Theor. Appl. Genet. 61, 129–133 (1982)

Cytogenetic Structure of Common Wheat Cultivars from or Introduced into Spain

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Summary. Chromosome arrangements of twenty-eight cultivars of common wheat, *Triticum aestivum* L., from or introduced into Spain are compared with that of 'Chinese Spring' taken as a pattern. All the cultivars analyzed differ from 'Chinese Spring' by one or two reciprocal translocations. When 12 out of 28 cultivars were compared it was concluded that a minimum number of thirteen interchanges are present, involving at least ten different chromosomes of the complement. The interest of a reappraisal of the rôle of interchanges in the evolution of Gramineae is pointed out.

Key words: Interchange – Chromosome arrangements – Common wheat – *Triticum aestivum*

Introduction

Common wheat, *Triticum aestivum* L., is an allohexaploid species ($2n=6\times=42$, AABBDD genome constitution) which behaves cytologically as a diploid, forming 21 bivalents at meiosis, due to the phenomenon named diploidization of polyploid wheats (Riley 1960). Thus, the formation of multivalent associations at meiosis in common wheat can be due either to the breakdown of mechanisms controlling homologous pairing or to heterozygosis for reciprocal translocations.

In considering the karyotypic orthoselection phenomenon, White (1965, 1973) stated that the new chromosomal arrangements can be found in populations in floating or fixed condition. In common wheat, an autogamous species, the varietal populations are homozygous for the chromosomal arrangement; however, they can differ from one another by reciprocal translocations. In these cases, intervarietal hybrids will be heterozygous for interchanges and form multivalent associations at meiosis (Sears 1953; Riley and Kimber 1961; Baker and McIntosh 1966; Riley et al. 1967; Diannelidis et al. 1969; Mettin et al. 1969; Mettin and Klein 1973; Law 1971; Zeller and Fischbeck 1971; Zeller and Sastrosumarjo 1972; Zeller 1973; Petrovic 1972; Larsen 1973; Baier et al. 1974).

In this paper chromosomal arrangement of several common wheat cultivars from, or introduced into, Spain are analyzed comparing them with 'Chinese Spring' taken as a pattern.

Materials and Methods

Twenty-eight cultivars of common wheat, *Triticum aestivum* L., were analyzed. Most of them arise from Spain and the others were introduced as commercial varieties some time ago. The cultivars analyzed were: 'Aragon 03', 'Aradi', 'Ariana 8', 'Aureo 23', 'Cabezorro', 'Cabezorro-2', 'Calatrava', 'Canaleja', 'Candeal de Castilla', 'Candeal de Teruel', 'Cascón', 'Caspino-4', 'Dimas', 'Florence Aurore', 'Hembrilla de Jaca', 'J-l', 'Magdalena', 'Mara', 'Mentana', 'MM-7', 'Pané 247', 'Rieti', 'Roma', 'San Bruno', 'Sin Tizón 35', 'Saria', 'Traquejos' and 'Yactana'.

On one hand the twenty-eight cultivars were crossed with the 'Chinese Spring' as male. On the other hand, twelve cultivars were crossed between them two by two in order to compare their respective chromosome arrangements.

Meiotic observations were made on pollen mother cells at metaphase I. Anthers were fixed in acetic alcohol 1:3 and PMCs stained with leuco-basic fuchsin according to Feulgen after the hydrolysis in 1N HCl at 60 °C for 11 min were squashed in a drop of acetic carmine. Meiotic observations were made on permanent slides mounted in Sandeural.

The chromosomal arrangements of each cultivar were deduced from the observation of meiotic configurations at metaphase I of the corresponding hybrids. Thus the presence of one or two quadrivalents was interpreted as the intervarietal hybrid being heterozygous for one or two independent interchanges, respectively. In consequence, it can be inferred that chromosomal arrangements of the two varieties differed in one or two independent reciprocal translocations. From the occurrence of an hexavalent or an octavalent hybrid it is inferred that the two varieties differ, respectively, in two or three interchanges in which one or more chromosomes have undergone sequential interchanges.

0040-5752/82/0061/0129/$ 1.00

Results

Analysis of Cytogenetic Structure

Critical configurations observed at metaphase I of the intervarietal hybrids ('Chinese Spring'×Cultivars) are shown in Table 1. Twenty-five out of the twenty-eight hybrids analyzed showed one quadrivalent (19 II+1 IV); the three remainder hybrids ('C.S'.×'Canaleja', 'C.S'.×'Candeal de Teruel' and 'C.S'.× 'Roma') showed two quadrivalents (17 II+2 IV). Thus, the three varieties 'Canaleja', 'Candeal de Teruel' and 'Roma' differ from 'Chinese Spring' in two independent interchanges, while the twenty-five remainders differ in only one.

The different frequencies with which multivalent associations are found at metaphase I can be taken as an indication of the different lengths of the chromosome segments involved in the interchanges of each hybrid combination. The higher the frequency of quadrivalents the longer the segments interchanged. So 'Cabezorro' cultivar shows the highest frequency (75%) while a number of cultivars show frequencies lower than 10% (the lowest corresponds to 'J-1' cultivar which shows 1%). Percentages ranging from 40 to 15% were considered intermediate values. In those cultivars which differ by two interchanges (for instance 'Canaleja') nothing can be accurately inferred from the high frequency (76%) of PMCs with one multivalent association since it was not possible to differentiate between the two interchanges.

In our material most of the intervarietal hybrids show a high percentage of chain quadrivalents. So it can be taken as an indication that the lengths of the chromosome segments interchanged are different. In 15 out of 28 intervarietal hybrids analyzed the frequency is 100%, suggesting that at least one of the chromosome segments involved in the interchange is very short.

Analysis of the Translocations and Estimation of the Number of Chromosomes Involved

The results obtained in the hybrid combinations between twelve cultivars are shown in Table 2. Fifty-nine

Table 1. Chromosome structures of common Spanish wheat cutlivars in comparison with 'Chinese Spring'. Analysis of meiotic configurations

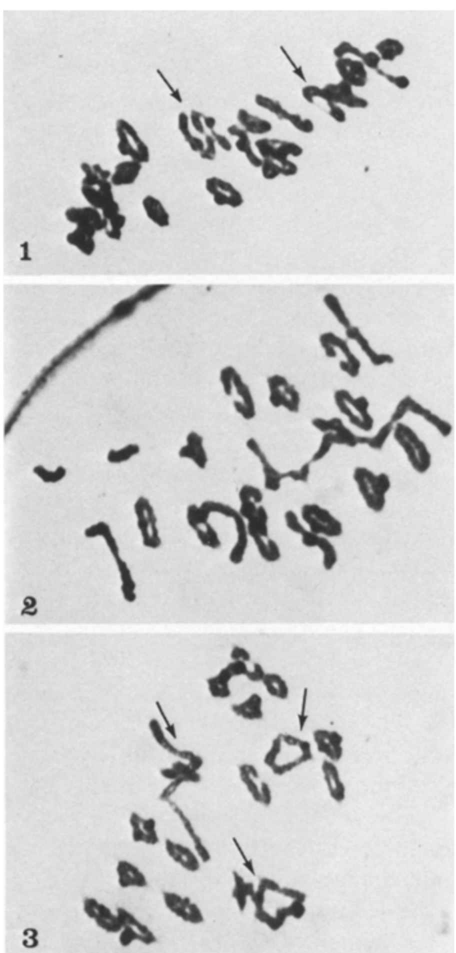
Cultivar crossed with 'Chinese Spring'	PMC	Critical configuration	Frequency of PMC in %			No. of interchanges	Quadrivalents in %	
			IV	III	2 IV		Ring	Chain
'Cabezorro'	100	1 IV	70.00	5.00	–	1	40.00	60.00
'Canaleja'	80	2 IV	63.75	7.50	5.00	2	37.50	62.50
'Cabezorro-2'[a]	90	I IV	47.78	3.33	–	2	39.53	60.47
'San Bruno'	101	1 IV	33.66	2.97	–	1	2.94	97.06
'Aragón-03'	100	1 IV	34.00	1.00	–	1	–	100.00
'C. Teruel'	89	2 IV	29.29	1.12	1.12	2	42.86	57.14
'Aradi'	100	1 IV	25.00	–	–	1	–	100.00
'Caspino-4'	95	1 IV	20.00	2.10	–	1	–	100.00
'Aureo-23'	100	1 IV	21.00	1.00	–	1	–	100.00
'Roma'	108	2 IV	17.59	–	1.85	2	–	100.00
'Saria'	119	1 IV	16.80	2.52	–	1	4.76	95.24
'Mara'	101	1 IV	17.82	–	–	1	–	100.00
'Yactana'	100	1 IV	13.00	2.00	–	1	–	100.00
'Magdalena'	103	1 IV	9.70	–	–	1	20.00	80.00
'Mentana'	104	1 IV	9.61	–	–	1	–	100.00
'C. Castilla'	93	1 IV	7.53	1.07	–	1	42.86	57.14
'Traquejos'	101	1 IV	7.92	–	–	1	37.50	62.50
'MM-7'	70	1 IV	7.14	–	–	1	40.00	60.00
'Sin Tizón-35'	70	1 IV	7.14	–	–	1	20.00	80.00
'Pané-247'	101	1 IV	5.94	–	–	1	–	100.00
'F. Aurore'	90	1 IV	4.44	–	–	1	50.00	50.00
'H. de Jaca'	100	1 IV	4.00	–	–	1	–	100.00
'Cascón'[b]	102	1 III	3.92	–	–	1	–	–
'Rieti'	128	1 IV	2.34	0.78	–	1	–	100.00
'Calatrava'	103	1 IV	2.91	–	–	1	–	100.00
'Ariana-8'	135	1 IV	2.22	–	–	1	33.33	66.67
'Dimas'	101	1 IV	1.98	–	–	1	–	100.00
'J-1'	100	1 IV	1.00	–	–	1	–	100.00

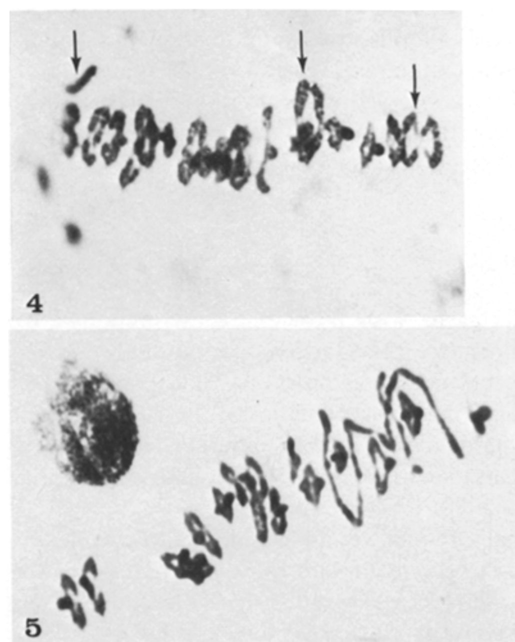
[a] The existence of two interchanges was inferred from intervarietal hybrid observations (see Table 2)

[b] The configuration corresponds to the cross with mono 2 D of 'Chinese Spring'

Table 2. Critical meiotic configurations of the hybrids between Spanish cultivars and their frequency in percentages

	CABEZORRO	S. BRUNO	C. CASTILLA	CANALEJA	ROMA	CASPINO-4	MENTANA	F. AURORE	MARA	CABEZORRO-2	C. DE TERUEL	YACTANA
CHINESE SPRING	1 IV	1 IV	1 IV	2 IV	2 IV	1 IV	1 IV	1 IV	1 IV	2 IV	2 IV	1 IV
CABEZORRO												
S. BRUNO	1 VI 8.2											
C. CASTILLA	1 VI 5.5	2 IV 1.6										
CANALEJA	3 IV 3.3	3 IV 0.9	3 IV 0.7									
ROMA	2 IV, 1 VI 1.3 16.7	2 IV, 1 VI 1.0 1.0	2 IV, 1 VI 1.2 0.8	2 IV 25.2								
CASPINO-4	1 VI 33.3	1 IV -	2 IV 2.4	2 IV, 1 VI 8.2 1.6	2 IV 2.3							
MENTANA	-	1 VI 8.8	1 IV 5.5	2 IV, 1 VI 31.8 4.6	2 IV, 1 VI 1.2 1.2	2 IV 1.8						
F. AURORE	2 IV 7.5	1 IV 16.1	1 IV 1.1	3 IV 0.7	2 IV 2.3	2 IV 1.4	1 IV 14.4					
MARA	-	2 IV 0.6	1 IV 18.8	3 IV 0.5	2 IV 2.0	2 IV 0.8	1 IV 14.0	2 IV 1.5				
CABEZORRO-2	1 IV 1.1	1 IV+1 VI 0.7	-	2 IV+1 VI 1.2	1 VIII 2.0	2 IV, 1 VI 1.0 14.9	1 IV+1 VI 1.0	2 IV, 1 VI 4.4 3.5	2 IV, 1 VI 1.1 5.5			
C. DE TERUEL	3 IV 51.6	-	1 IV+1 VI 19.6	3 IV, 1 IV+1 VI 1.9 1.9	2 IV+1 VI 0.8	1 IV+1 VI 12.8	-	1 IV, 1 VI 67.9 0.6	21 II 100	3 IV 2.3		
YACTANA	-	2 IV 0.7	1 IV 2.0	2 IV, 1 VI 4.8 1.2	2 IV 0.8	-	1 IV 1.1	2 IV 0.8	2 IV 0.6	1 VIII 0.6	2 IV, 1 VI 3.5 0.6	





Figs. 1–5. Meiotic configurations of hybrids between common wheat cultivars. **1** Metaphase I of the hybrid 'Florence Aurore' × 'Yactana' showing 2 IV; **2** Metaphase I of the hybrid 'S. Bruno' × 'Mentana' showing I VI; **3** Metaphase I of the hybrid 'Cabezorro' × 'C. de Teruel' showing 3 IV; **4** Metaphase I of the hybrid 'C. de Teruel' × 'C. de Castilla' showing 1 VI + 1 III + 1 I. The trivalent belongs to the critical IV; **5** Metaphase I of the hybrid 'Roma' × 'Cabezorro-2' showing 1 VIII

out of the 66 possible combinations were analyzed. Since all cultivars used as parents differed from 'Chinese Spring' cultivar by one or two interchanges, different critical configurations could be expected in the intervarietal hybrids as it is indicated below:

a) 2 IV: The two cultivars compared differ in two independent translocations (Fig. 1).

b) 1 VI: Both cultivars differ in two different interchanges but involving the same chromosome (Fig. 2).

c) 3 IV: The two cultivars differ in three independent translocations (Fig. 3).

d) 1 IV + 1 VI: Both cultivars differ in three interchanges but one of each cultivar involves the same chromosome, the third interchange being independent (Fig. 4).

e) 1 VIII: The two cultivars differ in three interchanges. Two independent translocations are carried by one of the cultivars and the two chromosomes involved in the interchanges of another cultivar are present in the former two translocations (Fig. 5).

As it can be seen in Table 2, all the above mentioned configurations were found in the hybrids analyzed. It is worthy of mention that in some cases the critical configuration is inferred from the PMCs observed. This is the case, for instance, of 'Cabezorr' × 'Roma' hybrids. In these hybrids the critical configuration written as 2IV, 1VI means that in some PMCs 2IV was observed while in others 1VI was seen; that is to say, the real critical configuration would be 1IV + 1VI but it was never found.

Table 3. An estimation of the interchanges present in the twelve Spanish cultivars analyzed

Cultivar	Interchanges	
	Number	Chromosomes involved[a]
'Cabezorro'	1	1 – 2
'San Bruno'	1	1 – 3
'Candeal de Castilla	1	2 – 4
'Canaleja'	2	5 – 6 and 7 – 8
'Roma'	2	1 – 4 and 5 – 6 or 7 – 8
'Caspino-4'	1	1 – 5, 6, 7, or 8 (arbitrarily fixed as 1 – 5)
'Mentana'	1	3 – 6, 7 or 8 (arbitrarily fixed as 3 – 6)
'Florence Aurore'	1	4 – 3 or 9 (inferred from its hybrids with S. Bruno)
'Mara'[b]	1	2 – 9 or 10
'Cabezorro-2'	2	1 – 2 and 4 – 6
'Candeal de Teruel'	2	4 – 5 and ? (the second one being unknown)
'Yactana'	1	2 – 5, 6, 7 or 8

[a] The numbering of chromosomes is arbitrary, and does not refer to any other conventional denomination

[b] The data available concerning the 'Mara' cultivar are not quite clear, probably due to the occurrence of a mixture of seeds

Discussion

Our results agree with those previously reported by other authors (see introduction) and strongly suggest that the occurrence of reciprocal translocations in common wheat is not the exception but the rule, since all the cultivars analyzed showed different chromosomal arrangements when compared with 'Chinese Spring' taken as a pattern.

The high frequencies of chain quadrivalents observed are in agreement with those reported by Baker and McIntosh (1966), suggesting that at least one of the segments involved in the interchange is small.

From the detailed analysis of Table 2 two main conclusions can be drawn, namely, 1) the twelve cultivars analyzed differ in a minimal number of thirteen reciprocal translocations, and 2) at least ten different chromosomes are involved in the interchanges. Both conclusions are reached according to the following rationale:

Let 1 and 2 be the chromosomes involved in the interchange carried by the 'Cabezorro' cultivar. Obviously the numbering of chromosomes is arbitrary. As the hybrid 'Cabezorro' × 'S. Bruno' forms an hexavalent, one can deduce that chromosomes 1 and 3 are involved in the interchange of 'San Bruno' cultivar.

As the hybrids of 'Candeal de Castilla' with 'Cabezorro' and 'San Bruno' have the critical configurations of 1 VI and 2 IV, respectively, one can deduce that 'Candeal de Castilla' has chromosomes 2 and 4 involved in the reciprocal translocation.

'Canaleja' cultivar differs from 'Chinese Spring' by two interchanges and its hybrids with 'Cabezorro', 'San Bruno' and 'Candeal de Castilla' cultivars show the 3 IV configuration, so it is deduced that the four chromosomes involved in the two reciprocal translocations are numbered 5, 6, 7 and 8.

A similar rationale could be applied to the remaining cultivars, 'Roma', 'Caspino-4', 'Mentana', 'Florence Aurore', 'Mara', 'Cabezorro-2', 'Candeal de Teruel' and 'Yactana'. The conclusions are summarized in Table 3.

The interchanges present in 'Canaleja' cultivar have been identified as 5B/7B and 4A/3D (Vega and Lacadena 1981). As its hybrids with the cultivars 'Cabezorro', 'San Bruno', 'Candeal de Castilla', 'Florence Aurore' and 'Mara' show the 3 IV configuration one can deduce that chromosomes 5B, 7B, 4A and 3D are not involved in the interchanges of such varieties.

However, as the hybrids of Canaleja with the cultivars 'Caspino-4', 'Mentana', 'Cabezorro-2', 'Candeal de Teruel' and 'Yactana' form hexavalent associations it can be inferred that their respective interchanges involve one of the four chromosomes 5B, 7B, 4A or 3D. Finally, the 'Roma' cultivar differs from 'Chinese Spring' by two independent interchanges (as 'Canaleja' cultivar does) and as the highest association found in the 'Roma' × 'Canaleja' hybrid was 2 IV, the possibility might be inferred that Roma cultivar carries one of the interchanges (5B/7B or 4A/3D) present in 'Canaleja' cultivar.

It is worth mentioning that from the point of view of the chromosome structure, all the cultivars of common wheat analyzed were monomorphic; that is to say, the chromosomal arrangements occurring during their evolution have been fixed in each cultivar.

The important rôle that polyploidy has played in the evolution of Gramineae is well known. However, the possible rôle of interchanges in their evolution has not been emphasized. From the karyotypic orthoselection point of view, it is worth noting that reciprocal translocations have been found at both inter- and intraspecific levels of several genera of Gramineae such as *Avena* (Ladinzinsky and Zohary 1971; Ladinzinsky 1973), *Secale* (Khush and Stebbins 1961; Khush 1962; Candela et al. 1979), *Hordeum* (Hunziker et al. 1973), *Briza* (Murray 1976), *Triticum*, etc.

The frequency with which reciprocal translocations appear in the *Gramineae* should stimulate a reappraisal of their rôle in the evolution of the taxon.

Acknowledgement

This grant has been supported by a grant from the Comision Asesora de Investigacion Cientifica y Técnica (No. 4204/79) of Spain.

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Received April 30, 1981
Communicated by R. Riley

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