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Chromosome structure of durum wheat

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Summary. Meiotic pairing was analyzed at metaphase I in ABRR triticale × rye hybrids to identify the arm homoeology of chromosomes of *Triticum turgidum*. Wheat chromosomes were identified using a C-banding technique. Results confirmed that the homoeologous relationships between chromosome arms of the A and B genomes in *T. turgidum* are the same as in *T. aestivum*, and that a double translocation involving *4AL, 5AL*, and *7BS* is present in *T. turgidum*. It is proposed that a pericentric inversion involving a substantial portion of chromosome *4A* is present in *T. turgidum* and *T. aestivum*.

Key words: Durum wheat – C-banding – Homoeologous pairing – Chromosome structure – Evolution

Introduction

Kihara (1924) reported the occurrence of 14 bivalents and 7 univalents in pentaploid wheat hybrids derived from crosses between *Triticum aestivum* ($2n=6x=42$) and *T. turgidum* ($2n=4x=28$). This indicated that the chromosomes of *T. turgidum* are homologous to those of the A and B genomes of *T. aestivum*, and that hexaploid wheat derived from tetraploid wheat as one of the parents.

The majority of chromosomes and their arms of *T. aestivum* cv. 'Chinese Spring' could be identified by means of C-banding in 'Chinese Spring' itself (Endo 1986) and in different wheat × rye hybrid genotypes (Naranjo et al. 1987, 1988 a, b). The analysis of homoeologous pairing at metaphase I in such hybrids allowed arm homoeology of most wheat chromosomes to be established. The presence in 'Chinese Spring' of a double translocation involving chromosome arms *4AL, 5AL,* and *7BS* was reported (Naranjo et al. 1987, 1988 a, b).

Chromosomes of *T. turgidum* present in hexaploid triticale cv 'Cachirulo' (AABBRR) could be distinguished by means of C-banding (Naranjo 1988). Their identification was carried out by studying pairing of chromosomes of the A and B genomes of *T. aestivum* cv 'Chinese Spring' in AABBDR triticale 'Cachirulo' × 'Chinese Spring' hybrids. The existence of normal homologous relationships between chromosomes of *T. turgidum* and *T. aestivum* was confirmed.

Chromosomes of rye, specially chromosome *5R*, induce homoeologous pairing in wheat-rye derivatives (Miller and Riley 1972; Riley et al. 1973; Naranjo et al. 1979; Naranjo and Palla 1982). In this work, the homoeologous relationships between arms of durum wheat chromosomes are identified by analysis of pairing at metaphase I in ABRR triticale × rye hybrids to confirm the presence of the double translocation *5AL/4AL/7BS* in *T. turgidum*.

Materials and methods

Hexaploid triticale cv 'Cachirulo' (AABBRR, $2n=6x=42$) was obtained from the cross *Triticum turgidum* ssp. *durum* cv 'Enano de Andujar' × *Secale cereale* cv 'Petkus' (Sánchez-Monge 1969). Triticale 'Cachirulo' was crossed with *S. cereale* cv 'Ailés' (RR, $2n=14$), and three ABRR plants ($2n=4x=28$) were analyzed. All three ABRR plants were grown in a controlled environment chamber at 16°–18 °C after vernalization for 8 weeks at 6°–8 °C.

Anthers at first metaphase of meiosis were fixed in 1:3 acetic acid:alcohol and were stored at 0°–4 °C for a minimum of 2 months. The fixed material was squashed and stained according to the C-banding technique of Giraldez et al. (1979). For the analysis of pairing, samples of 100 pollen mother cells (PMCs) per plant were scored.

Chromosomes of durum wheat were identified according to Naranjo (1988). Chromosome designations of *4A* and *4B* were interchanged in agreement with the resolutions of the 7th International Wheat Genetics Symposium (Cambridge 1988).

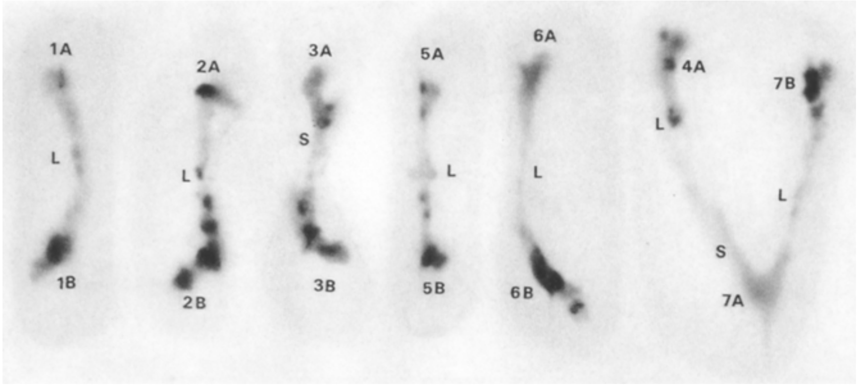

Fig. 1. Association between arms of homoeologous and non-homoeologous chromosomes of *T. turgidum* in ABRR hybrids. Configurations *1AL-1BL, 2AL-2BL, 3AS-3BS, 5AL-5BL* showing an interstitial chiasmata, *6AL-6BL, 4AL-7AS,* and *7AL-7BL*

Table 1. Frequency (%) of association between arms of homoeologous chromosomes of tetraploid wheat in ABRR triticale × rye hybrids [a]

Arms being bound	%	Arms being bound	%
1AS-1BS	5.3	*1AL-1BL*	47.7
2AS-2BS	36.3	*2AL-2BL*	81.0
3AS-3BS	28.7	*3AL-3BL*	47.0
4AS-4BS	0.3	*4AL-4BL*	0.3
5AS-5BS	14.7	*5AL-5BL*	14.0
6AS-6BS	8.0	*6AL-6BL*	45.0
7AS-7BS	0.3	*7AL-7BL*	20.0
		4AL-4BS	0.3

[a] 300 PMCs were scored. Arms *5AL* and *5BL* formed interstitial chiasmata; *6AS* and *6AL* were identified by pairing with *6BS* and *6BL*, respectively

Table 2. Frequency (%) of association between arms of non-homoeologous chromosomes of tetraploid wheat in ABRR triticale × rye hybrids [a]

Arms being bound	%
4BL-5AL-5BL	0.3
4BL-5AL	18.3
4AL-7AS	27.3
7BS-5BL	3.3
Others	1.0

[a] 300 PMCs were scored

Results and discussion

Chromosome *2A* derived from *T. turgidum* showed a telomeric C-band in one arm. Such an arm paired with *2BL* and the other one with *2BS*. The arms of chromosome *2A* that are homoeologous to *2BS* and *2BL* in 'Chinese Spring' could not be identified by C-banding in ABDR wheat × rye hybrids (Naranjo et al. 1987, 1988 a, b). As determined by the location of 13 sets of homoeoloci, Sharp and Soltes-Rak (1988) concluded that *2AS, 2BS,* and *2DS* of hexaploid wheat are homoeologous, as are *2AL, 2BL,* and *2DL.* Since chromosomes *2A* and *2B* derived from *T. turgidum* showed normal homologous relationships to chromosomes *2A* and *2B* from *T. aestivum* in AABBDR triticale × wheat hybrids (Naranjo 1988), the arm of chromosome *2A* derived from *T. turgidum* with the telomeric marker is *2AL* and the other one is *2AS*. Likewise, the arms of chromosome *7A* that could not be identified by C-banding in ABDR wheat × rye hybrids (Naranjo et al. 1987, 1988 a, b) were conspicuously marked in the plants analyzed here. The *7AL* arm carried a telomeric C-band while *7AS* was unbanded. Chromosome arms *6AS* and *6AL* from *T. turgidum* lacked apparent C-bands, and were identified by virtue of pairing with *6BS* and *6BL*, respectively.

Results of pairing at metaphase I between arms of wheat chromosomes in ABRR hybrids are given in Tables 1 and 2. Table 1 shows the frequency of association between arms of homoeologous chromosomes, and Table 2 shows the frequency of configurations formed by arms of non-homoeologous chromosomes. Figure 1 shows examples of metaphase I configurations formed by wheat chromosomes.

The frequency of association between the short arms of chromosomes of groups 1, 2, 3, 5, and 6 as well as between the long arms of chromosomes of groups 1, 2, 3, 6, and 7 identifies their homoeology relationships. The *4AL* arm seldom paired with *4BL* (0.3%), but did pair with *7AS* (27.3%). The presence in *4AL* of a considerable segment homoeologous to *7AS* can be deduced. Chromosome arm *5AL* formed interstitial chiasmata with *5BL* and terminal chiasmata with *4BL*. A terminal segment from *5AL* is homoeologous to *4BL*, while the rest of *5AL* is homoeologous to *5BL*. Chromosome arm *7BS* is to some extent homoeologous to *5BL*. Association of chromosome arms *4AS* and *4BS* was scarce. Other associations involving non-homoeologous chromosomes appeared with a total frequency of 1%.

As expected from the homology of *T. turgidum* chromosomes to 'Chinese Spring' A and B genome chromosomes (Naranjo 1988), the homoeologous relationships between arms of the A and B genome chromosomes in *T. turgidum* (Tables 1 and 2) are the same as in *T. aestivum* (Naranjo et al. 1987, 1988 a, b). This result confirms that the double translocation *5AL/4AL/7BS* detected in *T. aestivum* is present in *T. turgidum*. The chromosome structure of durum wheat agrees with the sequence of interchanges suggested by Naranjo et al. (1987, 1988 a), namely: an initial translocation *5AL/4AL* that took place during the evolution of *T. monococcum* (the donor of the A genome), and a second translocation *4AL/7BS* that arose in the primitive tetraploid. Evidence supporting the presence in *T. turgidum* of an interchange involving *4AL* and *7BS* was also reported by Gill and Chen (1987).

It is worth mentioning that associations between homoeologous arms or segments of the A and B genome chromosomes were much more frequent in ABRR hybrids than in *ph1b* and *5B*-deficient ABDR wheat × rye hybrids (Naranjo et al. 1987, 1988 a, b). This increase of homoeologous A-B pairing in ABRR hybrids was the result of the lack of competitive A-D pairing, which is preferential in ABDR hybrids, as well as B-D pairing.

Naranjo et al. (1987, 1988 a) proposed that a pericentric inversion involving a substantial portion of chromosome *4A* is present in *T. aestivum* but absent in *T. monococcum*. This hypothesis was based on the following findings: (i) the lack of homologous pairing either between telocentric *4AS* of 'Chinese Spring' and *T. monococcum* chromosomes (Chapman et al. 1976) or between *4AS* of diploid wheat and chromosomes of hexaploid wheat (Wazuddin and Driscoll 1986); (ii) the lack of homoeologous pairing between *4AS* and *4BS* or *4DS* of hexaploid wheat in ABDR wheat × rye hybrids (Naranjo et al. 1987, 1988 a, b); (iii) the location in 'Chinese Spring' of structural genes for isozymes of alcohol dehydrogenase (*Adh-1*), lypoxygenase (*Lpx*), phosphoglucomutase (*Pgm-1*) and NADH dehydrogenase (*Ndh-1*) on chromosome arms *4AL, 4BS*, and *4DS* (Hart and Langston 1977; Benito et al. 1984; Hart 1987), and the location of genes for isozymes of acid phosphatase (*Acph-2, -3, -4, -5, -6*, and *-8*) on *4AS, 4BL*, and *4DL* (Hart and Langston 1977). Two RFLP markers were recently reported to be located on the arm set *4AL, 4BS*, and *4DS*, and on the arm set *4AS, 4BL*, and *4DL*, respectively (Sharp et al. 1988).

The almost null frequency of association between *4AS* and *4BS* of *T. turgidum* in ABRR hybrids in addition to the rare association *4BS-4AL* (Table 1), and the regular pairing between chromosome pair *4A* of *T. turgidum* and *T. aestivum* in AABBDR hybrids (Naranjo 1988) indicate that the assumed pericentric inversion of *4A* would arise at the early tetraploid stage. Structure of chromosomes *4A, 5A*, and *7B* of *T. turgidum* as well as the sequence of changes occurred in the evolution: translocation *5AL/4AL* (1), translocation *4AL/7BS* (2), and the pericentric inversion of chromosome *4A* (3) are diagrammed in Fig. 2. Whether translocation *4AL/7BS* and the pericentric inversion of *4A* occurred in the order 2-3 or 3-2 in the primitive tetraploid remains undetermined.

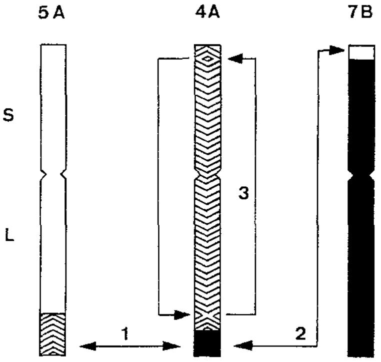

Fig. 2. Structure of chromosomes *4A, 5A*, and *7B* of *T. turgidum*. *1* represents translocation *5AL-4AL*, which occurred in the evolution of *T. monococcum*, *2* represents translocation *4AL-7BS*, and *3* represents a pericentric inversion of chromosome *4A*. *2* and *3* occurred at the early tetraploid stage but the order, *2–3* or *3–2*, could not be determined

References

Benito C, Figueiras AM, González-Jaen MT (1984) Phosphoglucomutase, a biochemical marker for group 4 chromosomes in the triticineae. Theor Appl Genet 68:555–557

Chapman V, Miller TE, Riley R (1976) Equivalence of the A genome of bread wheat and that of *Triticum urartu*. Genet Res 27:69–76

Endo TR (1986) Complete identification of common wheat chromosomes by means of the C-banding technique. Jpn J Genet 61:89–93

Gill BS, Chen PD (1987) Role of cytoplasm-specific introgression in the evolution of the polyploid wheats. Proc Natl Acad Sci USA 84:6800–6804

Giraldez R, Cermeño MC, Orellana J (1979) Comparison of C-banding patterns in the chromosomes of inbred lines and open pollinated varieties of rye, *Secale cereale* L. Z Pflanzenzuecht 83:40–48

Hart GE (1987) Genetic control of NADH dehydrogenase-1 and aromatic alcohol dehydrogenase-2 in hexaploid wheat. Biochem Genet 25:837–846

Hart GE, Langston PJ (1977) Chromosomal location and evolution of isozyme structural genes in hexaploid wheat. Heredity 39:263–277

Kihara H (1924) Cytologische und genetische Studien bei wichtigen Getreidearten mit besonderer Rücksicht auf das Verhalten der Chromosomen und die Sterilität in den Bastarden. Mem Coll Sci Kyoto Imp Univ 1:1–200

Miller TE, Riley R (1972) Meiotic chromosome pairing in wheat-rye combinations. Genet Iber 24:241–250

Naranjo T (1988) Identificación de los cromosomas de trigo del triticale "Cachirulo" por homologia con los de *Triticum aestivum*. An Aula Dei 19:55–62

Naranjo T, Palla O (1982) Genetic control of meiotic pairing in rye. Heredity 48:57–62

Naranjo T, Lacadena JR, Giraldez R (1979) Interaction between wheat and rye genomes on homologous and homoeologous pairing. Z Pflanzenzuecht 82:289–305

Naranjo T, Roca A, Goicoechea PG, Giraldez R (1987) Arm homoeology of wheat and rye chromosomes. Genome 29:873–882

Naranjo T, Roca A, Goicoechea PG, Giraldez R (1988 a) Chromosome structure of common wheat: Genome reassignment of chromosomes 4A and 4B. In: Proc 7th Int Wheat Genet Symp, Cambridge, pp 115–120

Naranjo T, Roca A, Giraldez R, Goicoechea PG (1988 b) Chromosome pairing in hybrids of *ph1b* mutant wheat with rye. Genome 30:639–646

Riley R, Chapman V, Miller TE (1973) The determination of meiotic chromosome pairing. In: Proc 4th Int Wheat Genet Symp, Columbia/MO, pp 731–738

Sánchez-Monge E (1969) La saga del Cachirulo. An Aula Dei 10:795–799

Sharp PJ, Soltes-Rak E (1988) Homoeologous relationships between wheat group 2 chromosome arms as determined by RFLP analysis. In: Proc 7th Int Wheat Genet Symp, Cambridge, pp 635–637

Sharp PJ, Desai S, Chao S, Gale MD (1988) Isolation, characterization and applications of a set of 14 RFLP probes identifying each homoeologous chromosome arm in the Triticeae. In: Proc 7th Int Wheat Genet Symp, Cambridge, pp 639–646

Wazuddin M, Driscoll CJ (1986) Chromosome constitution of polyploid wheats: introduction of diploid wheat chromosome 4. Proc Natl Acad Sci USA 83:3870–3874