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Confirmation of primitive chromosome structure in the hexaploid wheats*

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Summary. Hybrids between *Triticum aestivum* cv Chinese Spring (CS) and *T. dicoccoides* of chromosome type E_{1a} showed only a few or no trivalents at meiosis, but both trivalents and quadrivalents were shown by hybrids with six other types. Since there is strong evidence that the E_{1a} type has the primitive chromosome structure of *T. dicoccoides,* Chinese Spring can be said to have the primitive chromosome structure of the hexaploid wheats in regard to reciprocal translocation.

Key words: Hexaploid wheats – Primitive chromosome structure – Translocation – Chinese Spring – *Triticum dicoccoides*

Introduction

Chinese Spring (CS) is a cultivar of bread wheat, *Triticum aestivum* L. (AABBDD genome) and is widely used as a standard in genetics and cytogenetics of wheat. Riley et al. (1967) studied reciprocal translocations in hexaploid wheats with the AABBDD genome and compared their chromosome structures with those of tetraploid *T. dicoccoides* Körn. (AABB) and diploid *Ae. squarrosa* L. (DD), the two ancestral species of hexaploid wheats. They concluded that Chinese Spring has the primitive chromosome structure of hexaploid wheats. However, later studies revealed that translocations are frequently found between strains of *T. dicoccoides* (Rao and Smith 1968; Dagan and Zohary 1970; Kawahara and Tanaka 1978, 1983; Kawahara 1986, 1987). Therefore, a re-examination is needed to determine the primitiveness of the chromosome structure of Chinese Spring. This paper reports the chromosome pairings in hybrids between Chinese Spring and *T. dicoccoides* of seven types that have different reciprocal translocations.

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Materials and methods

Eleven strains of *T. dicoccoides* were used as the male parent in crossings with Chinese Spring. Strain numbers (KU-) and their reciprocal-translocation types are as follows: 108-5, 8817 and 8935 of the E_{1a} type; 108-2 and 108-3 of E_{1b}; 109 of E_2; 195 of E_3; 8915A of E_4; 1945 of E_5; and 1952 and 1957 of E_6. The E_{1a} type is the primitive chromosome structure of *T. dicoccoides* regarding reciprocal translocation (Kawahara 1984, 1986). The E_{1b} type differs from E_{1a} by one minor translocation and types E_2–E_6 differ from E_{1a} by one major translocation (Kawahara 1986, 1987).

The behavior of chromosomes was observed at first meiotic metaphase (MI) of the pollen mother cells (PMCs) in F_1 hybrids by the aceto-orcein squash technique.

Results

In two hybrids of Chinese Spring with E_{1a} type strains of *T. dicoccoides,* 108-5 and 8817, trivalents were observed at a very low frequency, 6.0%, while in another hybrid, CS×8935, no multivalent was observed (Table 1). In hybrids with all types other than E_{1a}, quadrivalents were formed. These were found at a low frequency, 1.5%–8.0%, in hybrids with 108-2 and 108-3, where about one-fifth of the cells had a trivalent, a quadrivalent or, rarely, both. On the other hand, quadrivalents were formed at a high frequency in hybrids with 109, 195, 8915A, 1945, 1952 and 1957, with

Table 1. Frequency of multivalents in hybrids between *Triticum aestivum* cv Chinese Spring and *T. dicoccoides*

Male parent	Type[a]	No. of PMCs observed	Percentage with indicated multivalents					No. of paired arms
			1 III	1 IV	1 III + 1 IV	2 III	2 IV	
108-5	E_{1a}	50	6.0	–	–	–	–	23.86
8817	E_{1a}	50	6.0	–	–	–	–	22.68
8935	E_{1a}	100	–	–	–	–	–	24.13
108-2	E_{1b}	65	21.5	1.5	–	–	–	–
108-3	E_{1b}	100	8.0	7.0	1.0	–	–	–
109	E_2	50	14.0	46.0	–	–	–	–
195	E_3	50	6.0	68.0	–	–	2.0	–
8915A	E_4	47	10.6	63.8	2.1	2.1	4.3	22.74
1945	E_5	33	21.2	66.7	–	–	–	22.58
1952	E_6	50	22.0	60.0	–	–	–	22.62
1957	E_6	50	20.0	50.0	–	–	–	22.14

[a] Translocation chromosome type of the male parent

the percentage of cells with a quadrivalent ranging from 46.0%–68.0%. PMCs with two quadrivalents were found in two hybrids, CS × 195 and CS × 8915A, but the frequency was low.

Since the number of paired arms did not differ greatly in the pentaploid hybrids examined (Table 1), the genetic background (which may affect the amount of homoeologous pairing) had little effect, if any, on the frequency of multivalents. Therefore, quadrivalents observed in these hybrids were considered to indicate structural heterozygosity of the chromosomes.

One minor translocation was found between E_{1a} and E_{1b} and a major translocation between E_{1a} and E_2–E_6 (Kawahara 1986, 1987). Since no quadrivalent was formed in hybrids of Chinese Spring with E_{1a}, the quadrivalents observed in hybrids other than E_{1a} must be due to translocations carried by the other types of *T. dicoccoides*. In haploid plants of Chinese Spring, bivalents are formed at meiosis at an average frequency ranging from 0.10–0.52 per cell (Miller and Chapman 1976; McGuire and Dvořák 1982). Therefore, trivalents formed in hybrids with 108-5 or 8817 are probably due to homoeologous pairing rather than to translocations between D and A or B genomes of Chinese Spring.

The present data clearly show that chromosomes of the A and B genomes of Chinese Spring have the same structure as the primitive type of *T. dicoccoides* in regard to translocation. However, chromosomes of the A and B genomes of Chinese Spring may not have the primitive hexaploid constitution in regard to other kinds of structural differentiation. In two hybrids with E_{1a}, CS × 108-5 and CS × 8935, PMCs at first meiotic anaphase were examined in addition to those at MI. Of 105 cells of the former, 6 had a bridge and a fragment. In the latter combination, a bridge with a fragment was recognized in 6 of the 260 cells observed. These hybrids were inferred to be heterozygous for at least one paracentric inversion. Although an extensive analysis was not made, these data may suggest that the chromosome of the A and B genomes of Chinese Spring do not have the primitive constitution concerning inversion.

Discussion

There is some controversy about the primitiveness of the chromosome structure of Chinese Spring. Riley et al. (1967) showed the existence of hexaploid wheat with the primitive chromosome structure by tracing the distribution of translocations. They assumed that in the initial hexaploid wheat, the structure of the chromosomes of the A and B genomes was identical with that of the chromosomes of the tetraploid from which it was derived. Similarly, the structure of the D genome must be identical with that of the chromosomes of the parental form of *Ae. squarrosa.* No multivalents were observed in hybrids of Chinese Spring with a strain of *Ae. squarrosa* (Riley and Chapman 1960) or with a strain of *T. dicoccoides* (Riley et al. 1967). Based on these observations, they concluded that Chinese Spring has the primitive chromosome structure of hexaploid wheats. Later, Larsen (1973) suggested that the chromosome structure of Chinese Spring was not as primitive as generally assumed. In hybrids between a synthetic hexaploid wheat and Chinese Spring monosomics, he observed multivalents, bridges and low pairings at meiosis. In the mitosis of the hybrids, morphological differences were recognized in chromosome 5D. In these two studies, only one strain each of *Ae. squarrosa, T. dicoccoides* and synthetic hexaploid wheat was used, without examining the cytogenetical relationship to other materials.

In the present study, the chromosome structure of the *dicoccoides* strains used is well clarified through intraspecific hybridization experiments. Kawahara and Tanaka (1978, 1983) and Kawahara (1986, 1987) found 1 minor and 5 major translocations among 46 strains of *T. dicoccoides*. The presumed ancestral chromosome arrangement, that of E_{1a}, was found widely throughout the distribution area of the species, but each translocation type was restricted to a single collection site. Further, the A genome of the E_{1a} type had the same chromosomal arrangement as that of the fundamental type of the diploid wheats in regard to translocation (Kawahara 1984). Based on these data, Kawahara (1984, 1986, 1987) concluded that type E_{1a} has the primitive chromosome structure of *T. dicoccoides* and that the other types studied, E_{1b}–E_6, have differentiated from this type by one translocation. Thus, the present data provide firm cytological evidence for the primitiveness of the translocation chromosome structure of Chinese Spring among hexaploid wheats.

No investigation of the structure of the D genome chromosomes was made in the present study. However, studies by Kihara et al. (1965) have clearly shown that structural differentiation in chromosomes is very rare in *Ae. squarrosa*. They examined more than 20 strains from various regions. Of these, only one strain from Iran had a translocation relative to the others. Two other strains collected from the same site had no translocation. Thus, 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 can be little doubt that Chinese Spring has the primitive chromosome structure of the hexaploid wheats in respect to translocation, as concluded by Riley et al. (1967). Nullisomic-tetrasomic compensation tests by Sears (1954) also support this conclusion.

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