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Cytogenetic Structure of Durum Wheat Cultivars from, or Introduced into, Spain

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With 8 figures and 4 tables

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Abstract

Chromosome arrangements of 48 cultivars of durum wheat, *Triticum turgidum* cv. *durum,* from Spain or introduced there are compared with those of the hexaploid 'Chinese Spring' and the tetraploid 'Senatore Capelli' taken as a standard (these two cultivars show the same chromosome arrangement for the A and B genomes). 21 out of the 48 cultivars analyzed show reciprocal translocations. All those cultivars differ by one interchange, except cv. 'Hércules' which contains two different interchanges involving three chromosomes. The interest in a reappraisal of the role played by reciprocal translocations as a cytogenetic mechanism in the evolution of *Gramineae* is pointed out.

Key words: *Triticum turgidum* — durum wheat — cytogenetic structure — reciprocal translocations — genome evolution

Allopolyploidy has played an important rôle in the evolution of *Gramineae.* However, in several genera a chromosomal polymorphism for reciprocal translocations has been found at both inter- and intraspecific levels. This is the case, for instance, in *Avena* (Ladizinsky and Zohari 1971, Ladizinsky 1973, Rajhathy and Thomas 1974), *Secale* (Khush and Stebbins 1961, Khush 1962, Candela et al. 1979), *Festuca* (Simönsen 1975), *Hordeum* (Hunziker et al. 1973), *Briza* (Murray 1976), *Lolium* (Simönsen 1973), *Triticum* (Baker and McIntosh 1966, Riley et al. 1967, Vega and Lacadena 1982).

In the genus *Triticum,* interchange polymorphism has been analyzed to a certain extent only in common wheat, *Triticum aestivum,* at an intervarietal

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level (for references see VEGA and LACADENA 1982). However, similar studies in tetraploid wheats are scarce; so, TANAKA and coworkers analysed the interchange polymorphism in *T. timopheevi* (TANAKA and ICHIKAWA 1972, TANAKA and ISHII 1975, KAWAHARA and TANAKA 1977). As far as we know, there is no systematic study in durum wheat.

In the present paper chromosomal arrangement of several durum wheat cultivars from Spain or introduced there are analyzed by crossing them with the hexaploid cv. 'Chinese Spring' and the tetraploid 'Senatore Capelli'.

Materials and Methods

48 cultivars of durum wheat, *Triticum turgidum* ($2n = 4x = 28$, AABB genome constitution), have been investigated; most of them are Spanish cultivars. Seed samples were kindly supplied by Dr. J. A. MARTÍN-SÁNCHEZ, Mahissa, Borjas Blancas (Lérida, Spain).

Chromosome arrangement of the hexaploid cultivar 'Chinese Spring' (*T. aestivum*, $2n = 6x = 42$, AABBDD genome constitution) and the tetraploid Italian cultivar 'Senatore Capelli' of durum wheat were taken as a standard, since both cultivars share the same chromosome pattern, their hybrids forming at metaphase I 14 bivalents plus 7 univalents ($7^{II}{}_A\, 7^{II}{}_B\, 7^{I}{}_D$).

The 48 durum cultivars were used as female parents: 22 cultivars were crossed with both tester cultivars (*Tab. 1*), 17 were crossed only with 'Chinese Spring' (*Tab. 2*) and 9 cultivars were crossed only with 'Senatore Capelli' (*Tab. 3*).

Meiotic analysis of hybrids was made at metaphase I of pollen mother cells from anthers fixed in 1 : 3 acetic : alcohol, stained with leucobasic fuchsin after hydrolysis with 1 N HCl at 60 °C for 11 min and squashed in a drop of acetic carmine. Observations were made on permanent slides mounted in Sandeural.

The number of PMCs observed in each hybrid was variable (ranging from 46 to 205) depending on the difficulty of interpretation.

Results

At the beginning, the durum wheat cultivars were only crossed with 'Chinese Spring' the chromosome structure of which has been generally accepted as the standard one. It was expected that the pentaploid hybrids (AABBD genome constitution) should show at metaphase I 14 bivalents plus 7 univalents ($7_A^{II}\, 7_B^{II}\, 7_D^{I}$) if the A and B chromosomes of the tetraploid cultivars did not differ from the corresponding chromosomes of 'Chinese Spring', while, if they differed by reciprocal translocations, then multivalent associations, bivalents and seven univalents should appear. However, in most of the pentaploid hybrids, PMCs with less than seven univalents were found. This indicated that some D chromosome was probably paired with its homoeologous A or B chromosomes and, in consequence, multivalent associations could be attributed not only to interchange heterozygosity but to homoeologous pairing, too. So, in order to overcome the difficulty of interpreting the observations, we decided to take as a standard the tetraploid 'Senatore Capelli' whose A and B genomes do not differ structurally from those of 'Chinese Spring'. The results obtained are shown in *Tables 1, 2* and *3*.

Among the hybrids with 'Chinese Spring' (*Tables 1* and *2*), only the 'Blanco de Llerena' cultivar did not show any multivalent (*Fig. 1*), while in

Tab. 1 Critical meiotic configurations at metaphase I of hybrids between durum wheat cultivars and 'Chinese Spring', hexaploid, and 'Senatore Capelli', tetraploid, cultivars

Cultivar	Cultivar × 'Chinese Spring'				Cultivar × 'Senatore Capelli'		
	PMC	critical configuration	frequency of PMC in %		PMC	critical configuration	frequency of PMC in % IV or III
			IV	III*)			
Alcalá la Real	156	IV	1.92	1.92	150	III	0.66
Alonso	101	IV	1.98	6.93	150	II	—
Alonso Perez Jurado	147	III	—	1.36	150	II	—
California de Alcalá la Real	156	III	—	1.28	150	II	—
Capeiti	125	IV	0.80	1.60	150	II	—
Caravaca-1	185	V	1.62	14.05	150	IV	0.66
Cascalvo Lucena y Montilla	125	IV	0.80	4.00	150	II	—
Casteldelmonte	106	IV	1.88	—	150	II	—
Crané	97	IV	3.09	4.12	150	IV	0.66
Fino Claro de Petrola	125	V	2.40	6.40	150	IV	2.00
Granja de Badajoz	202	IV	5.44	6.93	150	IV	2.00
Jerez 1936	108	III	—	3.69	150	II	—
Jerez 1937	148	IV	0.67	1.35	150	IV	3.33
Lakota	125	IV	2.40	13.60	150	II	—
Las Palmas-7	125	III	—	5.60	150	II	—
Las Palmas-8	119	III	—	1.68	150	II	—
Raspinegro de Mula	125	IV	1.60	2.40	150	IV	0.66
Recio de Almeria	108	III	—	2.77	150	II	—
Rubio de Badajoz	101	IV	0.99	5.94	150	II	—
Rubio de Belalcazar	114	IV	2.63	1.75	150	IV	1.33
Zoco de Yebel-Hebil	163	IV	1.84	1.23	150	IV	0.66
569/66	205	IV	1.46	6.34	77	IV	1.30

*) In the frequencies of PMCs with trivalents are included both those corresponding to cells with 6 univalents and those with 8 univalents.

the remaining hybrids, multivalent associations were observed. According to the maximum degree of association (critical configuration) found, and the frequency of PMCs in which such multivalent association appeared, these hybrids could be classified in four groups:

(1) Hybrids whose maximum association was a trivalent (*Figs. 2* and *3*). To this group belong 18 cultivars.

(2) Hybrids whose maximum association was a quadrivalent (*Fig. 4*). In this group the four cultivars 'Castelfusano', 'Castelporciano', 'Crané' and 'Granja de Badajoz' showed the multivalent in more than the 3% of the PMCs, while in the remaining 12 cultivars, the frequency of PMCs with the quadrivalent was lower than 3 per cent.

(3) Hybrids whose maximum association was a pentavalent (*Fig. 5*). This group includes the cultivars 'Caravaca-1', 'Fino Claro de Petrola' and 'Leeds' which showed a 1.08 %, 0.80 % and 0.57 % of PMCs with the multivalent, respectively.

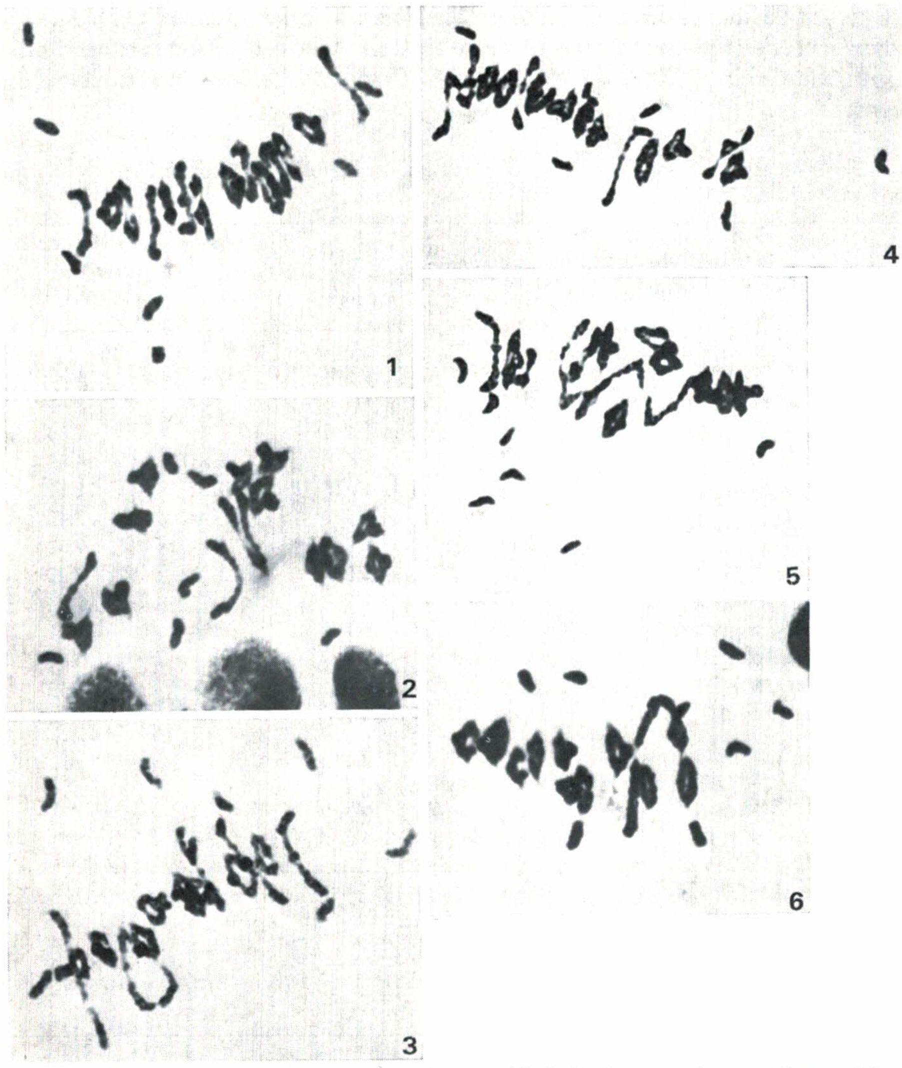
Tab. 2 Critical meiotic configurations at metaphase I of hybrids between durum wheat cultivars and 'Chinese Spring', hexaploid cultivar

Cultivar crossed with 'Chinese Spring'	PMC	Critical configuration	Frequency of PMC in %	
			IV	III*)
Bidi-17	46	III	—	4.35
Blanco de Llerena	110	II	—	—
Casalle-92	125	III	—	1.60
Castelfusano	83	IV	38.55	4.86
Castelporciano	90	IV	42.22	11.11
D	117	III	—	3.42
Haurani	125	III	—	9.60
Hércules	125	VI	51.20	7.20
Leeds	174	V	1.11	5.74
Raspinegro de Alcalá	132	III	—	1.51
Raspinegro de Alcolea	124	III	—	0.81
Raspinegro de Villanueva	124	III	—	2.42
Recio de Ronda	125	III	—	3.20
Rojal de Almeria	85	III	—	1.18
Ruso (Lérida)	125	III	—	8.00
Santa Coloma	100	III	—	2.00
Wells	125	III	—	0.80

*) In the frequencies of PMCs with trivalents are included both those corresponding to cells with 6 univalents and those with 8 univalents.

Tab. 3 Critical meiotic configurations at metaphase I of hybrids between durum wheat cultivars and 'Senatore Capelli'

Cultivar crossed with 'Senatore Capelli'	PMC	Critical configuration	Frequency of PMC in % IV or III
Claro Fino de Balazote	150	IV	1.33
Enano de Córdoba	150	IV	0.66
Enano de Jaén	150	II	—
Macolo de Jerez	150	II	—
Morisco de Tenerife-1	150	IV	2.00
Morisco de Tenerife-2	150	IV	51.33
Recio de Baza	150	IV	0.66
Rusello	84	IV	1.19
Valenciano negro	150	IV	2.00



Figs. 1—6 Meiotic configurations at metaphase I of hybrids between durum wheat cultivars and 'Chinese Spring'. *Fig. 1:* 14 II + 7 I. *Fig. 2:* 13 II + 1 III + 6 I. *Fig. 3:* 12 II + 1 III + 8 I. *Fig. 4:* 12 II + 1 IV + 7 I. *Fig. 5:* 12 II + 1 V + 6 I. *Fig. 6:* 11 II + 1 VI + 7 I.

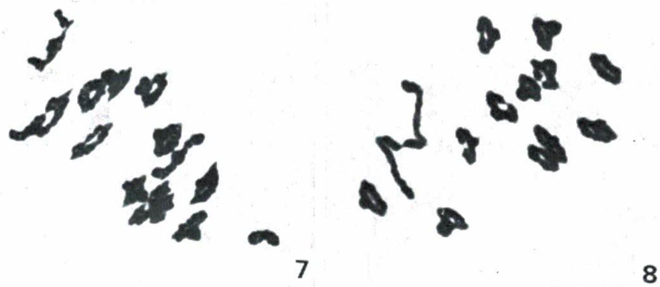
(4) Hybrids whose maximum association was a hexavalent (*Fig. 6*). To this group belongs only cv. 'Hércules'. The frequency of PMCs which showed the critical configuration was rather low (0.80 %).

The hybrids with 'Senatore Capelli' (*Tables 1* and *3*) could be classified in three groups:

(1) Hybrids which did not show any multivalent. This group includes 14 cultivars.

(2) Hybrids whose maximum association was a trivalent (*Fig. 7*). To this group belongs only cv. 'Alcalá la Real'.

(3) Hybrids whose maximum association was a quadrivalent (*Fig. 8*). This group includes 16 cultivars.



Figs. 7 and *8* Meiotic configurations at metaphase I of hybrids between durum wheat cultivars and 'Senatore Capelli'. *Fig. 7*: 12 II + 1 III + 1 I. *Fig. 8*: 12 II + 1 IV

Discussion

The results obtained confirm on the whole the existence of an intervarietal polymorphism for reciprocal translocations in *Triticum turgidum* cv. *durum*.

In the hybrids with 'Senatore Capelli', the results are of easy interpretation: 17 out of 31 hybrids show a quadrivalent which indicates that these 17 cultivars differ from 'Senatore Capelli' by a reciprocal translocation. Since the frequency of PMCs with a multivalent association (IV or III in the case of the 'Alcalá la Real' cultivar) is rather low in almost all hybrids (*Tables 1* and *3*), it can be inferred that the translocated segments are short. Only the hybrid corresponding to cv. 'Morisco de Tenerife-2' showed a rather high frequency (51.33 %) of PMCs with a quadrivalent. As the quadrivalent was always open (chain quadrivalent), one can conclude than one of the chromosome segments involved in the interchange was short and the other long. This predominance of chain quadrivalents is in agreement with the observations previously made in cultivars of common wheat, *T. aestivum,* compared with 'Chinese Spring' (Baker and McIntosh 1966, Vega and Lacadena 1982).

In the case of the hybrids with 'Chinese Spring' (*Tables 1* and *2*) the interpretation of the data obtained can be difficult since the presence of multivalents does not always correspond to interchange heterozygosity but to homoeologous pairing.

In all but one (cv. 'Wells') of the 18 hybrids analyzed, in which the maximum association was a trivalent, there were only 6 univalents (*Fig. 2*). This fact can be interpreted as one D chromosome being associated to other two chromosomes of the genomes A or B due to two possible causes, namely, (1) the presence of an interchange involving a chromosome of the D genome of 'Chinese Spring' or (2) homoeologous pairing between D and A or B chromosomes. The first assumption does not seem logical, since the existence of any translocations has not been detected in other studies carried out with 'Chinese

Spring' taken as standard (for reviews see BAIER et al. 1974, SUTKA 1978, VEGA and LACADENA 1982). In addition, if this were the case, the frequency of PMCs with the trivalent should be similar in all the hybrids analyzed; however, this does not happen.

On the other hand, the second assumption seems to be more logical since the presence, in a simple dose, of the suppressor chromosome 3D can influence homoeologous meiotic pairing as was already demonstrated by MELLO-SAMPAYO (1968) in pentaploid hybrids of wheat. In our observations, the finding of some PMCs with two trivalents and five univalents supports this assumption. The different frequencies of PMCs with a trivalent observed could be attributed to the efficiency of the genetic systems controlling meiotic pairing when acting on different genetic backgrounds.

According to this reasoning, one can conclude that the 18 cultivars analyzed do not differ structurally from 'Chinese Spring' taken as standard. Moreover, when six of these cultivars were tested with 'Senatore Capelli' (see *Table 1*), structural differences were not found, thus ratifying the above assumption.

In relation to the 16 hybrids with 'Chinese Spring' whose maximum association was a quadrivalent (*Tables 1* and *2*), we classified them in two groups according to the frequency with which the quadrivalents appeared in the PMCs (higher or lower than 3 %). In agreement with the minimum percentage previously stated by other authors in similar studies, we consider it reasonable to reject interchange heterozygosity in hybrids with frequencies lower than 3 %, the multivalent associations in these cases being attributable to homoeologous pairing. Altogether, among the 16 cultivars now under consideration, only four ('Castelfusano', 'Castelporciano', 'Crané' and 'Granja de Badajoz') are considered to differ structurally from 'Chinese Spring' taken as standard, since their frequencies of quadrivalents are high enough (38.55 %, 42.22 %, 3.09 % and 5.44 %, respectively). Moreover, this assumption was confirmed when the cultivars 'Crané' and 'Granja de Badajoz' were tested with the 'Senatore Capelli' taken as standard (*Table 1*).

Among the remainder 12 hybrids whose frequency of PMCs with quadrivalents was lower than 3 %, only those which showed quadrivalents when tested with the cultivar 'Senatore Capelli' taken as standard were considered to have structural differences. This is the case of the following six cultivars: 'Alcalá la Real', 'Jerez 1937', 'Raspinegro de Mula', Rubio de Belalcazar', 'Zoco de Yebel-Hebil' and '569/66' (*Table 1*).

Only the hybrid 'Hércules' × 'Chinese Spring' showed a hexavalent as maximum association (*Table 2*), although with low frequency (0.80 %); however, the frequency of PMCs with a quadrivalent was high (51.20 %). From these data one can conclude that 'Hércules' differs from 'Chinese Spring' by two different translocations involving three chromosomes, one of them being a very short translocated segment.

Finally, there are three cultivars ('Caravaca-1', 'Fino Claro de Petrola' and 'Leeds') whose hybrids with 'Chinese Spring' showed a pentavalent as maximum association (*Tables 1* and *2*). This pentavalent is interpreted as the homoeologous pairing of a D chromosome with a quadrivalent produced by an interchange heterozygosity. This assumption was confirmed on crossing the cultivars 'Caravaca-1' and 'Fino Claro de Petrola' with 'Senatore Capelli' taken as standard (*Table 1*).

Summing up, it can be concluded that 21 out of 48 cultivars of *Triticum turgidum* cv. *durum* analyzed differ from 'Chinese Spring' and 'Senatore Capelli' cultivars taken as reference (see *Table 4*).

Our results are in agreement with those obtained by Tanaka and Ishii (1975) and Kawahara and Tanaka (1977) in *Triticum timopheevi*, the other tetraploid species of the genus. The same authors have also reported the existence of reciprocal translocations in some wild lines of *T. timopheevi* ssp. *araraticum*. In conclusion, the occurrence of chromosomal polymorphism for reciprocal translocations in the genus *Triticum* becomes apparent at both hexaploid (previous work) and tetraploid (this work) levels. Thus, the genus *Triticum* behaves as the other genera of the *Gramineae: Avena, Briza, Festuca,*

Tab. 4 Chromosome structure of durum wheat cultivars in comparison with 'Chinese Spring' and 'Senatore Capelli' taken as standard

Cultivars carriers of interchanges	Number of interchanges	Cultivar with the same chromosome structure in comparison with standard
Alcalá la Real	1	Alonso
Caravaca-1	1	Alonso Pérez Jurado
Castelfusano	1	Bidi-17
Castelporciano	1	Blanco de Llerena
Claro Fino de Balazote	1	California de Alcalá la Real
Crané	1	Capeiti
Enano de Córdoba	1	Casalle-92
Fino Claro de Petrola	1	Cascalvo Lucena y Montilla
Hércules	2	Casteldelmonte
Granja de Badajoz	1	D
Jerez 1937	1	Enano de Jaén
Leeds	1	Haurani
Morisco de Tenerife-1	1	Jerez 1936
Morisco de Tenerife-2	1	Lakota
Raspinegro de Mula	1	Las Palmas-7
Recio de Baza	1	Las Palmas-8
Rubio de Belalcazar	1	Macolo de Jerez
Rusello	1	Raspinegro de Alcalá
Valenciano negro	1	Raspinegro de Alcolea
Zoco de Yebel-Hebil	1	Raspinegro de Villanueva
569/66	1	Recio de Almería
		Recio de Ronda
		Rojal de Almería
		Rubio de Badajoz
		Ruso (Lérida)
		Santa Coloma
		Wells

Hordeum, Lolium, Secale, etc. (see references in the Introduction). In consequence, the interest of a reappraisal of the rôle of interchanges in the evolution of *Gramineae* is pointed out. According to WHITE's (1975, 1977) karyotypic orthoselection phenomenon, interchanges can be found "fixed" or "floating" in autogamous or allogamous plant species, respectively.

Zusammenfassung

Cytogenetische Struktur von spanischen oder nach Spanien eingeführten *durum*-Weizensorten

Die Chromosomenanordnungen bei 48 Weizensorten (*Triticum turgidum* cv. *durum*), die in Spanien entweder entstanden oder eingeführt sind, wurden mit denen der hexaploiden Sorte 'Chinese Spring' und der tetraploiden 'Senatore Capelli' verglichen. Die zwei letztgenannten Sorten dienten als Standard (sie haben gleiche Chromosomenanordnungen für die A- und B-Genome).

Von den untersuchten 48 Sorten wiesen 21 Sorten reziproke Translokationen auf. Alle diese Sorten unterscheiden sich durch eine reziproke Translokation voneinander, mit Ausnahme der Sorte 'Hercules', die zwei verschiedene Translokationen enthält, an denen drei Chromosomen beteiligt sind.

Die Rolle der reziproken Translokation als cytogenetischer Mechanismus bei der Evolution der Gramineae wird diskutiert.

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