2IV + VI. This strain was not crossed to 1909C of the T_9 type. But the occurrence of multivalents in hybrids of 8460 with T_2 and T_4 differ from that of T_9 and this strain was named type T_{11}.

l. Type T_{12}

8715: 2IV was produced at a high frequency (78.8%) in 8715 x 107-1. Cells with IV (18.2%) and a cell (3.0%) with III + IV were also observed. In 196-1(T_2) x 8715, about half of the cells (54.4%) had 2IV and cells with 3IV (21.2%) or IV (12.1%) were also observed. Twelve cells were observed in 8715 x 8714A(T_6) and all had a chromosome configuration of 10II + 2IV. Of 18 PMCs observed in 8715 x 8784(T_8), 14 cells had X, three formed VIII and one had XII. The number of hybrids between this strain and other translocation types is rather small at present. But the occurrence of 2IV in hybrids with T_6 and X in those with T_8 has not been observed among the types with two major translocations between T_1. Therefore, the chromosome structure of 8715 would differ from those of T_9, T_{10} or T_{11} and was named type T_{12}.

m. Type T_{13}

8725: 2IV was observed in about half of the PMCs (52.8%) of 8725 x 8561(T_1). Cells with IV (37.7%), III (5.7%) and III + IV (1.9%) were also observed. In 8725 x 196-1(T_2), 2IV (39.4%) and IV (33.3%) were frequently observed. Occasionally, cells with V (9.1%), 3IV (9.1%), III (6.1%) and IV + V (3.0%) were observed. As 8725 produced 2IV and 196-1 produced IV in hybrids with T_1, a maximum of three translocations is expected between 196-1 and 8725. Probably 3IV was formed initially in PMCs of 8725 x 196-1 but these could only be maintained under favorable cellular circumstances. 3IV was observed in 48.5% of the PMCs in 8725 x 1908A(T_3). 3IV was also observed in hybrids with T_4 (75.8% in 8567 x 8725 and 48.5% in 8732 x 8725) and in those with T_6 (57.6% in 8725 x 8714A). IV + VI was observed in 45.5% and 2IV + VI in 39.4% of the PMCs of 8725 x 8784(T_8). In 1909C(T_9) x 8725, 4IV was observed at a high frequency (67.9%). In 1911(T_{10}) x 8725, 2IV + VIII was the most common (39.4%) followed by 2IV + VI (18.2%) and 2III + 2IV (9.1%). Two major translocations exist between T_1 and 1911 or 8725. So, four major translocations are expected between 1911 and 8725. In their hybrids, these transiocations probably produce 2IV + VI at meiosis. The occurrence of 2IV + VIII might be due to a minor translocation carried by 1911. 4IV was formed at a high frequency (65.2%) in 8460(T_{11}) x 8725. 8725 was not crossed to 8715 of T_{12}. But the latter strain formed 2IV or X in hybrids with T_6 or T_8, respectively, but the former produced 3IV or 2IV + VI in the corresponding hybrids. Therefore, the chromosome structure of this strain (8725) differs from those of T_9, T_{10}, T_{11} and T_{12} and was named type T_{13}.

n. Type T_{14}

8866*: Five hybrid combinations between T_1 and 8866 were observed at MI. Of these, 2IV was formed at a high frequency in 8822 x 8866 (61.1%) and 8866 x 8718A (67.9%) but at a low frequency in 107-1 x 8866 (14.8%), 8866 x 8827 (3.5%) and 8912 x 8866 (10.0%). In the latter hybrids, IV was observed at a high frequency, 50.8% in 107-1 x 8866, 87.7% in 8866 x 8827 and 58.0% in 8912 x 8866. III + IV was observed in 19.7% of the PMCs in 107-1 x 8866 and in 10.0% in 8912 x 8866. This strain, most probably, has two major translocations between T_1 but in some hybrid combinations, one or both of the two quadrivalents initially formed in the PMCs may have the tendency to greakdown into smaller configurations. In 8866 x 196-2(T_2), various combinations of multivalents were observed. Of these, the most common configuration was 2IV (24.5%), next was III + VI (15.1%), then IV (11.3%), III + 2IV, 2III + IV and IV + VI (9.4% each). The maximum multivalent association was 2IV + VI (5.7%). One or two major translocations are observed between T_1 and T_2 or T_{14}, respectively. So, three major translocations are expected between T_2 and T_{14} if the same translocation was not involved. Because IV + VI was observed more frequently than 3IV (1.9%), these three translocations would produce IV + VI in T_2 x T_{14}. The occurrence of 2IV + VI may be due to a minor translocation between T_1 and T_2. In 8866 x 1908A(T_3), 3IV was formed at a high frequency (55.9%). In T_4 x 8866, five hybrids including a reciprocal cross were observed. In all these hybrids, IV + VI was formed at a high frequency (61.9% in 8567 x 8866, 52.4% in 8866 x 8567, 57.6% in 8866 x 8572, 64.9% and 86.2% in two hybrids of the combination 8866 x 8732). IV + VI was also formed at high frequency in hybrids with T_6; 88.5% in 8714A x 8866, 84.0% in 8719 x 8866 and 67.5% in 8866 x 8719. 3IV was recognized in 66.7% of the cells in 8824A(T_7) x 8866 and in 84.8% in 8866 x 8824B(T_7). In 8866 x 8784(T_8), the most common multivalent association was IV + VIII (27.8%) followed by IV + VI (22.2%). 2IV + VI was formed at a high frequency in the following hybrids; 57.6% in 1909C(T_9) x 8866, 66.7% in 1911(T_{10}) x 8866, 54.5% in 8460(T_{11}) x 8866 and 56.1% in 8866 x 8725(T_{13}). In 8866 x 8715(T_{12}), 2IV was formed at a high frequency (87.9%). Thus, 8866 differs from T_9, T_{10}, T_{11}, T_{12} and T_{13} by four major translocations and was classified into type T_{14}.

o. type T_{15}

8713: IV + VI was observed at a high frequency (75.9%) in 8713 x 8561(T_1). Some cells with III + VI (13.8%) and a cell (3.4%) with VI, 2VI or 2III + VI were also recognized. Thus, this strain differs from T_1 by three major translocations and was classified into type T_{15}. In 8713 x 196-1(T_2), 15 PMCs were observed. Of these, three cells (20.0%)

had 2VI, other three had IV + VI and two had 2IV. The formation of 2VI is explained by four translocations expected between 8713 and 196-1. 2IV + VI was observed two-thirds (66.7%) of the PMCs in 1908A(T_3) x 8713. X was formed at a high frequency in 8567(T_4) x 8713(45.5%) and 8732(T_4) x 8713 (69.7%). In 8713 x 8719(T_6), IV + VI was formed at a high frequency (84.8%). Several cells with VI (9.1%), 2IV (3.0%) or 2IV + VI (3.0%) were also observed. In 8713 x 8784(T_8), 19 PMCs were observed. Of these, five cells produced X, four IV + VIII, three III + IX, two 2V and other two XII. A cell with 2IV, III + VI or V + VII was also observed. Because a miximum of five translocations is expected between 8713 and 8784, it is likely that XII was initially produced in the PMCs. The occurrence of IV + VIII, III + VI or V + VII would be the result of breakdown of XII into smaller configurations. VI + VIII was observed at a high frequency (69.7%) in 8469(T_{11}) x 8713. 2IV + VIII was observed in about half of the PMCs (51.5%) in 8713 x 8725(T_{13}). 84.8% of the PMCs in 8715(T_{12}) x 8713 and in 8866(T_{14}) x 8713 had VIII. In these combinations, a maximum of five translocations is expected but a higher valency of multivalents than VIII was not recognized. Probably, one of the three translocations between T_1 and T_{15} is common to one of the two between T_1 and T12, and another one would be the same translocation as one of those between T1 and T14.

p. unidentified

In the present study, all the strains observed were crossed to, at least, 107-1 of T. timopheevi or several other araraticum strains of the T_1 type. However, each strain was not crossed to strains of all translocation types other than T_1. Therefore, translocation type of 39 strains remain unidentified because of the lack of the available data.

Of these, 37 strains differ from T_1 by one major translocation. The remaining two strains, 1967 and 1972A, differ from T_1 by two translocations. Translocation types of these two strains would be different because different kinds of chromosome configurations were observed in their hybrids with 107-1 (see later). The stock numbers and the results obtained so far are as follows;

1907B (not T_1): IV was observed at a high frequency (87.9%) in 1907B x 1901(T_1). Crossings to types other than T_1 were not made.

1908B (neither T_1 nor T_2): III or IV was observed in 90.9% of the PMCs in 1908B x 1901(T_1). VI was observed in 48.0% of the PMCs in 1908B x 196-1(T_2), followed by III + VI (18.0%) and IV + VI (16.0%).

1938 (neither T_1 nor T_2): IV was observed at a high frequency (84.8%) in 1938 x 107-1. 2IV was observed in 75.8% of the PMCs in 1938 x 196-1(T_2).

1943 (not T_1): III or IV was observed in 81.8% of the cells in 1943 x 107-1.

1946 (not T_1): Most PMCs (88.9%) in 1946 x 107-1 had IV.

1950 (not T_1): Most PMCs (92.9%) in 1950 x 107-1 had IV.

1958 (neither T_1 nor T_2): IV was observed in 83.6% of the PMCs of 1958 x 107-1. In 1958 x 196-1(T_2), 2IV was observed in 36.4% of the PMCs and IV was observed in 31.8% of the cells.

1962 (neither T_1 nor T_3): IV was observed in 88.6% of the PMCs in 1962 x 107-1 and 2IV was observed at a high frequency (80.8%) in 1962 x 1908A(T_3).

1966 (not T_1): All the PMCs in 1966 x 107-1 had IV.

1967 (neither T_1 nor T_2): Most PMCs (93.5%) in 1967 x 107-1 had VI. This indicated the presence of two major translocations between

107-1 and 1967 and that a pair of chromosomes are involved in common. Three major translocations are expected between 1967 and 196-1(T_2) from the occurrence of IV + VI (49.2%).

1972A (not T_1): In 1972A x 107-1, 2IV was observed at a high frequency (66.7%) followed by IV (30.3%) and III + IV (3.0%). Therefore, two major translocations which share no chromosome in common are expected between 107-1 and 1972A.

1979A and 1979B (neither T_1 nor T_8): These two strains were established from one original sample. A hybrid between them produced no multivalents indicating the absence of translocation. Most PMCs in their hybrids with 107-1 (93.9% in both) had IV. IV was formed at a high frequency (75.8%) in 1979B x 8784(T_8).

1980A (neither T_1 nor T_3): IV was observed at a high frequency (87.5%) in 1980A x 107-1 and 80.6% of the cells in 1980A x 8784(T_8) had 2IV.

1980B (not T_1): All the cells observed in 1980B x 107-1 had IV.

1981A (not T_1): Most PMCs (93.1%) in 1981A x 107-1 had IV.

1981B (not T_1): IV was observed in most of the cells (93.8%) in 1981B x 107-1.

1982 (not T_1): IV was observed at a high frequency in a hybrid with 107-1 (89.4%).

1983 (not T_1): " " (86.0%).

1985 (neither T_1 nor T_3): IV was observed at a high frequency in a hybrid with 107-1 (89.4%). 2IV was observed at a high frequency (69.7%) in 1908A(T_3) x 1985.

1986 (not T_1): IV was observed at a high frequency in a hybrid with 107-1 (87.9%).

1987 (not T_1): IV was observed at a high frequency in hybrids with

107-1 (73.0% and 78.8%).

1988 (not T_1): Most PMCs in 1988 x 107-1 had IV (93.3%).

1990 (not T_1): 86.7% of the PMCs in 1990 x 107-1 had IV.

8497 (neither T_1, T_6 nor T_8): IV was observed in 90.9% of the cells in 8497 x 8561(T_1). 87.9% of the PMCs in 8497 x 8719(T_6) had 2IV. VIII was observed in 72.9% of the cells in 8497 x 8784(T_8).

8500 (neither T_1 nor T_8): IV was observed at a high frequency (75.7%) in 8500 x 8561(T_1). VIII was observed in 75.8% of the PMCs in 8500 x 8784(T_8).

8514A (neither T_1, T_4 nor T_6): IV was observed at a high frequency in hybrids with T_1; 90.9% in 8514A x 8718A and 85.7% in 8761 x 8514A. IV, 2IV or VI (68.2%, 22.7% or 9.1%, respectively) was observed in 8567(T_4) x 8514A. VI was observed in 54.5% of the PMCs in 8514A x 8719(T_6) followed by IV + VI (36.4%).

8521 (neither T_1, T_6 nor T_8): Most of the cells (93.9%) in 8521 x 107-1 had IV. 2IV and VIII were observed at a high frequency in 8521 x 8714(T_6) (68.2% in total) or 8521 x 8784(T_8) (54.5% in total).

8544 (neither T_1, T2, T_8 nor T_{14}): 98.0% of the PMCs in 8544 x 8561(T_1) had IV. IV (42.4%) and 2IV (30.3%) were the multivalents commonly observed in 8544 x 196-2(T_2). In 8544 x 8784(T_8), IV + VI was observed at a high frequency (81.8%). IV and 2IV were observed in 8544 x 8866(T_{14}) (29.4% and 5.9%, respectively).

8601 (neither T_1, T_2, T_4 nor T_6): All the PMCs in 8601 x 8561(T_1) had IV. About half of the cells (48.1%) in 8601 x 196-1(T_2) had 2IV. 2IV was observed at a high frequency (84.4%) in 8572(T_4) x 8601. Most of the cells (96.9%) in 8601 x 8719(T_6) had VI.

8662 (neither T_1, T_2, T_4 nor T_8): IV was observed at a high frequency in hybrids with T_1; 96.9% in 8561 x 8662 and 61.1% in the reciprocal cross. 2IV, IV, and 3IV were common in 8662 x 196-1(T_2); 34.2%, 31.6% and 21.2%, respectively. VI or VIII was observed at a high frequency in 8662 x 8719(T_6; 84.4%) or 8662 x 8784(T_8; 78.8%), respectively.

8668 (neither T_1, T_6 nor T_8): IV was observed in 78.0% of the PMCs in 8668 x 8561(T_1). 2IV was observed at a high frequency (85.3%) in 8668 x 8719(T_6). VIII, 2IV and III + V were frequently observed in 8668 x 8784(T_8); 42.4%, 27.3% and 18.2%, respectively.

8720 (neither T_1, T_6 nor T_{14}): IV was observed at a high frequency in hybrids with T_1; 86.4% in 8720 x 107-1 and 78.0% in 8720 x 8561. All the PMCs in 8720 x 8719(T_6) had VI. IV + VI was observed in 78.8% of the cells in 8720 x 8866(T_{14}).

8729 (neither T_1, T_6 nor T_8): IV was observed at a high frequency (84.0%) in 8729 x 8561(T_1). Most PMCs (92.9%) in 8729 x 8714A(T_6) had VI. In 8729 x 8784(T_8), 88.9% of the cells had VIII.

8733 (neither T_1, T_4, T_5, T_8 nor T_{14}): IV was observed at a low frequency in several hybrids between T_1; 36.0% in hybrids with 8469, 24.0% with 8593 and 26.0% with 8912. While, in 8733 x 8700(T_1), IV was observed at a high frequency (88.0%). VI was observed at a high frequency (84.8%) in 8733 x 8732(T_4). 26.1% of the PMCs in 8733 x 8674(T_5) had IV and 4.3% had 2IV. VIII was observed at a high frequency (72.0% and 66.7%) in hybrids with 8784(T_8). 69.2% of the PMCs in 8733 x 8866(T_{14}) had 3IV.

8734 (neither T_1 nor T_4): IV was observed at a low frequency (10.0%) in 8734 x 107-1. From these data, it may be inferred that a major translocation does not exist between 8734 and T_1. However, VI, an indication of two translocations, was observed at a high frequency (83.3%) in 8734 x 8732(T_4). Because 8732 differs from T_1 by one major translocation, 8734 is expected to differ from T_1 by one major translocation.

8944 (neither T_1, T_2, T_6, T_8 nor T_{14}): IV was observed at a high frequency in 8944 x 8561(T_1). The most common multivalent was IV (61.3%) in 8944 x 196-1(T_2), followed by 2IV (22.6%) and VI (12.9%). In 8944 x 8719(T_6), VI was observed at a high frequency (88.9%). In 8944 x 8784(T_8), 58.8% of the cells had VIII. 3IV (51.5%) or III + 2IV (30.3%) was commonly observed in 8944 x 8866(T_{14}).

8945 (neither T_1, T_6 nor T_{14}): IV was observed at a high frequency (89.4%) in 8945 x 107-1(T_1). VI or 3IV was observed at a high frequency in a hybrid with T_6 (8714A, 87.9%) or with T_{14} (8866, 81.9%), respectively.

Table Ic. Occurrence of multivalents in F_1 hybrids between strains of the timopheevi wheats

Cross combination	No. of cells observed	Per cent of cells with multivalents
107-1 x 8866	61	1IV 50.8, 1III+1IV 19.7, 2IV 14.8, 1III 11.5
196-1 x 8715	33	2IV 54.4, 3IV 21.2, 1IV 12.1, 1IV+1V 6.1, 2IV+1V 3.0, 2IV+1VI 3.0
196-2 x 107-1	100	none
" x " *	63	none
1907A x 107-1	35	1IV 94.3
" x 196-1	33	1VI 66.7, 1IV+1VI 15.2, 1III+1VI 12.1, 1VI 6.1
1907B x 1901	"	1IV 87.9
1908A x 196-1	50	1VI 58.0, 1IV 28.0, 2IV 6.0, 1III+1IV 2.0, 1III+1VI 2.0, 2III 2.0
" x 1909B	33	none
" x 1911	"	3IV 66.7, 2IV 33.3
" x 1985	"	2IV 69.7, 1IV 27.3, 1III+1IV 3.0
" x 8460	"	1IV+1VI 87.9, 1VI 6.1, 2IV 6.1
" x 8567	66**	2IV 92.4, 1III+1IV 4.5, 1IV 3.0
" x 8713	33	2IV+1VI 66.7, 3IV 18.2, 1IV+1VI 9.1, 2III+2IV 3.0, 2IV+1V 3.0
" x 8732	54	2IV 55.6, 1IV 37.0, 1III+1IV 7.4
" x " *	33	2IV 72.7, 1IV 24.2
" x 8784	50	1VIII 48.0, 1VII 18.0, 2IV 12.0, 1III+1V 8.0, 1VI 6.0, 1III+1IV 2.0, 2III 2.0, 3IV 2.0, 1IV+1VIII 2.0
" x 8824A	33	1VI 78.8, 1IV 15.2, 1V 6.1
" x 8824B	33	1VI 84.8, 1IV 9.1, 2III 3.0, 1III+1IV 3.0
1908B x 196-1	50	1VI 48.0, 1III+1VI 18.0, 1IV+1VI 16.0, 2IV 8.0, 1III+1IV 8.0, 1IV 2.0
" x 1901	33	1IV 87.9, 1III 3.0
1909A x 107-1	38	1IV 89.5, 1III 2.6
" x 1907A	33	none
" x 1908A	"	"
1909B x 107-1	"	1IV 97.0
" x 196-1	29	1VI 58.6, 1IV 27.6, 1IV+1VI 6.9, 2III 3.4, 1III+1IV 3.4
" x 1907A	33	none

* Observed in different years.
** Two plants were observed.

Table Ic. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
1909C x 107-1	33	2IV 57.6, 1IV 39.4, 1III+1IV 3.0
" x 196-1	66**	1IV+1VI 71.2, 1VI 9.1, 2IV 6.1, 1III+1IV 4.5, 2IV+1VI 4.5, 2III+1IV 1.5
" x 1911	29	2IV+1VI 79.3, 1III+1IV+1VI 13.0, 1IV+1VI 8.7, 2IV 4.3
" x 8714A	33	1IV+1VI 84.8, 2IV 9.1, 1VI 3.0, 1IV+1V 3.0
" x 8725	"	4IV 69.7, 1III+3IV 12.1, 3IV 9.1, 1III+2IV 9.1
" x 8732	"	2IV 78.8, 1III+1IV 18.2, 1IV 3.0
" x 8866	"	2IV+1VI 57.6, 3IV 24.2, 1IV+1VI 12.1, 2IV+1V 3.0 2IV 3.0
1911 x 107-1	37	2IV 81.1, 1IV 16.2, 1IV+1VI 2.7
" x " *	33	2IV 81.8, 1IV 15.2, 1III+1IV 3.0
" x 196-1	50	1IV+1VI 24.0, 3IV 24.0, 2IV+1VI 20.0, 2IV 12.0, 1Ⅲ+2IV 10.0, 2Ⅲ+2IV 4.0, 1Ⅲ+1IV 2.0, 2Ⅲ+1IV 2.0, 2IV+1V 2.0
" x 8460	33	2IV+1VI 90.9, 1IV+1VI 9.1
" x 8714A	33	3IV 78.8, 2IV 15.2, 1III+2IV 6.1
" x 8725	"	2IV+1VⅢ 39.4, 2IV+1VI 18.2, 2Ⅲ+2IV 9.1, 1Ⅲ+2IV+1V 6.1, 1Ⅲ+2IV 6.1, 1IV+1VⅢ 6.1, 1Ⅲ+1VⅢ 3.0, 1IV+1VI 3.0 1Ⅲ+1IV+1VI 3.0, 3IV 3.0, 4IV 3.0
" x 8732	"	1IV+1VI 93.9, 1VI 3.0, 1IV 3.0
" x 8784	17	1IV+1VⅢ 23.5, 1Ⅲ+1IV+1V 17.6, 1IV+1VI 17.6, 2Ⅲ+1IV 11.8, 1Ⅲ+2IV 11.8, 2IV 5.6, 3IV 5.6, 1Ⅲ+1VⅢ 5.6
" x 8866	33	2IV+1VI 66.7, 3IV 9.1, 1Ⅲ+1IV+1VI 6.1, 2IV+1V 6.1, 1IV+1VI 3.0, 2Ⅲ+2IV 3.0, 1Ⅲ+2IV 3.0, 2Ⅲ+1IV 3.0
1914 x 107-1	50	none
" x 196-1	30	1IV 40.0, 1III 13.3, 1VI 6.7, 2IV 3.3
1923 x 107-1	33	none
1924 x 107-1	"	"
1925 x 107-1	25	"
1926A x 107-1	33	"
1927 x 107-1	"	"
1928 x 107-1	"	"
1929 x 107-1	29	"
1931 x 107-1	66**	"

Table Ic. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
1932 x 107-1	30	none
1933 x 107-1	61	1IV 1.6
" x 1908A	33	1IV 97.0
1934 x 107-1	"	1IV 3.0
1935 x 107-1	31	none
1936 x 107-1	27	"
1937 x 107-1	51	"
1938 x 107-1	33	1IV 84.8
" x 196-1	"	2IV 75.8, 1IV 15.2, 1III+1IV 9.1
1939 x 107-1	30	none
1943 x 107-1	33	1IV 78.8, 1III 3.0
1946 x 107-1	27	1IV 88.9
1950 x 107-1	28	1IV 92.9
1958 x 107-1	61	1IV 83.6
" x 196-1	44	2IV 36.4, 1IV 31.8, 1III+1IV 13.6, 1III+2IV 11.4, 3IV 2.3, 2III 2.3, 2III+1IV 2.3
1960 x 107-1	31	1IV 12.9
1962 x 107-1	35	1IV 88.6
" x 1908A	26	2IV 80.8, 1IV 19.2
1963 x 107-1	28	none
" x 1908A	29	1IV 89.7
1964 x 107-1	27	none
1965 x 107-1	25	"
1966 x 107-1	23	1IV 100
1967 x 107-1	31	1VI 93.5, 1IV 6.5
" x 196-1	21	1IV+1VI 42.9, 1VI 23.8, 2IV 19.0, 1IV 4.8, 1VIII 4.8, 1IV+1VIII 4.8
1969 x 107-1	31	none
" x 196-1	34	1IV 64.7, 2IV 11.8, 1III 5.9
1972A x 107-1	33	2IV 66.7, 1IV 30.3, 1III+1IV 3.0
1978A x 107-1	66**	none
1979A x 107-1	33	1IV 93.9

Table Ic. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
1979B x 107-1	33	1IV 93.9, 1III 3.0
" x 1979A	20	none
" x 8784	33	1VI 75.8, 2III 21.1, 1 V 3.0
1980A x 107-1	32	1IV 87.5
" x 1908A	31	2IV 80.6, 1IV 19.4
1980B x 107-1	33	1IV 100
1981A x 107-1	23	1IV 91.3
1981B x 107-1	33	1IV 93.9
1982 x 107-1	66**	1IV 89.4
1983 x 107-1	43	1IV 86.0, 1VI 9.3
1985 x 107-1	66**	1IV 89.4
1986 x 107-1	33	1IV 87.9
1987 x 107-1	37	1IV 73.0, 1III 2.7
" x " *	33	1IV 78.8, 2IV 12.1
1988 x 107-1	"	1IV 93.9
1990 x 107-1	30	1IV 86.7
8456 x 8561	30	none
8460 x 196-1	26	2IV 57.7, 3IV 38.5, 2III+1IV 3.8
" x 8561	57	2IV 70.2, 1IV 22.8, 1VI 3.5, 1IV+1VI 1.8
" x 8567	33	1VIII 90.9, 1VI 6.1, 1III+1V 3.0
" x 8572	"	1VIII 90.9, 1VI 6.1, 1X 3.0
" x 8674	59**	1IV+1VI 52.5, 2IV 16.9, 1VI 10.2, 1III+1VI 5.1, 2III+1IV 3.4, 1IV 3.4, 1IV+1V 1.7, 1III+1V 1.7, 1III+1IV 1.7, 2VI 1.7, 2III 1.7
" x 8713	33	1VI+1VIII 69.7, 2VI 21.2, 2III+1VI 3.0 1III+2V 3.0, 1IV+1VIII 3.0
" x 8719	30	1IV+1VI 83.3, 1VI 16.7
" x 8725	66**	4IV 65.2, 3IV 22.7, 1III+3IV 6.1, 1III+2IV 3.0, 2IV 3.0
" x 8732	26	1VIII 76.9, 1VI 7.7, 1III+1V 3.8, 1VII 3.8, 2IV 3.8, 1IV 3.8
" x 8784	33	1VI 78.8, 1IV 12.1, 2III 9.1
" x 8866	"	2IV+1VI 54.5, 3IV 21.2, 1IV+1VI 12.1, 1III+2IV 6.1, 2III+1IV 3.0, 1VI 3.0
8469 x 8561	"	none

Table Ic. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
8478 x 8561	50	none
8491 x 8561	"	"
8497 x 8561	"	1IV 90.0
" x 8719	33	2IV 87.9, 1IV 12.1
" x 8784	"	1VIII 72.9, 1VI 9.1, 1III+1V 6.1, 1X 6.1, 2IV 3.0, 1IV+1VI 3.0
8500 x 8561	37	1IV 75.7
" x 8784	33	1VIII 75.8, 1III+1V 12.1, 1IV 3.0, 1V 3.0, 1VI 3.0, 2IV 3.0
8514A x 8718A	55	1IV 90.9
" x 8719	33	1VI 54.5, 1IV+1VI 36.4, 1IV 6.1, 2IV 3.0
" x 8732	"	2IV 84.8, 3IV 12.1, 1IV 3.0
8521 x 107-1	"	1IV 93.9
" x 8714A	22	2IV 68.2, 1IV 13.6, 1III+1IV 9.1, 1III 4.5, 2III+1IV4.5
" x 8784	33	1VIII 54.5, 1VI 15.2, 1III+1V 15.2, 2IV 6.1, 2III 6.1, 1III+1IV 3.0
8528A x 107-1	38	1IV 2.6
" x 8719	32	1IV 93.8
8529 x 107-1	33	none
" x 8714A	30	1IV 90.0
8543 x 8561	50	none
8544 x 196-1	33	1IV 42.4, 2IV 30.3, 1VI 12.1, 1IV+1VI 6.1, 1V 3.0, 1IV+1V 3.0
" x 8561	50	1IV 98.0
" x 8784	33	1IV+1VI 81.8, 1VI 6.1, 2IV 6.1, 2III+1IV 6.1
" x 8866	34	1IV 29.4, 2IV 5.9
8551 x 196-1	33	1IV 57.6, 1III 12.1, 1III+1IV 6.1, 2IV 3.0
" x 8561	36	1IV 2.8
" x 8719	33	1IV 100
8561 x 8662	32	1IV 96.9, 2III 3.1
" x 8718A	50	none

Table Ic. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
8567 x 8514A	22	1IV 68.2, 2IV 22.7, 1VI 9.1
" x 8561	69**	1IV 79.7, 1VI 1.4, 1III 1.4
" x 8572	33	none
" x 8713	"	1X 45.5, 1VIII 36.4, 1VI 6.1, 1IV+1VI 6.1, 1VII 3.0, 2V 3.0
" x 8714A	27	1VI 85.2, 1IV 7.4, 1V 3.7, 1III 3.7
" x 8725	33	3IV 75.8, 2IV 18.2, 1III+2IV 6.1
" x 8732	"	none
" x 8866	21	1IV+1VI 61.9, 1VI 14.3, 1III+1IV 9.5, 1III+1VI 9.5, 2IV 4.8
8572 x 196-1	55	2IV 67.3, 1IV 23.6, 3IV 9.1
" x 8601	45	2IV 84.4, 1IV 15.6
" x 8674	33	1VI 39.4, 2III 39.4, 1III 12.1, 1IV 9.1
" x 8714A	30	1VI 86.7, 2IV 6.7, 1IV 3.3, 1V 3.3
" x 8784	33	1VI 93.9, 1VIII 6.1
8593 x 107-1	50	1IV 2.0
" x 8561	26	1IV 3.8
8597 x 8561	50	none
8601 x 196-1	27	2IV 48.1, 1VI 18.5, 1IV 18.5, 1IV+1VI 7.4, 2III+1IV 3.7, 1IV+1V 3.7
" x 8514A	72	1VI 90.3, 1IV 4.2, 2III 4.2
" x " *	32	1VI 93.8, 1IV 6.3
" x 8561	29	1IV 100
" x 8719	32	1VI 96.9, 1IV 3.1
8616 x 8561	50	none
8662 x 196-1	38	2IV 34.2, 1IV 31.6, 3IV 21.1, 1III+1IV 5.3, 1III 2.6, 2III 2.6, 2IV 2.6, 1IV+1VI 2.6
" x 8561	72	1IV 61.1, 1III 11.1, 2III 1.4
" x 8719	32	1VI 84.4, 2III 9.4, 1V 3.1, 1VIII 3.1
" x 8784	27	1VIII 77.8, 1VI 11.1, 1III+1IV 7.4, 1VII 3.7
8668 x 8561	50	1IV 78.0
" x 8719	34	2IV 85.3, 1IV 8.8, 1III+1IV 5.9
" x 8784	33	1VIII 42.4, 2IV 27.3, 1III+1V 18.2, 1VI 6.1, 1III 3.0, 1VII 3.0

Table Ic. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
8673 x 8561	50	none
8674 x 1908A	33	1VI 93.9, 1 V 3.0, 1IV 3.0
" x 8593	59	1IV 37.3, 1III 1.7
" x 8784	33	1VIII 57.6, 2IV 30.3, 1III+1IV 3.0, 1III+1V 3.0 1 V 3.0, 1VII 3.0
8682 x 1908A	64	1IV 60.9, 2IV 20.3, 1III+1IV 3.1, 1III 3.1, 2III 1.6, 2IV 1.6, 1VI 1.6
" x 8700	36	1IV 83.3, 1III 16.7,
8697 x 8561	100	none
8707 x 8700	30	1IV 3.3
8709 x 8700	50	none
8711 x 8561	100	"
8712 x 8561	50	"
8713 x 196-1	15	2VI 20.0, 1IV+1VI 20.0, 2IV 13.3, 1VII 6.7, 3IV 6.7, 1IV+1V 6.7, 2III+1IV 6.7, 1III+2IV 6.7, 1IV+1VII 6.7, 1III+1V+1VI 6.7
" x 8561	29	1IV+1VI 75.9, 1III+1VI 13.8, 1VI 3.4, 2IV 3.4, 2III+1IV 3.4
" x 8719	33	1IV+1VI 84.8, 1VI 9.1, 2IV 3.0, 2IV+1VI 3.0
" x 8725	"	2IV+1VIII 51.5, 3IV 18.2, 1IV+1VIII 9.1, 1III+1IV+1VIII 9.1, 2IV 6.1, 1IV+1VI 3.0, 4IV 3.0
" x 8784	19	1X 26.3, 1IV+1VIII 21.1, 1III+1IX 15.8, 2V 10.5, 1XII 10.5, 2IV 5.3, 1III+1VI 5.3, 1V+1VII 5.3
8714A x 1908A	60**	1IV 58.3, 2IV 20.0, 1III 13.3
" x 8567	20	1VI 70.0, 1VIII 20.0, 1IV+1VI 10.0
" x 8784	24	1VI 37.5, 1VIII 37.5, 1IV 12.5, 2III 4.2, 2IV 4.2, 1X 4.2
" x 8827	38	1IV 94.7
" x 8866	61**	1IV+1VI 88.5, 1III+1VI 4.9, 1IV+1V 3.3, 1IV 1.6, 1VI 1.6
8715 x 107-1	33	2IV 78.8, 1IV 18.2, 1III+1IV 3.0
" x 8713	"	1VIII 84.8, 1VI 9.1, 2IV 3.0, 1III+1IV 3.0
" x 8714A	12	2IV 100
" x 8784	18	1X 77.8, 1VIII 16.7, 1XII 5.6
8718A x 8674	67	1IV 92.5, 1VI 1.5
" x 8714A	23	1IV 100

Table Ic. (continued)

Cross combination		No. of cells observed	Per cent of cells with multivalents
8719	x 8514A	50	1VI 92.0, 1IV 6.0
"	x 8674	79	2IV 75.9, 1IV 13.9, 1III+1IV 8.9, 2III 1.3
"	x 8714A	50	none
"	x 8784	38	1VI 44.7, 1VIII 26.3, 2IV 13.2, 2III 5.3, 1IV 2.6
"	x 8866	50	1IV+1VI 84.0, 1III+1VI 10.0, 1VI 6.0
8720	x 107-1	22	1IV 86.4, 1III 4.5
"	x 8561	50	1IV 78.0, 1III 4.0
"	x 8719	33	1VI 100
"	x 8866	"	1IV+1VI 78.8, 1IV 6.1, 2IV 6.1, 2Ⅲ+1IV 6.1, 1Ⅲ+1VI 3.0
8724	x 8718A	24	1IV 4.2
"	x 8719	33	1IV 87.9, 1III 9.1
8725	x 196-1	"	2IV 39.4, 1IV 33.3, 1V 9.1, 3IV 9.1, 1Ⅲ 6.1, 1IV+1V 3.0
"	x 1908A	"	3IV 48.5, 2IV 39.4, 1Ⅲ+2IV 9.1, 1Ⅲ+1IV 3.0
"	x 8561	53	2IV 52.8, 1IV 37.7, 1III 5.7, 1III+1IV 1.9
"	x 8714A	33	3IV 57.6, 2IV 39.4, 1IV 3.0
"	x 8784	"	1IV+1VI 45.5, 2IV+1VI 39.4, 2IV 6.1, 1VI 3.0, 1III+1VI 3.0, 1III+1IV+1VI 3.0
8729	x 8561	50	1IV 84.0, 1III 10.0
"	x 8714A	28	1VI 92.9, 1IV 3.6, 2III 3.6
"	x 8784	27	1VIII 88.9, 1VI 11.1
8731	x 107-1	39	none
"	x 8700	43	"
8732	x 1908A	56	2IV 76.8, 1IV 10.7, 1III+1IV 7.1, 1III+2IV 1.8
"	x 8572	33	none
"	x 8674	64	1VI 78.1, 1IV 7.8, 2III 7.8, 1III 4.7, 1V 1.6
"	x " *	33	1VI 63.6, 2III 24.2, 1IV 12.1
"	x 8713	"	1X 69.7, 1VIII 21.2, 1IV+1VI 6.1, 2V 3.0
"	x 8714A	40	1VI 92.5, 1IV 5.0, 2III 2.5
"	x 8719	"	1VI 82.5, 1IV 7.5
"	x 8725	33	3IV 48.5, 2IV 36.4, 1III+2IV 12.1, 1III+1IV 3.0

Table Ic. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
8733 x 8469	50	1IV 36.0
" x 8593	"	1IV 24.0
" x 8674	23	1IV 26.1, 2IV 4.3
" x 8700	50	1IV 88.0
" x 8732	33	1VI 84.8, 1IV 12.1, 2IV 3.0
" x 8784	50	1VIII 72.0, 1X 12.0, 1VI 10.0, 1XII 2.0, 1VII 2.0, 1VI 2.0
" x " *	24**	1VIII 66.7, 1VI 12.5, 2IV 12.5, 1III+1V 4.2, 1VII 4.2
" x 8866	26	3IV 69.2, 2IV 26.9, 1III+2IV 3.8
" x 8912	50	1IV 26.0, 1III 2.0
8734 x 107-1	"	1IV 10.0
" x 8732	24	1VI 83.3, 2III 8.3, 1IV 4.2, 1V 4.2
8735 x 107-1	33	1III 3.0
" x " *	"	1IV 6.1
8742 x 8718A	25	none
8761 x 107-1	50	"
" x 8514A	21	1IV 85.7, 2IV 4.8
" x 8561	50	none
8770 x 196-1	39	1IV 64.1, 1III 10.3, 1III+1IV 2.6
" x 8761	26	none
8779 x 8561	50	"
8784 x 107-1	"	2III 38.0, 1VI 30.0, 1IV 26.0
" x 8718A	"	1VI 96.0, 1IV 4.0
" x 8732	"	1VI 98.0, 2III 2.0
" x 8824A	33	1IV 87.9
" x 8827	50	1VI 92.0, 1IV 8.0
8797 x 107-1	38	1IV 10.5, 1III 2.6
" x 8784	43	1VI 37.2, 1IV 30.2, 1IV+1VI 7.0, 2IV 2.3, 1X 2.3
8799B x 107-1	33	none
8802 x 196-1	27	1IV 63.0, 2IV 14.8, 1III 3.7
" x 8761	34	1IV 2.9

Table Ic. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
8819 x 196-1	32	1IV 62.5, 1III 6.3, 1III+1IV 6.3, 2IV 3.1
" x 8827	39	none
8821B x 107-1	30	"
" x 8593	50	"
" x 8948	"	"
8822 x 8827	33	"
" x 8866	36	2IV 61.1, 1III+1IV 22.2, 1IV 16.7
8824A x 107-1	66**	1IV 87.9, 1III 3.0
" x 8719	33	1VI 100
" x 8732	"	1VI 93.9, 1III 3.0, 1IV 3.0
" x 8824B	66**	none
" x 8866	33	3IV 66.7, 2IV 27.3, 1III+2IV 6.1
8824B x 8561	50	1IV 64.0, 1III 2.0
" x 8714A	30	1VI 96.7, 1IV 3.3
" x 8732	66**	1VI 95.5, 1IV 3.0, 1 V 1.5
" x 8784	33	1IV 93.9, 1III 6.1
8827 x 107-1	66**	none
" x 8674	51	1IV 76.5, 1III 5.9
" x 8928	50	1IV 2.0
8831 x 107-1	33	none
" x 8732	"	1IV 97.0, 1III 3.0
8866 x 196-1	53	2IV 24.5, 1III+1IV 15.1, 1IV 11.3, 1III+2IV 9.4, 2III+1IV 9.4, 1IV+1VI 9.4, 2IV+1VI 5.7, 1IV+1V 3.8, 1III 1.9, 1V 1.9, 1VI 1.9, 2III 1.9, 2III+1VI 1.9, 3IV 1.9
" x 1908A	68	3IV 55.9, 1III+2IV 22.1, 2IV 17.6, 1III+1IV 2.9, 1IV+1VI 1.5
" x 8567	21	1IV+1VI 52.4, 2IV 28.6, 1VI 9.5, 1III+1IV 4.8, 1IV+1V 4.8
" x 8572	33	1IV+1VI 57.6, 2III+1IV 12.1, 1IV+1V 12.1, 2IV 9.1, 1VI 6.1, 1III+1VI 3.0
" x 8713	"	1VIII 84.8, 1VI 6.1, 2IV 6.1, 1III+1V 3.0
" x 8715	"	2VI 87.9, 1IV+1VI 12.1
" x 8718A	53	2IV 67.9, 1IV 26.4, 1III+1IV 1.9

Table Ic. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
8866 x 8719	40	1IV+1VI 67.5, 1Ⅲ+1VI 25.0, 2IV 5.0, 1VI+1VⅢ 2.5
" x 8725	66**	2IV+1VI 56.1, 1IV+1VI 36.4, 1Ⅲ+1VI 3.0, 3IV 1.5, 1Ⅲ+1IV+1VI 1.5, 3IV+1VI 1.5
" x 8732	37	1IV+1VI 64.9, 1X 13.5, 1VI 8.1, 2III+1IV 5.4, 2IV 5.4, 1IV 2.7
" x " *	29	1IV+1VI 86.2, 2IV 6.7, 1VI 3.4, 1VIII 3.4
" x 8784	36**	1IV+1VⅢ 27.8, 1IV+1VI 22.2, 1Ⅲ+1IV+1V 8.3, 1IV+1V 5.6, 1VⅢ 5.6, 1IV 5.6, 2VI 2.8, 3IV 2.8, 2Ⅲ 2.8, 3Ⅲ 2.8, 1VI 2.8, 1Ⅲ+1IV 2.8, 1Ⅲ+1V 2.8, 1Ⅲ+1VI 2.8, 1Ⅲ+1VⅡ 2.8
" x 8824B	33	3IV 84.8, 2IV 15.2
" x 8827	57	1IV 87.7, 2IV 3.5, 1III 3.5
8880 x 107-1	66**	none
" x 8714A	39	1IV 92.3
8884 x 107-1	33	1IV 3.0
" x 8514A	50	1IV 90.0, 1VI 2.0
" x 8719	26	1IV 53.8
" x 8732	50	1IV 98.0, 1III 2.0
8890 x 107-1	"	none
8907 x 107-1	"	1IV 6.0, 1III 2.0
8912 x 8709	"	none
" x 8797	"	1IV 4.0, 1III 2.0
" x 8866	"	1IV 58.0, 2IV 10.0, 1III+1IV 10.0, 1III 10.0
8913 x 107-1	28	none
" x 196-1	33	1IV 57.6, 2IV 21.2, 1III 6.1, 1III+1IV 3.0
8924 x 107-1	30	none
" x 8561	"	"
" x 8912	50	"
8926 x 107-1	66**	"
" x 1908A	25	1IV 88.0
8928 x 107-1	50	none
8933 x 107-1	33	none
" x " *	66**	"
" x 8719	33	1IV 100

Table Ic. (continued)

Cross combination	No. of cells observed	Per cent of cells with multivalents
8940 x 107-1	57	none
" x " *	33	"
" x 196-2	"	1IV 9.1
" x 8719	29	1IV 79.3, 1III 6.9
" x 8827	41**	none
" x 8947	33	"
8944 x 196-1	31	1IV 61.3, 2IV 22.6, 1VI 12.9, 1III 3.2
" x 8561	50	1IV 86.0, 1III 8.0
" x 8719	27	1VI 88.9, 1IV 7.4, 2III 3.7
" x 8784	34	1VIII 58.8, 1VI 20.6, 2IV 8.8, 1IV 5.9, 1VII 2.9, 1III+1V 2.9
" x 8866	33	3IV 51.5, 1III+2IV 30.3, 2IV 15.2, 1III+1IV 3.0
8945 x 107-1	"	1IV 84.8, 1III 9.1
" x 8714A	"	1VI 87.9, 1IV 6.1, 2III 6.1
" x 8866	"	3IV 81.8, 1III+2IV 12.1, 2IV 6.1
8947 x 107-1	100**	none
" x 8827	33	"
8948 x 8718A	37	"
" x 8947	50	"

APPENDIX II.

Chromosome pairings in F_1 hybrids

Table IIa. Chromosome pairings in F_1 hybrids between strains of the diploid wheats

Cross combination	No. of cells observed	Chromosome pairings*				Xta per cell
		I	II	III	IV	
101-1 x 103	50	-	7.00 (7)	-	-	13.80
101-2 x "	"	-	7.00 (7)	-	-	13.54
102 x "	"	-	7.00 (7)	-	-	13.42
1501 x "	"	-	5.16 (5-7)	-	0.92 (0-1)	13.44
1519 x "	"	-	5.16 (5-7)	-	0.92 (0-1)	13.58
3621 x "	"	-	7.00 (7)	-	-	13.64
3636 x "	"	-	7.00 (7)	-	-	13.66
8082 x "	"	-	7.00 (7)	-	-	13.74
8143 x "	"	-	7.00 (7)	-	-	13.74

* Means and ranges(in parentheses).

Table IIb. Chromosome pairings in F_1 hybrids between T. dicoccoides and the diploid wheats

Cross combination	Envir. cond.*	No. of cells observed	Chromosome pairings**				Xta per cell
			I	II	III	IV	
108-2 x 103	G	33	7.91	5.73	0.55	-	10.24
			(6-10)	(4-7)	(0-1)		
"	F	33	8.39	5.39	0.61	-	9.79
			(6-11)	(4-7)	(0-2)		
108-3 x 101-3	G	50	8.78	5.36	0.50	-	8.46
			(6-11)	(4-7)	(0-1)		
108-3 x 103	G	33	8.09	5.72	0.79	-	10.27
			(6-11)	(4-7)	(0-2)		
"	F	33	8.09	5.55	0.61	-	10.15
			(5-11)	(4-7)	(0-2)		
109 x 101-3	G	60	8.68	5.83	0.22	-	10.60
			(6-11)	(5-7)	(0-1)		
109 x 103	G	33	8.58	5.67	0.36	-	10.55
			(6-11)	(4-7)	(0-2)		
195 x 103	F	33	8.70	5.97	0.12	-	9.73
			(4-11)	(5-7)	(0-1)		
1945 x 103	G	50	9.88	5.50	0.04	-	7.64
			(8-15)	(3-6)	(0-1)		
1957 x 103	F	33	9.00	4.64	0.30	0.45	9.15
			(7-11)	(3-6)	(0-1)	(0-1)	
1978B x 103	G	33	8.85	5.76	0.21	-	9.70
			(5-13)	(4-7)	(0-2)		
8915A x 103	F	50	8.48	5.42	0.54	-	10.48
			(6-11)	(2-7)	(0-2)		
8935 x 103	F	50	8.42	5.96	0.22	-	10.68
			(6-11)	(4-7)	(0-2)		

* Environmental conditions: F=Field, G=Glasshouse.

** Means and ranges(in parentheses).

Table IIc. Chromosome pairings in F_1 hybrids between *T. araraticum* or *T. timopheevi* and the diploid wheats

Cross combination	Envir. cond.*	No. of cells observed	Chromosome pairings**						Xta per cell
			I	II	III	IV	V	VI-VIII	
107-1 x 101-1	G	50	6.74 (4-9)	4.98 (1-7)	0.70 (0-3)	0.50 (0-2)	0.04 (0-1)	-	10.66
107-1 x 104-1	G	62	7.10 (4-9)	5.35 (3-8)	0.40 (0-2)	0.44 (0-2)	0.05 (0-1)	-	10.66
196-1 x 101-1	G	50	8.66 (5-15)	4.56 (3-7)	0.44 (0-2)	0.40 (0-2)	0.06 (0-1)	-	9.14
196-1 x 103	F	33	8.52 (6-13)	4.58 (3-7)	0.58 (0-1)	0.21 (0-1)	0.15 (0-1)	-	8.85
196-2 x 101-1	G	64	7.27 (5-11)	4.84 (3-7)	0.86 (0-3)	0.33 (0-1)	0.03 (0-1)	-	9.37
196-2 x 101-3	G	59	6.56 (5-9)	5.27 (4-7)	0.78 (0-2)	0.22 (0-1)	0.14 (0-1)	-	10.25
196-2 x 103	G	33	6.85 (5-11)	4.91 (3-7)	0.85 (0-2)	0.33 (0-1)	0.09 (0-1)	-	10.12
1908A x 101-1	G	60	7.22 (5-11)	5.23 (3-7)	0.40 (0-3)	0.38 (0-1)	0.12 (0-1)	-	10.27
1908A x 101-3	G	42	7.07 (4-11)	5.02 (4-7)	0.69 (0-3)	0.45 (0-1)	-	-	9.87
1908A x 103	G	33	7.12 (5-9)	5.27 (4-7)	0.64 (0-2)	0.24 (0-1)	0.09 (0-1)	-	10.09

* Environmental conditions: F=Field, G=Glasshouse.
** Means and ranges(in parentheses)

Table IIc. (continued)

Cross combination	Envir. cond.*	No. of cells observed	Chromosome pairings**						Xta per cell
			I	II	III	IV	V	VI-VIII	
1909C x 103	G	50	7.06 (4-12)	4.86 (2-7)	0.68 (0-4)	0.42 (0-1)	0.10 (0-1)	-	10.06
1911 x 103	G	37	7.03 (5-9)	3.70 (2-6)	0.95 (0-4)	0.27 (2-7)	0.27 (0-1)	0.11VI (0-1) 0.08VIII (0-1)	10.27
8460 x 103	G	50	7.52 (5-11)	5.78 (4-7)	0.58 (0-2)	0.02 (0-1)	0.02 (0-1)	-	8.42
"	F	33	7.18 (5-11)	5.67 (5-7)	0.79 (0-2)	0.03 (0-1)	-	-	9.03
8674 x 103	G	50	8.08 (5-11)	5.26 (3-7)	0.44 (0-1)	0.22 (0-1)	0.04 (0-1)	-	8.66
8700 x 103	F	50	8.38 (5-13)	5.14 (4-7)	0.62 (0-2)	0.12 (0-1)	-	-	8.40
8725 x 103	G	50	8.88 (6-13)	4.00 (2-6)	0.68 (0-3)	0.52 (0-2)	-	-	7.84
8732 x 101-1	G	46	7.33 (5-9)	5.48 (3-7)	0.46 (0-2)	0.28 (0-1)	0.04 (0-1)	-	9.94

Table IIc. (continued)

Cross combination	Envir. cond.*	No. of cells observed	Chromosome pairings**						Xta per cell
			I	II	III	IV	V	VI-VIII	
8784 x 101-1	G	44	7.84 (5-12)	5.55 (3-8)	0.48 (0-2)	0.16 (0-1)	-	-	8.85
8784 x 103	F	50	7.40 (5-11)	5.40 (3-7)	0.48 (0-2)	0.24 (0-1)	0.08 (0-1)	-	9.68
8821B x 101-1	G	54	7.02 (5-10)	5.50 (4-8)	0.46 (0-1)	0.35 (0-1)	0.04 (0-1)	-	10.21
8821B x 103	F	50	7.74 (6-13)	5.30 (4-7)	0.46 (0-2)	0.32 (0-1)	-	-	9.36
8822 x 103	F	50	7.58 (5-12)	5.40 (3-7)	0.50 (0-2)	0.18 (0-1)	0.08 (0-1)	-	9.12
8866 x 101-1	G	45	7.60 (5-11)	5.53 (4-7)	0.42 (0-2)	0.27 (0-1)	-	-	8.78

Table IId. Chromosome pairings and seed fertilities in F_1 hybrids between strains of *T. dicoccoides*

Cross * combination	No. of cells	Chromosome pairings **					Seed fert.(%)
		I	II	III	IV	V -VIII	
108-1 x 108-3	50	0.24 (0-2)	13.80 (12-14)	-	0.04 (0-1)	-	69.1
108-2 x 108-3	50	0.16 (0-2)	13.92 (13-14)	-	-	-	83.8
108-3 x 195	38	0.08 (0-2)	11.92 (10-14)	0.03 (0-1)	1.00 (0-2)	-	-
108-3 x 1957	33	0.61 (0-6)	11.36 (9-14)	0.06 (0-1)	1.12 (0-2)	-	-
108-3 x 1978B	54	0.31 (0-2)	13.63 (11-14)	0.02 (0-1)	0.09 (0-1)	-	-
108-3 x 8808	66	0.18 (0-2)	13.52 (11-14)	-	0.20 (0-1)	-	-
108-4 x 108-3	38	0.58 (0-2)	13.34 (12-14)	0.11 (0-1)	0.11 (0-1)	-	-
108-5 x 108-3	64	-	13.79 (12-14)	-	0.02 (0-1)	-	48.2
109 x 108-3	83	0.08 (0-2)	12.28 (11-14)	0.08 (0-2)	0.65 (0-1)	0.08VI (0-1)	63.0
109 x 195	38	0.08 (0-1)	10.37 (10-12)	0.08 (0-1)	1.74 (0-2)	-	-
109 x 1945	33	0.09 (0-1)	9.94 (9-10)	0.09 (0-1)	1.85 (1-2)	0.06VI (0-1)	-
109 x 8808	33	0.48 (0-2)	11.79 (11-12)	0.15 (0-1)	0.79 (0-1)	0.03V 0.03VI (0-1) (0-1)	-
110 x 108-3	83	0.14 (0-4)	13.88 (12-14)	-	0.02 (0-1)	-	88.2
195 x 108-3	25	-	12.00 (12)	-	1.00 (1)	-	3.2
195 x 109	33	0.12 (0-2)	10.67 (10-14)	0.06 (0-1)	1.55 (0-2)	0.03VI (0-1)	-
195 x 1945	25	0.04 (0-1)	11.04 (9-12)	0.48 (0-2)	0.16 (0-1)	0.04V 0.60VI (0-1) (0-1)	-
195 x 1978B	33	-	11.88 (10-12)	-	1.06 (0-2)	-	-
195 x 8808	66	0.44 (0-3)	11.45 (10-13)	0.17 (0-1)	1.02 (0-2)	0.02VI (0-1)	-

* Same as Table Ia.

** Means and ranges (in parentheses).

Table IId. (continued)

Cross * combination	No. of cells	Chromosome pairings**					Seed fert.(%)
		I	II	III	IV	V -VIII	
1921 x 108-2	33	0.58 (0-4)	12.48 (10-14)	0.09 (0-1)	0.55 (0-1)	-	74.8
1921 x 109	30	0.17 (0-2)	10.00 (9-12)	0.03 (0-1)	1.73 (1-2)	0.13VI (0-1)	-
1921 x 195	66	0.03 (0-1)	12.03 (12-14)	0.03 (0-1)	0.95 (0-1)	-	-
1921 x 8817	33	0.15 (0-3)	13.70 (11-14)	0.03 (0-1)	0.09 (0-1)	-	-
1921 x 8915A	33	-	11.88 (10-14)	-	1.06 (0-2)	-	-
1945 x 1921	33	-	11.94 (10-12)	-	1.03 (1-2)	-	20.3
1945 x 1959B	33	-	12.00 (12)	-	1.00 (1)	-	81.3
1945 x 1976B	33	0.03 (0-1)	12.00 (10-14)	0.03 (0-1)	0.97 (0-1)	-	44.7
1945 x 1978B	33	-	12.06 (12-14)	-	0.97 (0-1)	-	87.9
1945 x 8915A	66	0.05 (0-1)	10.58 (10-12)	0.05 (0-1)	1.67 (0-2)	-	-
1947 x 8935	33	-	14.00 (14)	-	-	-	63.3
1948 x 108-3	74	0.08 (0-2)	13.50 (11-14)	-	0.23 (0-1)	-	-
1948 x 109	33	-	12.18 (12-14)	-	0.91 (0-1)	-	72.0
1948 x 1921	33	-	13.94 (12-14)	-	0.03 (0-1)	-	-
1949 x 108-3	38	0.21 (0-2)	12.21 (12-14)	0.11 (0-1)	0.76 (0-1)	-	-
1949 x 109	33	0.24 (0-2)	10.33 (10-12)	0.18 (0-2)	1.64 (0-2)	-	76.9
1949 x 1921	33	0.03 (0-1)	12.06 (10-14)	0.03 (0-1)	0.94 (0-1)	-	67.2
1951 x 108-3	33	0.18 (0-2)	13.91 (13-14)	-	-	-	-
1951 x 109	66	0.12 (0-2)	12.06 (11-14)	0.06 (0-2)	0.89 (0-1)	-	85.8

Table IId. (continued)

Cross * combination	No. of cells	Chromosome pairings **					Seed fert.(%)
		I	II	III	IV	V - VIII	
1952 x 108-3	33	0.30 (0-4)	12.45 (11-14)	-	0.70 (0-1)	-	-
1952 x 109	35	-	10.37 (10-12)	-	1.71 (0-2)	0.03VI (0-1) 0.03VIII (0-1)	-
1952 x 1921	33	-	11.76 (10-14)	-	1.12 (0-2)	-	-
1952 x 8915A	33	0.12 (0-2)	10.39 (10-12)	0.06 (0-1)	1.73 (1-2)	-	-
1953 x 8935	33	-	14.00 (14)	-	-	-	72.7
1955 x 1991	33	-	14.00 (14)	-	-	-	-
1957 x 109	33	0.09 (0-2)	10.48 (10-14)	0.03 (0-1)	1.67 (0-2)	0.03VI (0-1)	51.6
1957 x 195	55	0.15 (0-2)	9.76 (8-12)	0.04 (0-1)	2.05 (1-3)	-	-
1957 x 1945	33	-	10.18 (10-12)	-	1.91 (1-2)	-	-
1957 x 1952	33	-	13.88 (12-14)	-	0.06 (0-1)	-	-
1957 x 8536	33	0.18 (0-2)	12.09 (11-14)	-	0.91 (0-1)	-	60.5
1959A x 109	33	-	11.88 (11-12)	-	0.88 (0-1)	0.12VI (0-1)	85.5
1959A x 8937B	33	0.24 (0-2)	13.82 (12-14)	-	0.03 (0-1)	-	75.0
1959B x 1921	33	-	13.57 (12-14)	-	0.21 (0-1)	-	73.6
1959B x 1949	33	-	12.00 (12)	-	1.00 (1)	-	64.2
1959B x 8536	33	0.06 (0-2)	13.97 (13-14)	-	-	-	75.4
1972B x 108-3	34	0.03 (0-1)	13.65 (12-14)	0.03 (0-1)	0.15 (0-1)	-	-
1972B x 8915A	33	0.09 (0-2)	12.09 (11-14)	0.03 (0-1)	0.91 (0-1)	-	-

Table IId. (continued)

Cross* combination	No. of cells	Chromosome pairings**					Seed fert.(%)
		I	II	III	IV	V-VIII	
1974 x 1991	33	0.12 (0-2)	13.94 (13-14)	-	-	-	-
1974 x 8915A	33	-	12.12 (12-14)	-	0.94 (0-1)	-	-
1976B x 108-3	28	-	13.86 (12-14)	-	0.07 (0-1)	-	-
1976B x 109	33	0.27 (0-2)	11.97 (11-14)	0.15 (0-1)	0.79 (0-1)	0.03VI (0-1)	51.4
1976B x 1949	33	0.03 (0-1)	12.12 (12-14)	0.03 (0-1)	0.91 (0-1)	-	31.4
1976B x 1959B	33	-	14.00 (14)	-	-	-	64.5
1976B x 1978B	33	-	14.00 (14)	-	-	-	56.1
1978B x 108-3	50	0.06 (0-2)	13.38 (12-14)	0.02 (0-1)	0.28 (0-1)	-	-
1978B x 109	33	0.12 (0-2)	12.09 (11-14)	-	0.88 (0-1)	0.03VI (0-1)	0.0
1978B x 1957	33	-	12.73 (12-14)	-	0.64 (0-1)	-	-
1978B x 1959B	33	-	14.00 (14)	-	-	-	38.4
1978B x 8915A	33	0.06 (0-2)	11.97 (11-12)	-	1.00 (1)	-	-
1991 x 108-3	34	0.26 (0-2)	13.71 (12-14)	0.03 (0-1)	0.06 (0-1)	-	-
1991 x 109	33	0.12 (0-2)	12.09 (11-14)	0.06 (0-1)	0.88 (0-1)	-	64.5
8528A x 108-3	51	-	13.96 (12-14)	-	0.02 (0-1)	-	8.0
8536 x 108-2	58	0.24 (0-2)	13.67 (12-14)	-	0.10 (0-1)	-	76.0
8536 x 108-5	50	-	13.96 (12-14)	-	0.02 (0-1)	-	-
8536 x 108-5	27	-	14.00 (14)	-	-	-	69.5

Table IId. (continued)

Cross* combination	No. of cells	Chromosome pairings **					Seed fert.(%)
		I	II	III	IV	V-VIII	
8536 x 109	23	0.22 (0-2)	11.91 (11-14)	0.04 (0-1)	0.83 (0-1)	0.09VI (0-1)	65.0
8536 x 8821C	34	-	13.94 (12-14)	-	0.03 (0-1)	-	79.2
8536 x 8915B	50	0.12 (0-2)	13.12 (11-14)	-	0.38 (0-1)	0.02VI (0-1)	51.2
8536 x 8943	25	0.24 (0-2)	13.88 (13-14)	-	-	-	70.6
8539 x 108-3	50	0.32 (0-2)	13.80 (12-14)	-	0.02 (0-1)	-	-
8541 x 108-3	33	0.42 (0-2)	13.09 (11-14)	0.06 (0-1)	0.30 (0-1)	-	62.5
8541 x 108-5	50	0.04 (0-2)	13.98 (13-14)	-	-	-	50.5
8736A x 108-5	50	-	13.96 (12-14)	-	0.02 (0-1)	-	39.4
8736A x 8817	50	0.12 (0-2)	13.86 (12-14)	-	0.04 (0-1)	-	59.3
8736A x 8821C	50	-	13.96 (12-14)	-	0.02 (0-1)	-	61.2
8736A x 8536	22	0.18 (0-2)	13.91 (13-14)	-	-	-	80.1
8736A x 8915B	50	0.16 (0-2)	13.36 (12-14)	-	0.28 (0-1)	-	41.7
8736A x 8943	37	0.16 (0-2)	13.92 (13-14)	-	-	-	51.8
8736B x 108-3	50	0.90 (0-3)	13.46 (11-14)	0.06 (0-1)	-	-	76.0
8736B x 108-5	50	-	14.00 (14)	-	-	-	47.7
8737 x 108-3	25	-	13.20 (12-14)	0.40 (0-1)	-	-	65.1
8737 x 108-5	100	0.04 (0-2)	13.98 (13-14)	-	-	-	12.7
8737 x 108-5	74	0.15 (0-2)	13.69 (12-14)	0.01 (0-1)	0.11 (0-1)	-	50.0

Table IId. (continued)

Cross * combination	No. of cells	Chromosome pairings**					Seed fert.(%)
		I	II	III	IV	V-VIII	
8804 x 108-3	50	0.20 (0-2)	13.90 (13-14)	-	-	-	74.0
8816A x 108-2	28	0.61 (0-3)	13.11 (11-14)	0.11 (0-1)	0.21 (0-1)	-	87.7
8816A x 109	48	-	11.90 (10-14)	-	0.90 (0-2)	0.10VI (0-1)	-
8816B x 108-3	50	0.12 (0-2)	13.86 (12-14)	-	0.04 (0-1)	-	77.5
8817 x 108-2	29	0.34 (0-2)	13.62 (11-14)	-	0.10 (0-1)	-	68.9
8817 x 108-5	50	-	14.00 (14)	-	-	-	-
8817 x 8536	50	0.20 (0-4)	13.90 (12-14)	-	-	-	85.3
8817 x 8821C	50	-	14.00 (14)	-	-	-	67.7
8817 x 8915B	50	0.24 (0-4)	13.44 (12-14)	-	0.22 (0-1)	-	8.2
8817 x 8935	23	-	14.00 (14)	-	-	-	83.0
8817 x 8943	50	0.12 (0-2)	13.94 (13-14)	-	-	-	79.7
8821A x 108-3	50	0.04 (0-2)	13.86 (12-14)	-	0.06 (0-1)	-	72.0
8821C x 108-3	66	0.03 (0-2)	13.68 (12-14)	-	0.15 (0-1)	-	75.4
8821C x 8943	50	-	13.92 (12-14)	-	0.04 (0-1)	-	51.6
8915A x 108-3	67	0.27 (0-2)	12.42 (10-14)	0.09 (0-1)	0.66 (0-2)	-	73.6
8915A x 109	33	-	11.12 (11-12)	-	0.12 (0-1)	0.88VI (0-1)	-
8915A x 195	33	0.24 (0-2)	10.27 (10-12)	0.06 (0-1)	1.76 (1-2)	-	5.8
8915A x 1921	33	0.09 (0-2)	11.55 (9-12)	0.03 (0-1)	1.18 (0-2)	-	-

Table IId. (continued)

Cross* combination	No. of cells	Chromosome pairings**					Seed
		I	II	III	IV	V-VIII	
8915A x 8915B	66	0.15 (0-2)	13.92 (13-14)	-	-	-	44.5
8915B x 108-3	38	0.68 (0-3)	12.24 (9-14)	0.11 (0-1)	0.63 (0-1)	-	78.4
8915B x 108-5	61	0.16 (0-2)	12.72 (11-14)	0.03 (0-1)	0.57 (0-1)	-	43.3
8915B x 109	33	0.03 (0-1)	11.15 (11-12)	0.15 (0-2)	0.12 (0-1)	0.79VI (0-1)	36.6
8915B x 195	33	0.12 (0-2)	10.79 (9-14)	-	1.58 (0-2)	-	-
8915B x 8821C	50	0.04 (0-2)	13.42 (12-14)	-	0.28 (0-1)	-	53.2
8935 x 108-3	54	0.06 (0-3)	13.69 (11-14)	0.02 (0-1)	0.13 (0-1)	-	69.5
8935 x 108-5	50	-	14.00 (14)	-	-	-	74.4
8935 x 8536	50	-	14.00 (14)	-	-	-	59.4
8935 x 8736A	50	0.36 (0-4)	13.82 (12-14)	-	-	-	58.6
8935 x 8821C	50	-	14.00 (14)	-	-	-	74.6
8935 x 8915B	50	0.12 (0-2)	13.38 (12-14)	-	0.28 (0-1)	-	49.3
8935 x 8943	50	0.76 (0-4)	13,62 (12-14)	-	-	-	59.2
8937B x 108-3	50	0.12 (0-2)	13.94 (13-14)	-	-	-	31.2
8937B x 108-5	50	0.12 (0-2)	13.94 (13-14)	-	-	-	74.2
8941 x 108-2	55	0.07 (0-2)	12.82 (12-14)	0.04 (0-1)	0.55 (0-1)	-	70.8
8941 x 108-5	50	0.08 (0-2)	13.88 (12-14)	-	0.04 (0-1)	-	40.3
8942 x 108-2	24	0.79 (0-2)	13.13 (11-14)	0.04 (0-1)	0.21 (0-1)	-	84.2

Table IId. (continued)

Cross* combination	No. of cells	Chromosome pairings**					Seed fert. (%)
		I	II	III	IV	V-VIII	
8942 x 108-3	50	0.34 (0-2)	13.40 (12-14)	0.02 (0-1)	0.20 (0-1)	-	72.5
8942 x 195	33	0.06 (0-2)	12.03 (10-14)	-	0.97 (0-2)	-	31.0
8943 x 108-3	33	0.30 (0-2)	13.15 (12-14)	0.06 (0-1)	0.30 (0-1)	-	78.6
8943 x 108-5	50	0.08 (0-2)	13.96 (13-14)	-	-	-	54.8
8943 x 8536	50	0.08 (0-2)	13.96 (13-14)	-	-	-	90.3
8943 x 8915A	50	0.08 (0-2)	13.48 (13-14)	-	0.24 (0-1)	-	66.1

Table IIe. Chromosome pairings and seed fertilities in F_1 hybrids between strains of the timopheevi wheats

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
107-1 x 8866	61	0.38 (0-3)	11.34 (9-14)	0.31 (0-1)	1.00 (0-2)	-	-	-	0.0
196-1 x 8715	33	0.45 (0-2)	9.39 (7-12)	-	2.03 (1-3)	0.09 (0-1)	0.03 (0-1)	-	-
196-2 x 107-1	100	0.16 (0-2)	13.92 (13-14)	-	-	-	-	-	31.3
196-2 x 107-1	63	0.06 (0-2)	13.97 (13-14)	-	-	-	-	-	-
1907A x 107-1	35	-	12.11 (12-14)	-	0.94 (0-1)	-	-	-	-
1907A x 196-1	33	0.18 (0-2)	10.48 (9-12)	0.12 (0-1)	0.21 (0-1)	-	0.94 (0-1)	-	-
1907B x 1901	33	-	12.24 (12-14)	-	0.88 (0-1)	-	-	-	-
1908A x 196-1	50	0.08 (0-2)	11.20 (9-14)	0.08 (0-2)	0.42 (0-2)	-	0.60 (0-1)	-	-
1908A x 1909B	33	-	14.00 (14)	-	-	-	-	-	-
1908A x 1911	33	-	8.67 (8-10)	-	2.67 (2-3)	-	-	-	-
1908A x 1985	33	0.03 (0-1)	10.55 (01-12)	0.03 (0-1)	1.70 (1-2)	-	-	-	-

* Same as Table Ic.

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	Ⅲ	IV	V	VI	VII-XII	
1908A x 8460	33	-	9.18 (9-11)	-	1.00 (0-2)	-	0.94 (0-1)	-	-
1908A x 8567	66	0.05 (0-1)	10.06 (10-12)	0.05 (0-1)	1.92 (1-2)	-	-	-	-
1908A x 8713	33	0.03 (0-1)	7.36 (7-9)	0.06 (0-2)	2.09 (1-3)	0.03 (0-1)	0.76 (0-1)	-	-
1908A x 8732	54	0.07 (0-1)	10.74 (10-12)	0.07 (0-1)	1.56 (1-2)	-	-	-	-
1908A x 8732	33	-	10.61 (10-14)	-	1.70 (0-2)	-	-	-	-
1908A x 8784	50	0.20 (0-1)	10.00 (8-11)	0.14 (0-2)	0.34 (0-3)	0.08 (0-1)	0.06 (0-1)	0.18VII (0-1) 0.50VⅢ (0-1)	-
1908A x 8824A	33	0.06 (0-1)	11.15 (11-12)	-	0.15 (0-1)	0.06 (0-1)	0.79 (0-1)	-	-
1908A x 8824B	33	0.09 (0-2)	11.12 (10-12)	0.09 (0-2)	0.12 (0-1)	-	0.82 (0-1)	-	-
1908B x 196-1	50	0.50 (0-3)	10.06 (9-12)	0.26 (0-1)	0.42 (0-2)	-	0.82 (0-1)	-	-
1908B x 1901	33	0.09 (0-2)	12.15 (11-14)	0.03 (0-1)	0.88 (0-1)	-	-	-	-
1909A x 107-1	38	0.13 (0-2)	12.03 (11-14)	0.08 (0-1)	0.89 (0-1)	-	-	-	-
1909A x 1907A	33	-	14.00 (14)	-	-	-	-	-	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
1909A x 1908A	33	-	14.00 (14)	-	-	-	-	-	-
1909B x 107-1	33	-	12.06 (12-14)	-	0.97 (0-1)	-	-	-	-
1909B x 196-1	29	0.03 (0-1)	11.10 (9-12)	0.10 (0-2)	0.38 (0-1)	-	0.66 (0-1)	-	-
1909B x 1907A	33	-	14.00 (14)	-	-	-	-	-	-
1909C x 107-1	33	0.03 (0-1)	10.79 (10-12)	0.03 (0-1)	1.58 (1-2)	-	-	-	-
1909C x 196-1	64	0.05 (0-1)	9.16 (7-11)	0.08 (0-2)	0.97 (0-2)	-	0.92 (0-1)	-	-
1909C x 1911	29	0.10 (0-1)	7.24 (7-10)	0.10 (0-1)	1.83 (1-2)	-	0.97 (0-1)	-	-
1909C x 8714A	33	0.03 (0-1)	9.15 (9-11)	-	1.06 (0-2)	0.03 (0-1)	0.88 (0-1)	-	-
1909C x 8725	33	0.21 (0-1)	6.36 (6-8)	0.21 (0-1)	3.61 (2-4)	-	-	-	-
1909C x 8732	33	0.18 (0-1)	10.06 (10-12)	0.18 (0-1)	1.79 (1-2)	-	-	-	-
1909C x 8866	33	0.03 (0-1)	7.58 (7-10)	-	2.12 (1-3)	0.03 (0-1)	0.70 (0-1)	-	-
1911 x 107-1	37	-	10.30 (9-12)	-	1.81 (1-2)	-	0.03 (0-1)	-	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
1911 x 107-1	33	0.03 (0-1)	10.30 (10-12)	0.03 (0-1)	1.82 (1-2)	-	-	-	-
1911 x 196-1	50	0.14 (0-1)	8.28 (7-10)	0.24 (0-2)	1.96 (1-3)	0.02 (0-1)	0.44 (0-1)	-	-
1911 x 8460	33	-	7.18 (7-9)	-	1.91 (1-2)	-	1.00 (1)	-	-
1911 x 8714A	33	0.12 (0-2)	8.27 (7-10)	0.06 (0-1)	2.79 (2-3)	-	-	-	-
1911 x 8725	33	0.30 (0-3)	6.67 (6-9)	0.36 (0-2)	1.91 (0-4)	0.06 (0-1)	0.24 (0-1)	0.48VIII (0-1)	-
1911 x 8732	33	-	9.15 (9-12)	-	0.97 (0-1)	-	0.97 (0-1)	-	-
1911 x 8784	17	0.29 (0-2)	8.35 (8-9)	0.59 (0-2)	1.24 (0-3)	0.18 (0-1)	0.18 (0-1)	0.29VIII (0-1)	-
1911 x 8866	33	0.15 (0-1)	7.24 (7-9)	0.21 (0-2)	1.97 (1-3)	0.06 (0-1)	0.76 (0-1)	-	-
1914 x 107-1	50	0.04 (0-2)	13.98 (13-14)	-	-	-	-	-	-
1914 x 196-1	30	0.27 (0-2)	12.53 (10-14)	0.13 (0-1)	0.47 (0-2)	-	0.07 (0-1)	-	62.2
1923 x 107-1	33	-	14.00 (14)	-	-	-	-	-	64.1
1924 x 107-1	33	-	14.00 (14)	-	-	-	-	-	74.6

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
1925 x 107-1	25	-	14.00 (14)	-	-	-	-	-	-
1926A x 107-1	33	0.06 (0-2)	13.97 (13-14)	-	-	-	-	-	29.5
1927 x 107-1	33	-	14.00 (14)	-	-	-	-	-	89.2
1928 x 107-1	33	0.06 (0-2)	13.97 (13-14)	-	-	-	-	-	74.4
1929 x 107-1	29	0.07 (0-2)	13.97 (13-14)	-	-	-	-	-	-
1931 x 107-1	66	0.03 (0-2)	13.98 (13-14)	-	-	-	-	-	90.4
1932 x 107-1	30	0.07 (0-2)	13.97 (13-14)	-	-	-	-	-	-
1933 x 107-1	61	-	13.97 (12-14)	-	0.02 (0-1)	-	-	-	-
1933 x 1908A	33	-	12.06 (12-14)	-	0.97 (0-1)	-	-	-	-
1934 x 107-1	33	-	13.94 (12-14)	-	0.03 (0-1)	-	-	-	80.0
1935 x 107-1	31	-	14.00 (14)	-	-	-	-	-	-
1936 x 107-1	27	-	14.00 (14)	-	-	-	-	-	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges) I	II	III	IV	V	VI	VII-XII	Seed fert.(%)
1937 x 107-1	51	0.12 (0-4)	13.94 (12-14)	-	-	-	-	-	-
1938 x 107-1	33	-	12.30 (12-14)	-	0.85 (0-1)	-	-	-	72.1
1938 x 196-1	33	0.09 (0-1)	10.30 (10-12)	0.09 (0-1)	1.76 (1-2)	-	-	-	68.3
1939 x 107-1	30	-	14.00 (14)	-	-	-	-	-	-
1943 x 107-1	33	0.09 (0-2)	12.33 (12-14)	0.03 (0-1)	0.79 (0-1)	-	-	-	71.2
1946 x 107-1	27	0.07 (0-2)	12.19 (11-14)	-	0.89 (0-1)	-	-	-	-
1950 x 107-1	28	-	12.14 (12-14)	-	0.93 (0-1)	-	-	-	-
1958 x 107-1	61	-	12.33 (12-14)	-	0.84 (0-1)	-	-	-	-
1958 x 196-1	44	0.84 (0-2)	10.07 (8-12)	0.34 (0-2)	1.50 (0-3)	-	-	-	-
1960 x 107-1	31	-	13.74 (12-14)	-	0.13 (0-1)	-	-	-	-
1962 x 107-1	35	-	12.23 (12-14)	-	0.89 (0-1)	-	-	-	-
1962 x 1908A	26	-	10.38 (10-12)	-	1.81 (1-2)	-	-	-	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
1963 x 107-1	28	-	14.00 (14)	-	-	-	-	-	-
1963 x 107-1	29	-	12.21 (12-14)	-	0.90 (0-1)	-	-	-	-
1964 x 107-1	27	-	14.00 (14)	-	-	-	-	-	-
1965 x 107-1	25	-	14.00 (14)	-	-	-	-	-	-
1966 x 107-1	23	0.09 (0-2)	11.96 (11-12)	-	1.00 (1)	-	-	-	-
1967 x 107-1	31	-	11.06 (11-12)	-	0.06 (0-1)	-	0.94 (0-1)	-	-
1967 x 196-1	21	0.38 (0-2)	9.62 (8-12)	-	0.90 (0-2)	-	0.67 (0-1)	0.10VIII (0-1)	-
1969 x 107-1	31	0.06 (0-2)	13.97 (13-14)	-	-	-	-	-	-
1969 x 196-1	34	0.12 (0-2)	12.09 (10-14)	0.06 (0-1)	0.88 (0-2)	-	-	-	-
1972A x 107-1	33	-	10.61 (10-12)	0.03 (0-1)	1.64 (0-2)	0.03 (0-1)	-	-	12.3
1978A x 107-1	66	-	14.00 (14)	-	-	-	-	-	54.5
1979A x 107-1	33	0.18 (0-2)	12.03 (11-14)	-	0.94 (0-1)	-	-	-	66.0

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
1979B x 107-1	33	0.09 (0-2)	12.03 (11-14)	0.03 (0-1)	0.94 (0-1)	-	-	-	-
1979B x 1979A	20	0.20 (0-2)	13.90 (13-14)	-	-	-	-	-	-
1979B x 8784	33	0.03 (0-1)	11.00 (11)	0.42 (0-2)	0.03 (0-1)	0.76 (0-1)	-	-	-
1980A x 107-1	32	-	12.25 (12-14)	-	0.88 (0-1)	-	-	-	-
1980A x 1908A	31	-	10.39 (10-12)	-	1.81 (1-2)	-	-	-	-
1980B x 107-1	33	-	12.00 (12)	-	1.00 (1)	-	-	-	73.2
1981A x 107-1	23	-	12.17 (12-14)	-	0.91 (0-1)	-	-	-	-
1981B x 107-1	33	-	12.12 (12-14)	-	0.94 (0-1)	-	-	-	75.0
1982 x 107-1	66	0.09 (0-2)	12.16 (11-14)	-	0.89 (0-1)	-	-	-	-
1983 x 107-1	43	0.05 (0-2)	11.98 (11-14)	-	0.86 (0-1)	-	0.09 (0-1)	-	-
1985 x 107-1	66	0.06 (0-2)	12.18 (11-14)	-	0.89 (0-1)	-	-	-	86.0
1986 x 107-1	33	0.06 (0-2)	12.21 (11-14)	-	0.88 (0-1)	-	-	-	-

Table IIe. (continued)

Cross* combination	No. of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
1987 x 107-1	37	0.08 (0-2)	12.46 (11-14)	0.03 (0-1)	0.73 (0-1)	-	-	-	-
1987 x 107-1	33	0.06 (0-2)	11.91 (10-14)	-	1.03 (0-2)	-	-	-	-
1988 x 107-1	33	-	12.12 (12-14)	-	0.94 (0-1)	-	-	-	76.8
1990 x 107-1	30	0.13 (0-2)	12.20 (11-14)	-	0.87 (0-1)	-	-	-	-
8456 x 8561	30	-	14.00 (14)	-	-	-	-	-	-
8460 x 196-1	26	0.15 (0-2)	9.12 (8-10)	0.08 (0-2)	2.35 (1-3)	-	-	-	-
8460 x 8561	57	0.04 (0-2)	10.53 (9-14)	-	1.65 (0-2)	-	0.05 (0-1)	-	74.3
8460 x 8567	33	-	10.06 (10-11)	0.03 (0-1)	-	0.03 (0-1)	0.06 (0-1)	0.91VIII (0-1)	-
8460 x 8572	33	-	10.03 (9-11)	-	-	-	0.06 (0-1)	0.91VIII (0-1) 0.03X (0-1)	-
8460 x 8674	59	0.22 (0-2)	9.46 (8-12)	0.19 (0-2)	0.97 (0-2)	0.03 (0-1)	0.71 (0-1)	-	-
8460 x 8713	33	0.03 (0-1)	7.27 (7-8)	0.09 (0-2)	0.03 (0-1)	0.06 (0-2)	1.15 (0-2)	0.73VIII (0-1)	-
8460 x 8719	30	-	9.33 (9-11)	-	0.83 (0-1)	-	1.00 (1)	-	-

Table IIe. (continued)

Cross* combination	No. of cells	Chromosome pairings (means and ranges) I	II	III	IV	V	VI	VII-XII	Seed fert. (%)
8460 x 8725	66	0.15 (0-2)	6.61 (6-10)	0.09 (0-1)	3.59 (2-4)	-	-	-	-
8460 x 8732	26	0.04 (0-1)	10.15 (10-12)	0.04 (0-1)	0.12 (0-2)	0.04 (0-1)	0.08 (0-1)	0.04VII (0-1) 0.77VIII (0-1)	-
8460 x 8784	33	-	11.12 (11-12)	0.18 (0-2)	0.12 (0-1)	-	0.79 (0-1)	-	-
8460 x 8866	33	0.06 (0-1)	7.70 (7-11)	0.12 (0-2)	2.00 (0-3)	-	0.70 (0-1)	-	-
8469 x 8561	33	-	14.00 (14)	-	-	-	-	-	98.5
8478 x 8561	50	-	14.00 (14)	-	-	-	-	-	81.5
8491 x 8561	50	0.08 (0-2)	13.96 (13-14)	-	-	-	-	-	93.8
8497 x 8561	50	0.08 (0-2)	12.16 (11-14)	-	0.90 (0-1)	-	-	-	90.5
8497 x 8719	33	-	10.24 (10-12)	-	1.88 (1-2)	-	-	-	-
8497 x 8784	33	-	10.00 (9-11)	0.06 (0-1)	0.09 (0-2)	0.06 (0-1)	0.12 (0-1)	0.73VIII (0-1) 0.06X (0-1)	-
8500 x 8561	37	0.05 (0-2)	12.46 (11-14)	-	0.76 (0-1)	-	-	-	76.3
8500 x 8784	33	0.03 (0-1)	10.12 (10-12)	0.12 (0-1)	0.09 (0-2)	0.15 (0-1)	0.03 (0-1)	0.76VIII (0-1)	-

Table IIe. (continued)

Cross* combination	No. of cells	Chromosome pairings (means and ranges)							Seed fert. (%)
		I	II	III	IV	V	VI	VII-XII	
8514A x 8718	55	-	12.18 (12-14)	-	0.91 (0-1)	-	-	-	67.8
8514A x 8719	33	0.06 (0-2)	10.27 (9-12)	-	0.48 (0-2)	-	0.91 (0-1)	-	-
8514A x 8732	33	-	9.82 (8-12)	-	2.09 (1-3)	-	-	-	-
8521 x 107-1	33	0.55 (0-2)	11.85 (11-14)	-	0.94 (0-1)	-	-	-	-
8521 x 8714A	22	0.68 (0-5)	10.05 (8-12)	0.23 (0-2)	1.64 (0-2)	-	-	-	-
8521 x 8784	33	0.09 (0-2)	10.18 (10-11)	0.30 (0-2)	0.15 (0-2)	0.15 (0-1)	0.15 (0-1)	0.05VIII (0-1)	-
8528A x 107-1	38	0.11 (0-2)	13.89 (12-14)	-	0.03 (0-1)	-	-	-	-
8528A x 8719	32	-	12.13 (12-14)	-	0.94 (0-1)	-	-	-	-
8529 x 107-1	33	0.06 (0-2)	13.97 (13-14)	-	-	-	-	-	-
8529 x 8714A	30	-	12.20 (12-14)	-	0.90 (0-1)	-	-	-	-
8543 x 8561	50	-	14.00 (14)	-	-	-	-	-	97.4
8544 x 196-1	33	0.48 (0-4)	10.82 (9-12)	-	1.12 (0-2)	0.06 (0-1)	0.18 (0-1)	-	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
8544 x 8561	50	0.16 (0-2)	11.96 (11-14)	-	0.98 (0-1)	-	-	-	85.7
8544 x 8784	33	-	9.18 (9-11)	0.12 (0-2)	1.00 (1-2)	-	0.88 (0-1)	-	-
8544 x 8866	34	0.29 (0-2)	13.03 (10-14)	-	0.41 (0-2)	-	-	-	61.9
8551 x 196-1	33	0.97 (0-2)	11.85 (10-14)	0.18 (0-1)	0.70 (0-2)	-	-	-	-
8551 x 9561	36	-	13.94 (12-14)	-	0.03 (0-1)	-	-	-	-
8551 x 8719	33	-	12.00 (12)	-	1.00 (1)	-	-	-	-
8561 x 8662	32	0.06 (0-2)	11.94 (11-12)	0.06 (0-2)	0.97 (0-1)	-	-	-	-
8561 x 8718	50	-	14.00 (14)	-	-	-	-	-	96.2
8567 x 8514	22	-	11.45 (10-12)	-	1.14 (0-2)	-	0.09 (0-1)	-	79.7
8567 x 8561	69	0.07 (0-1)	12.30 (11-14)	0.01 (0-1)	0.80 (0-1)	-	0.01 (0-1)	-	91.9
8567 x 8572	33	0.06 (0-2)	13.97 (13-14)	-	-	-	-	-	-
8567 x 8713	33	0.03 (0-1)	9.52 (9-11)	-	0.06 (0-1)	0.06 (0-2)	0.12 (0-1)	0.03VII, 0.36VIII, 0.45X (0-1) (0-1) (0-1)	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
8567 x 8714A	27	0.07 (0-1)	11.11 (11-12)	0.04 (0-1)	0.07 (0-1)	0.04 (0-1)	0.85 (0-1)	-	-
8567 x 8725	33	0.18 (0-2)	8.30 (8-10)	0.06 (0-1)	2.74 (2-3)	-	-	-	-
8567 x 8732	33	0.06 (0-2)	13.97 (13-14)	-	-	-	-	-	-
8567 x 8866	21	0.19 (0-1)	9.43 (9-11)	0.19 (0-1)	0.81 (0-2)	-	0.86 (0-1)	-	-
8572 x 196-1	55	0.11 (0-2)	10.24 (8-12)	-	1.85 (1-3)	-	-	-	-
8572 x 8601	45	0.04 (0-2)	10.29 (10-12)	-	1.84 (1-2)	-	-	-	-
8572 x 8674	33	0.30 (0-4)	11.12 (9-12)	0.91 (0-2)	0.09 (0-1)	-	0.39 (0-1)	-	-
8572 x 8714A	30	-	10.93 (10-12)	0.03 (0-1)	0.17 (0-2)	0.03 (0-1)	0.87 (0-1)	-	-
8572 x 8784	33	-	10.94 (10-11)	-	-	-	0.94 (0-1)	0.06VIII (0-1)	-
8593 x 107-1	50	0.24 (0-2)	13.84 (12-14)	-	0.02 (0-1)	-	-	-	3.1
8593 x 8561	26	-	13.92 (12-14)	-	0.04 (0-1)	-	-	-	-
8597 x 8561	50	0.12 (0-2)	13.94 (13-14)	-	-	-	-	-	100.0

Table IIe. (continued)

Cross* combination	No. of cells	Chromosome pairings (means and ranges)							Seed fert. (%)
		I	II	III	IV	V	VI	VII-XII	
8601 x 196-1	27	0.26 (0-2)	10.30 (9-12)	0.07 (0-2)	1.30 (0-2)	0.04 (0-1)	0.26 (0-1)	-	-
8601 x 8514A	72	-	11.08 (11-14)	0.08 (0-2)	0.04 (0-1)	-	0.90 (0-1)	-	70.5
8601 x 8514A	32	-	11.06 (11-12)	-	0.06 (0-1)	-	0.94 (0-1)	-	-
8601 x 8561	29	0.07 (0-2)	11.97 (11-12)	-	1.00 (1)	-	-	-	-
8601 x 8719	32	-	11.03 (11-12)	-	0.03 (0-1)	-	0.97 (0-1)	-	-
8616 x 8561	50	0.12 (0-2)	13.94 (13-14)	-	-	-	-	-	91.7
8662 x 196-1	38	0.13 (0-2)	10.24 (8-12)	0.13 (0-2)	1.71 (0-3)	-	0.03 (0-1)	-	-
8662 x 8561	72	2.08 (0-6)	11.53 (9-14)	0.14 (0-2)	0.61 (0-1)	-	-	-	-
8662 x 8719	32	0.16 (0-2)	10.91 (10-11)	0.19 (0-2)	-	0.03 (0-1)	0.84 (0-1)	0.03VIII (0-1)	-
8662 x 8784	27	0.11 (0-1)	10.11 (10-11)	0.07 (0-1)	0.07 (0-1)	-	0.11 (0-1)	0.04VII (0-1) 0.78VIII (0-1)	-
8668 x 8561	50	0.16 (0-2)	12.36 (11-14)	-	0.78 (0-1)	-	-	-	85.5
8668 x 8719	34	0.06 (0-1)	10.18 (10-12)	0.06 (0-1)	1.85 (1-2)	-	-	-	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)								Seed fert.(%)
		I	II	Ⅲ	IV	V	VI	VII-XII		
8668 x 8784	33	0.06 (0-1)	10.12 (10-12)	0.21 (0-1)	0.55 (0-2)	0.18 (0-1)	0.06 (0-1)	0.03VII (0-1)	0.42VⅢ (0-1)	-
8673 x 8561	50	0.12 (0-2)	13.94 (13-14)	-	-	-	-	-		94.1
8674 x 1908A	33	0.15 (0-2)	10.97 (10-12)	-	0.03 (0-1)	0.03 (0-1)	0.94 (0-1)	-		-
8674 x 8593	59	0.29 (0-2)	13.08 (11-14)	0.02 (0-1)	0.37 (0-1)	-	-	-		97.3
8674 x 8784	33	0.15 (0-2)	10.00 (9-11)	0.06 (0-1)	0.64 (0-2)	0.06 (0-1)	-	0.03VII (0-1)	0.58VⅢ (0-1)	-
8682 x 1908A	64	0.25 (0-3)	11.59 (9-14)	0.09 (0-2)	1.05 (0-2)	-	0.02 (0-1)	-		-
8682 x 8700	36	0.22 (0-3)	11.97 (11-12)	0.17 (0-1)	0.83 (0-1)	-	-	-		-
8697 x 8561	100	0.16 (0-2)	13.92 (13-14)	-	-	-	-	-		94.4
8707 x 8700	30	0.20 (0-2)	13.83 (12-14)	-	0.03 (0-1)	-	-	-		-
8709 x 8700	50	0.28 (0-4)	13.86 (12-14)	-	-	-	-	-		93.0
8711 x 8561	100	0.04 (0-2)	13.98 (13-14)	-	-	-	-	-		95.2
8712 x 8561	50	0.28 (0-2)	13.86 (13-14)	-	-	-	-	-		-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
8713 x 196-1	15	0.53 (0-2)	8.53 (7-10)	0.27 (0-2)	1.00 (0-3)	0.13 (0-1)	0.67 (0-2)	0.13VII (0-1)	-
8713 x 8561	29	0.14 (0-1)	9.10 (9-11)	0.21 (0-2)	0.86 (0-2)	-	0.93 (0-1)	-	-
8713 x 8719	33	0.06 (0-2)	9.12 (7-11)	-	0.97 (0-2)	-	0.97 (0-1)	-	-
8713 x 8725	33	0.09 (0-1)	6.88 (6-10)	0.09 (0-1)	2.03 (1-4)	-	0.03 (0-1)	0.70VIII (0-1)	-
8713 x 8784	19	0.11 (0-2)	8.47 (7-10)	0.21 (0-1)	0.32 (0-2)	0.26 (0-1)	-	0.11VII,0.21VIII, 0.16IX (0-1) (0-1) (0-1) 0.26X, 0.11XII (0-1) (0-1)	-
8714A x 1908A	60	0.17 (0-2)	11.75 (10-14)	0.13 (0-1)	0.98 (0-2)	-	-	-	-
8714A x 8567	20	-	10.60 (9-11)	-	0.10 (0-1)	-	0.80 (0-1)	0.20VIII (0-1)	76.5
8714A x 8784	24	-	10.63 (9-12)	0.08 (0-2)	0.21 (0-2)	-	0.38 (0-1)	0.38VIII 0.04X (0-1) (0-1)	54.2
8714A x 8827	38	0.05 (0-2)	12.08 (11-14)	-	0.95 (0-1)	-	-	-	40.1
8714A x 8866	61	0.08 (0-1)	9.08 (9-12)	0.05 (0-1)	0.93 (0-1)	0.03 (0-1)	0.95 (0-1)	-	7.4
8715 x 107-1	33	0.09 (0-2)	10.33 (9-12)	0.03 (0-1)	1.79 (1-2)	-	-	-	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
8715 x 8713	33	0.03 (0-1)	10.09 (10-11)	0.03 (0-1)	0.09 (0-1)	-	0.09 (0-1)	0.85VIII (0-1)	-
8715 x 8714A	12	-	10.00 (10)	-	2.00 (2)	-	-	-	-
8715 x 8784	18	-	9.11 (8-10)	-	-	-	-	0.17VIII, 0.78X, 0.06XII (0-1) (0-1) (0-1)	-
8718A x 8674	67	0.12 (0-2)	12.04 (11-14)	-	0.93 (0-1)	-	0.02 (0-1)	-	76.0
8718A x 8714A	23	-	12.00 (12)	-	1.00 (1)	-	-	-	76.9
8719 x 8514A	50	0.04 (0-2)	11.10 (11-13)	-	0.06 (0-1)	-	0.92 (0-1)	-	66.3
8719 x 8674	79	0.09 (0-1)	10.29 (10-12)	0.11 (0-2)	1.75 (0-2)	-	-	-	22.2
8719 x 8714A	50	-	14.00 (14)	-	-	-	-	-	82.9
8719 x 8784	38	0.11 (0-1)	11.08 (10-14)	0.11 (0-2)	0.16 (0-2)	-	0.45 (0-1)	0.26VIII (0-1)	54.6
8719 x 8866	50	0.10 (0-1)	9.12 (9-11)	0.10 (0-1)	0.84 (0-1)	-	1.00 (1)	-	38.7
8720 x 107-1	22	0.05 (0-1)	12.18 (12-14)	0.05 (0-1)	0.86 (0-1)	-	-	-	-
8720 x 8561	50	0.12 (0-2)	12.32 (11-14)	0.04 (0-1)	0.78 (0-1)	-	-	-	89.2

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges) I	II	Ⅲ	IV	V	VI	VII-XII	Seed fert.(%)
8720 x 8719	30	-	11.00 (11)	-	-	-	1.00 (1)	-	-
8720 x 8866	33	0.03 (0-1)	9.24 (9-12)	0.15 (0-2)	1.03 (0-2)	-	0.82 (0-1)	-	-
8724 x 8718A	24	0.25 (0-2)	13.79 (12-14)	-	0.04 (0-1)	-	-	-	-
8724 x 8719	33	0.15 (0-2)	12.03 (11-14)	0.09 (0-1)	0.88 (0-1)	-	-	-	-
8725 x 196-1	33	0.91 (0-3)	10.30 (7-12)	0.06 (0-1)	1.42 (0-3)	0.12 (0-1)	-	-	-
8725 x 1908A	33	0.12 (0-1)	8.85 (8-10)	0.12 (0-1)	2.45 (1-3)	-	-	-	-
8725 x 8561	53	0.08 (0-1)	10.94 (10-14)	0.08 (0-1)	1.45 (0-2)	-	-	-	85.1
8725 x 8714A	33	0.06 (0-2)	8.88 (7-12)	-	2.55 (1-3)	-	-	-	-
8725 x 8784	33	0.24 (0-2)	8.18 (7-11)	0.06 (0-1)	1.39 (0-2)	-	0.94 (0-1)	-	-
8729 x 8561	50	0.10 (0-1)	12.12 (12-14)	0.10 (0-1)	0.84 (0-1)	-	-	-	73.0
8729 x 8714A	28	-	11.04 (11-12)	0.07 (0-2)	0.04 (0-1)	-	0.93 (0-1)	-	-
8729 x 8784	27	-	10.11 (10-11)	-	-	-	0.11 (0-1)	0.89VIII (0-1)	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
8731 x 107-1	39	0.05 (0-2)	13.97 (13-14)	-	-	-	-	-	-
8731 x 8700	43	0.19 (0-2)	13.91 (13-14)	-	-	-	-	-	-
8732 x 1908A	56	0.09 (0-1)	10.32 (8-14)	0.09 (0-1)	1.57 (0-2)	-	-	-	44.7
8732 x 8572	33	0.06 (0-2)	13.97 (13-14)	-	-	-	-	-	-
8732 x 8674	64	0.06 (0-1)	11.13 (11-12)	0.20 (0-2)	0.08 (0-1)	0.02 (0-1)	0.78 (0-1)	-	54.0
8732 x 8674	33	0.06 (0-2)	11.09 (11-12)	0.48 (0-2)	0.12 (0-1)	-	0.64 (0-1)	-	-
8732 x 8713	33	-	9.21 (9-10)	-	0.06 (0-1)	0.06 (0-2)	0.06 (0-1)	0.21VIII (0-1) 0.70X (0-1)	-
8732 x 8714A	40	-	11.05 (11-12)	0.05 (0-2)	0.05 (0-1)	-	0.93 (0-1)	-	35.0
8732 x 8719	40	-	11.38 (11-14)	-	0.08 (0-1)	-	0.83 (0-1)	-	63.8
8732 x 8725	33	0.33 (0-2)	8.70 (8-10)	0.15 (0-1)	2.45 (1-3)	-	-	-	-
8733 x 8469	50	0.04 (0-2)	13.26 (11-14)	-	0.36 (0-1)	-	-	-	86.5
8733 x 8593	50	0.12 (0-2)	13.46 (12-14)	-	0.24 (0-1)	-	-	-	81.9

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (neans and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
8733 x 8674	23	0.70 (0-6)	12.96 (10-14)	-	0.35 (0-2)	-	-	-	71.0
8733 x 8700	50	0.20 (0-2)	12.14 (11-14)	-	0.88 (0-1)	-	-	-	81.7
8733 x 8732	33	-	11.09 (10-12)	-	0.18 (0-2)	-	0.85 (0-1)	-	-
8733 x 8784	50	0.04 (0-2)	9.96 (8-12)	-	0.02 (0-1)	-	0.10 (0-1)	0.74VIII,0.12X,0.02XII (0-1) (0-1) (0-1)	48.9
8733 x 8784	24	0.04 (0-1)	10.13 (10-11)	0.04 (0-1)	0.25 (0-2)	0.04 (0-1)	0.13 (0-1)	0.04VII 0.67VIII (0-1) (0-1)	-
8733 x 8866	26	0.04 (0-1)	8.54 (8-10)	0.04 (0-1)	2.69 (2-3)	-	-	-	-
8733 x 8912	50	0.46 (0-4)	13.22 (11-14)	0.02 (0-1)	0.26 (0-1)	-	-	-	76.0
8734 x 107-1	50	0.16 (0-2)	13.72 (12-14)	-	0.10 (0-1)	-	-	-	6.0
8734 x 8732	24	0.04 (0-1)	11.04 (11-12)	0.17 (0-2)	0.04 (0-1)	0.04 (0-1)	0.83 (0-1)	-	-
8735 x 107-1	33	0.33 (0-2)	13.79 (12-14)	0.03 (0-1)	-	-	-	-	-
8735 x 107-1	33	-	13.88 (12-14)	-	0.06 (0-1)	-	-	-	5.9
8742 x 8718A	25	-	14.00 (14)	-	-	-	-	-	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
8761 x 107-1	50	0.12 (0-2)	13.94 (13-14)	-	-	-	-	-	43.7
8761 x 8514A	21	0.10 (0-2)	12.05 (10-14)	-	0.95 (0-2)	-	-	-	70.4
8761 x 8561	50	-	14.00 (14)	-	-	-	-	-	96.1
8770 x 196-1	39	0.23 (0-2)	12.36 (10-14)	0.13 (0-1)	0.67 (0-1)	-	-	-	-
8770 x 8761	26	-	14.00 (14)	-	-	-	-	-	-
8779 x 8561	50	0.04 (0-2)	13.98 (13-14)	-	-	-	-	-	90.8
8784 x 107-1	50	0.04 (0-2)	11.42 (10-14)	0.76 (0-2)	0.26 (0-1)	-	0.30 (0-1)	-	4.7
8784 x 8718A	50	-	11.04 (11-12)	-	0.08 (0-1)	-	0.96 (0-1)	-	40.9
8784 x 8732	50	0.04 (0-2)	10.98 (10-11)	0.04 (0-2)	-	-	0.98 (0-1)	-	27.4
8784 x 8824A	33	-	12.24 (12-14)	-	0.88 (0-1)	-	-	-	-
8784 x 8827	30	0.04 (0-2)	11.06 (10-12)	-	0.08 (0-1)	-	0.92 (0-1)	-	39.7
8797 x 107-1	38	0.18 (0-2)	13.66 (11-14)	0.03 (0-1)	0.11 (0-1)	-	-	-	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
8797 x 8784	43	-	11.72 (9-14)	-	0.42 (0-2)	-	0.44 (0-1)	0.02X (0-1)	43.7
8799B x 107-1	33	0.06 (0-2)	13.97 (13-14)	-	-	-	-	-	51.7
8802 x 196-1	27	0.04 (0-1)	12.07 (10-14)	0.04 (0-1)	0.93 (0-2)	-	-	-	-
8802 x 8761	34	0.12 (0-2)	13.88 (13-14)	-	0.03 (0-1)	-	-	-	-
8819 x 196-1	32	0.56 (0-2)	12.03 (10-14)	0.13 (0-1)	0.75 (0-2)	-	-	-	-
8819 x 8827	39	-	14.00 (14)	-	-	-	-	-	-
8821B x 107-1	30	0.20 (0-2)	13.90 (13-14)	-	-	-	-	-	-
8821B x 8593	50	0.04 (0-2)	13.98 (13-14)	-	-	-	-	-	81.3
8821B x 8948	50	-	14.00 (14)	-	-	-	-	-	98.7
8822 x 8827	33	-	14.00 (14)	-	-	-	-	-	-
8822 x 8866	36	0.22 (0-1)	10.33 (10-12)	0.22 (0-1)	1.61 (1-2)	-	-	-	-
8824A x 107-1	66	0.03 (0-1)	12.18 (12-14)	0.03 (0-1)	0.88 (0-1)	-	-	-	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
8824A x 8719	33	-	11.00 (11)	-	-	-	1.00 (1)	-	-
8824A x 8732	33	0.03 (0-1)	11.06 (11-12)	0.03 (0-1)	0.03 (0-1)	-	0.94 (0-1)	-	-
8824A x 8824B	66	0.03 (0-2)	13.98 (13-14)	-	-	-	-	-	-
8824A x 8866	33	0.06 (0-1)	8.55 (8-10)	0.06 (0-1)	2.67 (2-3)	-	-	-	-
8824B x 8561	50	0.06 (0-2)	12.66 (12-14)	0.02 (0-1)	0.64 (0-1)	-	-	-	85.0
8824B x 8714A	30	-	11.03 (11-12)	-	0.03 (0-1)	-	0.97 (0-1)	-	-
8824B x 8732	66	0.05 (0-2)	11.02 (10-12)	-	0.03 (0-1)	0.02 (0-1)	0.95 (0-1)	-	-
8824B x 8784	33	0.06 (0-1)	12.00 (12)	0.06 (0-1)	0.94 (0-1)	-	-	-	-
8827 x 107-1	66	0.06 (0-2)	13.97 (13-14)	-	-	-	-	-	-
8827 x 8674	51	0.57 (0-2)	12.10 (11-14)	0.06 (0-1)	0.76 (0-1)	-	-	-	54.8
8827 x 8928	50	0.08 (0-2)	13.92 (12-14)	-	0.02 (0-1)	-	-	-	93.2
8831 x 107-1	33	-	14.00 (14)	-	-	-	-	-	-

Table IIe. (continued)

Cross* combination	No. of cells	Chromosome pairings (means and ranges)							Seed fert. (%)
		I	II	III	IV	V	VI	VII-XII	
8831 x 8732	33	0.03 (0-1)	12.00 (12)	0.03 (0-1)	0.97 (0-1)	-	-	-	-
8866 x 196-1	53	0.62 (0-3)	9.51 (6-12)	0.53 (0-2)	1.34 (0-3)	0.06 (0-1)	0.19 (0-1)	-	-
8866 x 1908A	68	0.37 (0-3)	8.37 (7-10)	0.25 (0-1)	2.51 (1-3)	-	0.02 (0-1)	-	38.4
8866 x 8567	21	0.19 (0-2)	9.48 (9-11)	0.05 (0-1)	1.19 (0-2)	0.05 (0-1)	0.62 (0-1)	-	20.6
8866 x 8572	33	0.21 (0-2)	9.18 (8-11)	0.27 (0-1)	1.00 (0-2)	0.12 (0-1)	0.67 (0-1)	-	-
8866 x 8713	33	-	10.06 (10-11)	0.03 (0-1)	0.12 (0-2)	0.03 (0-1)	0.06 (0-1)	0.85VIII (0-1)	-
8866 x 8715	33	-	8.12 (8-9)	-	0.12 (0-1)	-	1.88 (1-2)	-	-
8866 x 8718A	53	0.06 (0-2)	10.66 (10-14)	0.02 (0-1)	1.64 (0-2)	-	-	-	21.8
8866 x 8719	40	0.25 (0-1)	9.03 (8-10)	0.25 (0-1)	0.80 (0-2)	-	0.93 (0-1)	0.03VIII (0-1)	-
8866 x 8725	66	0.11 (0-3)	7.74 (5-9)	0.05 (0-1)	1.59 (0-1)	-	0.98 (0-1)	-	-
8866 x 8732	37	-	9.30 (9-12)	0.11 (0-2)	0.84 (0-2)	-	0.73 (0-1)	0.14X (0-1)	7.0
8866 x 8732	29	-	9.17 (9-11)	-	1.00 (0-2)	-	0.90 (0-1)	0.03VIII (0-1)	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges) I	II	III	IV	V	VI	VII-XII	Seed fert.(%)
8866 x 8732	36	0.22 (0-2)	8.92 (8-12)	0.31 (0-3)	0.83 (0-3)	0.17 (0-1)	0.03 (0-2)	0.03VII (0-2) 0.33VIII (0-1)	-
8866 x 8824B	33	0.12 (0-2)	8.24 (7-10)	-	2.85 (2-3)	-	-	-	-
8866 x 8827	57	0.04 (0-1)	12.04 (10-14)	0.04 (0-1)	0.95 (0-2)	-	-	-	40.7
8880 x 107-1	66	-	14.00 (14)	-	-	-	-	-	2.4
8880 x 8714A	39	0.05 (0-2)	12.13 (11-14)	-	0.92 (0-1)	-	-	-	-
8884 x 107-1	33	-	13.94 (12-14)	-	0.03 (0-1)	-	-	-	-
8884 x 8514	50	0.08 (0-2)	12.10 (11-14)	-	0.90 (0-1)	-	0.02 (0-1)	-	41.0
8884 x 8719	26	-	12.92 (12-14)	-	0.54 (0-1)	-	-	-	59.0
8884 x 8732	50	0.02 (0-1)	12.00 (12)	0.02 (0-1)	0.98 (0-1)	-	-	-	66.0
8890 x 107-1	50	0.08 (0-2)	13.96 (13-14)	-	-	-	-	-	1.3
8907 x 107-1	50	0.14 (0-4)	13.78 (12-14)	0.02 (0-1)	0.06 (0-1)	-	-	-	13.1
8912 x 8709	50	0.16 (0-2)	13.92 (13-14)	-	-	-	-	-	53.1

Table IIe. (continued)

Cross* combination	No. of cells	Chromosome pairings (means and ranges) I	II	III	IV	V	VI	VII-XII	Seed fert.(%)
8912 x 8797	50	0.14 (0-2)	13.82 (12-14)	0.02 (0-1)	0.04 (0-1)	-	-	-	55.8
8912 x 8866	50	0.24 (0-2)	11.82 (10-14)	0.20 (0-1)	0.88 (0-2)	-	-	-	65.7
8913 x 107-1	28	0.07 (0-2)	13.96 (13-14)	-	-	-	-	-	-
8913 x 196-1	33	0.15 (0-2)	11.73 (10-14)	0.09 (0-1)	1.03 (0-2)	-	-	-	-
8924 x 107-1	30	-	14.00 (14)	-	-	-	-	-	-
8924 x 8561	30	0.07 (0-2)	13.97 (13-14)	-	-	-	-	-	96.9
8924 x 8912	50	0.28 (0-4)	13.86 (12-14)	-	-	-	-	-	94.0
8926 x 107-1	66	0.18 (0-2)	13.91 (13-14)	-	-	-	-	-	-
8926 x 1908A	25	0.08 (0-2)	12.20 (11-14)	-	0.88 (0-1)	-	-	-	-
8928 x 107-1	50	-	14.00 (14)	-	-	-	-	-	36.3
8933 x 107-1	33	-	14.00 (14)	-	-	-	-	-	-
8933 x 107-1	66	-	14.00 (14)	-	-	-	-	-	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
8933 x 8719	33	-	12.00 (12)	-	1.00 (1)	-	-	-	-
8940 x 107-1	57	0.04 (0-2)	13.98 (13-14)	-	-	-	-	-	83.0
8940 x 107-1	33	0.06 (0-2)	13.97 (13-14)	-	-	-	-	-	-
8940 x 196-2	33	-	13.82 (12-14)	-	0.09 (0-1)	-	-	-	-
8940 x 8719	29	0.14 (0-2)	12.24 (12-14)	0.07 (0-1)	0.79 (0-1)	-	-	-	61.4
8940 x 8827	41	-	14.00 (14)	-	-	-	-	-	-
8940 x 8947	33	0.18 (0-2)	13.91 (13-14)	-	-	-	-	-	-
8944 x 196-1	31	0.16 (0-2)	11.35 (10-12)	0.03 (0-1)	1.06 (0-2)	-	0.13 (0-1)	-	-
8944 x 8561	50	0.08 (0-1)	12.12 (12-14)	0.08 (0-1)	0.86 (0-1)	-	-	-	87.5
8944 x 8719	27	-	11.07 (11-12)	0.07 (0-2)	0.07 (0-1)	-	0.89 (0-1)	-	-
8944 x 8784	34	0.26 (0-4)	10.21 (10-11)	0.03 (0-1)	0.24 (0-2)	0.03 (0-1)	0.21 (0-1)	0.03VII (0-1) 0.59VIII (0-1)	-
8944 x 8866	33	0.39 (0-2)	8.33 (8-10)	0.33 (0-1)	2.48 (1-3)	-	-	-	-

Table IIe. (continued)

Cross* combination	No.of cells	Chromosome pairings (means and ranges)							Seed fert.(%)
		I	II	III	IV	V	VI	VII-XII	
8945 x 107-1	33	0.09 (0-1)	12.12 (12-14)	0.09 (0-1)	0.85 (0-1)	-	-	-	-
8945 x 8714A	33	-	11.06 (11-12)	0.12 (0-2)	0.06 (0-1)	-	0.88 (0-1)	-	-
8945 x 8866	33	0.12 (0-1)	8.12 (8-10)	0.12 (0-1)	2.82 (2-3)	-	-	-	-
8947 x 107-1	100	0.04 (0-2)	13.98 (13-14)	-	-	-	-	-	-
8947 x 8827	33	0.12 (0-2)	13.94 (13-14)	-	-	-	-	-	-
8948 x 8718	37	-	14.00 (14)	-	-	-	-	-	89.2
8948 x 8947	50	-	14.00 (14)	-	-	-	-	-	-

Table IIf. Chromosome pairings in F_1 hybrids between T. aestivum cv. Chinese Spring and T. dicoccoides

Cross combination	Envir. cond.*	No. of cells observed	Chromosome pairings**				Xta per cell
			I	II	III	IV	
184-1 x 108-2	G	30	7.80 (6-14)	13.40 (9-14)	0.13 (0-1)	-	-
184-2 x 108-2	G	35	7.46 (6-10)	13.29 (11-14)	0.29 (0-1)	0.03 (0-1)	-
184-1 x 108-3	G	50	7.88 (6-11)	13.30 (10-14)	0.04 (0-1)	0.10 (0-1)	-
184-2 x 108-3	G	50	7.70 (6-11)	13.32 (11-14)	0.14 (0-1)	0.06 (0-1)	-
184-2 x 108-5	F	50	7.70 (6-9)	13.56 (12-14)	0.06 (0-1)	-	23.86
184-1 x 109	G	50	8.30 (7-13)	12.22 (11-14)	0.14 (0-1)	0.46 (0-1)	-
184-1 x 195	G	50	7.90 (7-13)	12.02 (10-14)	0.06 (0-1)	0.72 (0-2)	-
910 x 1957	F	50	7.78 (6-11)	12.28 (10-14)	0.22 (0-1)	0.50 (0-1)	22.14
910 x 8915A	F	47	7.89 (6-11)	11.81 (10-14)	0.17 (0-2)	0.74 (0-2)	22.74
910 x 8935	F	100***	7.44 (7-11)	13.78 (12-14)	-	-	24.13

* Environmental conditions: F=Field, G=Glasshouse.
** Means and ranges(in parentheses).
*** Two plants were observed.