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Cytogenetic analysis of structural rearrangements in three varieties of common wheat, *Triticum aestivum*

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Summary. The winter wheat varieties 'Starke' and 'Cappelle Desprez' and the spring wheat 'Chinese Spring' were analysed for structural chromosome rearrangements that resulted in the formation of multivalents in F_1 hybrids. The analyses were carried out using hybrids involving euploids, monosomic and ditelosomic stocks, and double-monotelodisomic constructs. The study confirmed that 'Cappelle Desprez' differs from 'Chinese Spring' in a reciprocal translocation between chromosomes 5B and 7B (Riley et al. 1967); a translocation involving chromosomes 3B and 3D could not be verified. Furthermore, the analysis showed that 'Starke' differs from 'Chinese Spring' in a reciprocal translocation between chromosomes 7A and 7D. Both translocations have a coefficient of multivalent realisation of about 0.84. Further multivalents in euploid 'Starke', in euploid and some aneuploid stocks of 'Cappelle Desprez', and in euploid as well as various types of aneuploid hybrids between all three varieties could nearly all be explained hypothesizing that chromosome 2B of both 'Starke' and 'Cappelle Desprez' is a duplication-deficiency chromosome. In the hypothesis a part of the long arm of 2B is missing and replaced by a duplicated part of the long arm of chromosome 2D. The multivalents of this rearrangement showed an average coefficient of realisation of about 0.09.

Key words: Common wheat – *Triticum aestivum* – Structural rearrangements – Translocation – Interchange – Duplication-deficiency – Aneuploidy

Introduction

As early as 1956 Burnham listed the occurrence of several structural rearrangements between chromosomes, especially translocations, within and between species of *Triticum* and *Aegilops*.

In common wheat, *Triticum aestivum*, such translocations often differentiate varieties (see surveys by Larsen 1973; Vega and Lacadena 1982; and also reports by Petrović 1972; Baier et al. 1974; Bourgeois et al. 1978; Košner and Bareš 1979; Lange et al. 1981). In plants heterozygous for a reciprocal translocation a multivalent may be formed at meiosis. The frequency of multivalent formation (referred to as coefficient of multivalent realisation) varies and is supposed to be related to the length of the translocated chromosome segments.

Several of the earlier papers on the production of aneuploid stocks in common wheat (Sears 1953; Person 1956; Unrau et al. 1956; Kuspira 1963) reported the occurrence of translocations and discussed the possible consequences of multivalent formation in relation to the use of aneuploids in cytogenetic studies.

The multivalents may increase the incidence of 'univalent shift' and the chromosomal structure of new aneuploid stocks, obtained through backcrossing, may remain different from that of the recurrent parent. Thus, Quinn and Driscoll (1970) as well as Law and Worland (1973) reported a strong gametic or zygotic selection for one of the two translocation chromosomes involved in a multivalent. The selection was supposed to be brought about by certain genes, making it difficult to recover the rearranged chromosome in an aneuploid condition. Also it can be expected that the frequency and distribution of chiasmata is being influenced by the translocation breakpoints. This could hamper the recovery of homozygosity or of the true genotype of the recurrent parent in backcrosses.

Thus, translocations are troubling factors in the production and use of aneuploid stocks of common wheat. Therefore, to minimize possible complications, the chromosomal structure of varieties used in cytogenetic experiments with aneuploids should be studied in advance. In addition, such knowledge might be useful in studies of the history of varieties and on the intraspecific evolution of common wheat.

The number of translocations differentiating two varieties and the coefficient of multivalent realisation can be estab-

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lished by studying meiosis of euploid F_1 hybrids (Riley et al. 1967; Petrović 1972; Bourgeois et al. 1978; Vega and Lacadena 1982). In such studies, the variety 'Chinese Spring' is often used as a reference, primarily because it is considered to have the original chromosome structure (Riley et al. 1967). More specific information can be obtained if a variety is crossed to all monosomics of another variety, followed by an analysis of multivalent formation in the monosomic F_1 hybrids (Baker and McIntosh 1966; Morris and Sears 1967; and others). In this way the chromosomes involved in a translocation can be identified. Linde-Laursen and Larsen (1974) described the use of double-monotelodisomic stocks to establish with full certainty that two chromosomes are involved in the same translocation. More recently, Gill and Kimber (1977) and Lapitan et al. (1984) used C-banding to recognize translocations and other structural changes in wheat-rye hybrids. Fominaya and Jouve (1985) studied C-banding patterns in wheat chromosomes at meiosis and were able to identify several chromosomes involved in translocation multivalents.

The present study was initiated in the seventies. The aim was to study in detail the translocations that exist in the Swedish winter wheat variety 'Starke' relative to the varieties 'Cappelle Desprez' and 'Chinese Spring'. This knowledge was wanted because 'Starke' was being used as a recipient variety for the introduction of monosomics and telosomics by backcrossing. The study revealed a discrepancy as to a previously published translocation differentiating 'Cappelle Desprez' and 'Chinese Spring' (Riley et al. 1967) and rendered it probable that structural rearrangements other than translocations may exist in common wheat. The origin of such rearrangements as well as the consequences of structural rearrangements for cytogenetic studies using aneuploid wheat will be discussed. A preliminary report has been published earlier (Lange et al. 1981).

Material and methods

The plant material consisted of various stocks of three varieties of common wheat, *Triticum aestivum* (L.) Thell.: 'Starke' (ST), 'Cappelle Desprez' (CD), and 'Chinese Spring' (CS). The Swedish variety 'Starke' was known to be composed of a mixture of lines; therefore, a selection of the original variety provided by Dr. G. Olsson (Svalöv, Sweden) was used. The material of 'Cappelle Desprez' included a euploid line and 20 monosomics (CD mono $5B^L$–$7B^L$, a translocation chromosome, was missing) and was made available by Dr. C. N. Law (Cambridge, UK). Several types of aneuploid 'Chinese Spring', viz. monosomics, monotelosomics, ditelosomics and double-monotelodisomics, as well as euploid plants were included in this study. Most stocks were produced by Dr. E. R. Sears (Columbia, Missouri, USA) and made available by himself or by Dr. R. Riley or Dr. C. N. Law (Cambridge, U.K.), or were produced from the original stocks (cf. Linde-Laursen and Larsen 1974).

Crosses were made to produce euploid and various types of aneuploid F_1 hybrids between the varieties. Hybrid seed was germinated on moist filter paper at 22–25 °C. If the mitotic chromosome number was needed to select the correct cytotype in segregating offspring, root-tip squashes were made. Tips of germinal roots of about 1.5 cm were collected and pretreated with 1-bromonaphthalene (4 h in a saturated solution or 5 h in a 0.1% aqueous solution of a mixture of 1 ml 1-bromonaphthalene and 100 ml absolute ethanol). The root tips were fixed in glacial acetic acid (overnight), followed by storage in acetic ethanol (1 : 3) for at least 24 h, or were fixed in 45% aceto-carmine for two or more days. Hydrolysis was carried out in 1N hydrochloric acid at 60 °C for 10 min, followed by staining with leuco-basic fuchsin and squashing in 45% acetic acid.

Meiotic chromosomes were studied in pollen mother cells (PMCs). Anthers were fixed in acetic ethanol (1 : 3), washed in 70% ethanol and in distilled water. Hydrolysis was carried out in 1N hydrochloric acid at 60 °C for 6–10 min, followed by staining with leuco-basic fuchsin and squashing in 45% acetic acid, sometimes with orcein or carmine or with haematoxylin according to Wittmann (1965). Both mitotic and meiotic preparations were made permanent by dry-ice freezing (Jacobsen 1965).

The programme mainly consisted of meiotic analyses. Euploid varieties and their euploid F_1 hybrids were studied to establish the number of multivalents at metaphase I and the distribution of multivalents over the cells. Monosomic hybrids between 'Cappelle Desprez' (20 chromosomes) and 'Starke', monosomic and monotelodisomic hybrids between 'Chinese Spring' (21 chromosomes) and 'Starke', monotelodisomic hybrids between 'Chinese Spring' and 'Cappelle Desprez' (4 chromosomes), and two monosomics of 'Cappelle Desprez' were analysed to establish the chromosomes involved in multivalent configurations at metaphase I. In all cases the critical cells were recorded. In the monosomic condition a critical cell would show a trivalent without univalent, and in the monotelodisomic cells the telosome would be part of the multivalent, irrespective of the fact that the translocation breakpoint is situated in the telosome or in the missing arm of the same chromosome. Some double-monotelodisomic hybrids between 'Chinese Spring' and both 'Starke' and 'Cappelle Desprez' were analysed to verify that two chromosomes were involved in the same multivalent. Thus, various types of critical cells were recorded.

As usual the multivalents will be presented by Roman figures: III = trivalent, IV = quadrivalent, etc. If, e.g., a trivalent contains a telosome or a quadrivalent contains two telosomes this will be notated as IIIt and IVtt, respectively.

Results

Euploid varieties and their F_1 hybrids

The results of studying metaphase I in PMCs of euploids of the three varieties and of their euploid F_1 hybrids are summarized in Table 1. In two hybrids both reciprocal F_1s were analysed; the results were similar, thus, the data were pooled. In all three hybrids plants were grown and analyses were carried out at two locations (Denmark and The Netherlands); again the results were similar, and the data were pooled.

All cells with trivalents had at least as many univalents as there were trivalents. Consequently, the trivalents were considered quadrivalents which had fallen apart in a trivalent and a univalent. For unknown reasons the proportion of quadrivalents that showed this irregularity differed markedly among the three hybrids.

Only 'Chinese Spring' did not show any multivalent configuration. In 'Starke' and 'Cappelle Desprez' about

Table 1. Number of PMCs with multivalents in euploids of three varieties of common wheat, 'Starke' (ST), 'Cappelle Desprez' (CD), and 'Chinese Spring' (CS), and their euploid F_1 hybrids

Variety or F_1 hybrid	No. of cells	Multivalents per cell								
		None	1 III	1 IV	2 III	1 III + 1 IV	2 IV	1 III + 2 IV	3 IV	Others
ST euploid	335	317	1	17						
CD euploid	120	116		4						
CS euploid	180	180								
CD × ST	176	2	2	30		10	124	1	6	1[b]
CS × ST	122	21	7	64	1	15	12	1		1[a]
CS × CD	451	42	35	340	1	12	19	1	1	

[a] 1 VI; [b] 1 IV + 1 VI

Table 2. Number of PMCs with multivalents in monosomic F_1 hybrids (2n = 41) between monosomics of 'Cappelle Desprez' and euploid 'Starke'. In brackets, the number of critical cells (III without I)

Monosomic	No. of cells	Multivalents per cell								
		None	1 III	1 IV	2 III	1 III + 1 IV	2 IV	2 III + 1 IV	1 III + 2 IV	3 IV	Others
1 A	27			3		2	10		5	7	
2 A	26			3		3	16			3	1[b]
3 A	26	1	1	6		1	15		1	1	
4 A	31	1	1	12		2	12			2	1[b]
5 A	25	1		4			16		2	1	1[b]
6 A	30	1		7		2	14		1	2	3[b,b,e]
7 A	29 (21)		5 (3)	2	4 (4)	15 (12)	1	1 (1)	1 (1)		
1 B	28		1	9		3	10		2	3	
2 B	91 (4)	3	3 (1)	25		5 (1)	46	1	3 (2)	5	
3 B	113	10	4	40	1	16	35	1	3	3	
4 B	30			11		4	14			1	
5 B^S–7 B^S	71 (46)	4	17 (12)	12	1 (1)	30 (27)	1		6 (6)		
6 B	29	1	1	5		3	13		2	2	2[a,d]
1 D	52 (1)	5	3	21	1 (1)	4	13		3	2	
2 D	82 (7)	3	1	26		6 (1)	39	1 (1)	6 (5)		
3 D	92 (1)	12	2	35		8 (1)	32			5	2[c,e]
4 D	53	1	1	10		3	28		2	5	3[b,e,f]
5 D	29	1		12		5	8			2	1[a]
6 D	27	2	1	5		7	9			2	1[b]
7 D	27 (15)		2 (2)	4	1	16 (10)		2 (1)	2 (2)		

[a] 1 VI; [b] 1 IV + 1 VI; [c] 1 IV + 1 VII; [d] 2 IV + 1 V; [e] 2 IV + 1 VI; [f] 3 III + 1 IV

4% of the cells had one multivalent (Fig. 1 A), indicating the occurrence of structural rearrangements. The observation of multivalents in 'Cappelle Desprez' confirms the findings of Petrović (1972) and Bourgeois et al. (1978). In the three F_1 hybrids multivalents were observed in the majority of the cells, with a maximum of three per cell (Fig. 1 B). Thus, in the two varieties only two chromosomes seem to be involved in a rearrangement. In the F_1 hybrids the number is higher. Disregarding the occurrence of three cells (in two combinations) with three multivalents and two cells with a hexavalent, at least four chromosomes in hybrids between 'Chinese Spring' and both 'Starke' and 'Cappelle Desprez', and at least six chromosomes in hybrids between the latter varieties are involved in rearrangements.

Aneuploid F_1 hybrids

'Cappelle Desprez' × 'Starke'. Meiosis was analysed in monosomic F_1 hybrids from crosses between monosomic 'Cappelle Desprez' and euploid 'Starke'. It was known (Law and Worland 1973) that mono 5B and mono 7B of 'Cappelle Desprez' were different from the ones in 'Chinese Spring' because monosomic lines carrying the translocation chromosome $5B^S$–$7B^S$ were the only ones that were recovered from crosses between

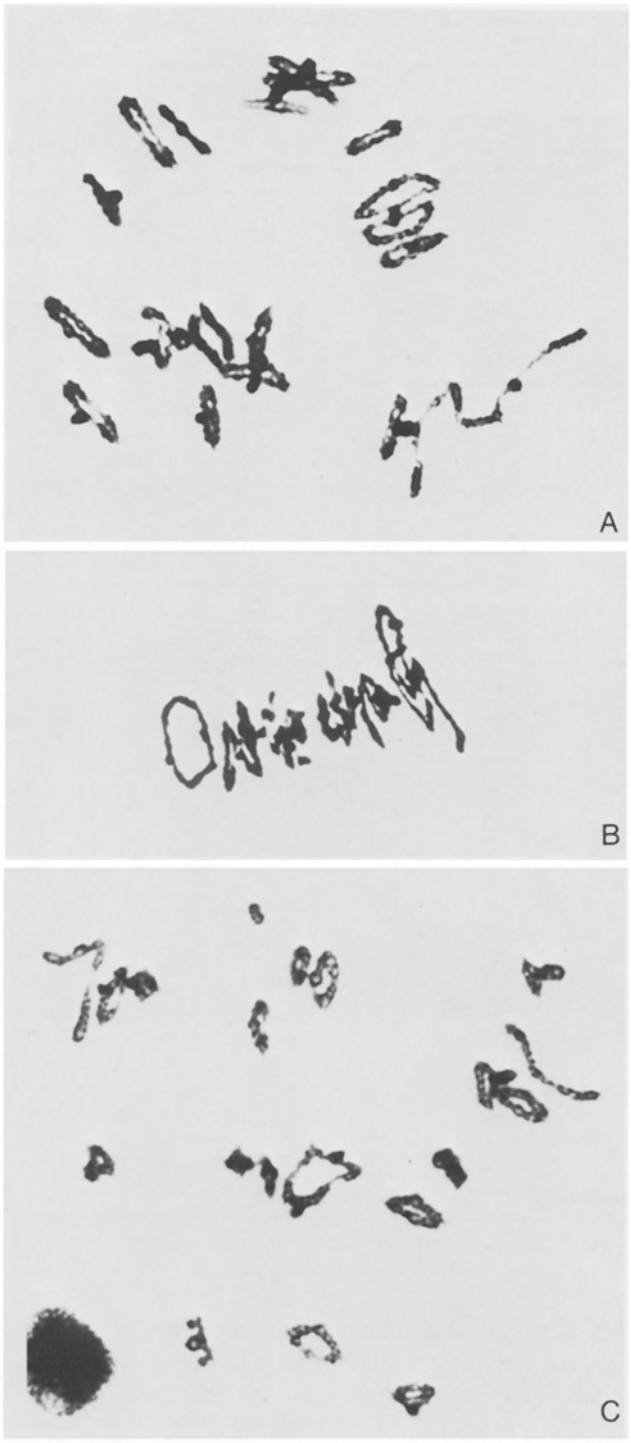

Fig. 1 A–C. Meiotic metaphases with multivalents originating from structural rearrangements. **A** Euploid 'Cappelle Desprez': 1 IV + 19 II. **B** Euploid F_1 hybrid between 'Starke' and 'Cappelle Desprez': 3 IV (2 rings and 1 zig-zag) + 15 II. **C** Pseudocritical cell in monotelodisomic F_1 hybrid between euploid 'Starke' and 'Chinese Spring' ditelosomic 2B: 1 IV + 1 III + 17 II + telo I

mono 5B or mono 7B of 'Chinese Spring' and 'Cappelle Desprez'. Thus, mono $5B^L$–$7B^L$ of 'Cappelle Desprez' was missing. The results of the analysis of the 20 monosomic types are summarized in Table 2.

The first concern was the critical cells, which are considered to indicate that the missing chromosome is homologous to parts of the chromosomes of the multivalent configuration. High frequencies of critical cells were found in mono 7A, mono $5B^S$–$7B^S$, and mono 7D; low frequencies were found in mono 2B and mono 2D; finally in both mono 1D and mono 3D one critical cell was observed. This led to the tentative conclusion that the six chromosomes involved in rearrangements between 'Cappelle Desprez' and 'Starke' are 7A, 2B, 5B, 7B, 2D and 7D. The critical cells in mono 1D and mono 3D will be discussed later.

Most multivalents were trivalents and quadrivalents. For unknown reasons the proportion of quadrivalents that fell apart in a trivalent and a univalent, excluding the monosomic types with critical cells, was higher than in the euploid F_1 hybrid. Some cells showed multivalents with more than four chromosomes: a pentavalent, several hexavalents and a septavalent. These configurations were rare and will be discussed later.

'Chinese Spring' × 'Starke'. These F_1 hybrids were studied in either the monosomic or the monotelodisomic condition. All 21 chromosomes were analysed and the results are summarized in Table 3. High frequencies of critical cells were found in mono 7A and 7D as well as in telo 7A and 7D. In telo 2D a low frequency of critical cells was observed, together with pseudocritical cells: cells in which a trivalent and a telosomic univalent occurred without further univalents. Telo 2B showed a low frequency of pseudocritical cells (Fig. 1 C). Finally, telo 3B showed one critical cell among a high number non-critical ones. These results led to the tentative conclusion that chromosomes 7A, 2B, 2D and 7D are involved in structural rearrangements between 'Chinese Spring' and 'Starke', but that in the case of chromosomes 2B and 2D the pseudocritical cells need special attention.

In these aneuploid hybrids the proportion of quadrivalents that fell apart in a trivalent and a univalent was much lower than in the euploid combination. Two cells had three multivalents, and no multivalents with more than four chromosomes were observed.

'Chinese Spring' × 'Cappelle Desprez'. The structural rearrangements between 'Chinese Spring' and 'Cappelle Desprez' were studied earlier. Riley et al. (1967) reported two translocations. One of them involved the chromosomes 5B and 7B; it was confirmed by Law and Worland (1973) and had a high coefficient of multivalent realisation. The other one was between chromosomes 3B and 3D, and had a low coefficient of multivalent realisation. Law (1971) mentioned the same

Table 3. Number of PMCs with multivalents in monosomic (2n = 41) and monotelodisomic (2n = 42t) F_1 hybrids between aneuploid types of 'Chinese Spring' and euploid 'Starke'. In brackets, the number of critical cells (for monosomics: III without I; for monotelodisomics: IIIt or IVt), or if marked with * the number of pseudocritical cells (III + It without I)

Monosomic	No. of cells	Multivalents per cell						Telosomic	No. of cells	Multivalents per cell					
		None	1 III	1IV	2 III	1 III + 1 IV	2 IV			None	1 III	1 IV	1 III + 1 IV	2 IV	Others
								1 A^L	80	22		50		8	
2 A	36	9	1	20		1	5								
3 A	17	1		12		2	2	3 A^a	11	5		5		1	
								4 A^a	25	5		17	1	1	1[b]
								5 A^L	36	17		14		5	
								6 A^S	21	9		8	1	3	
7 A	17 (7)	5	11 (6)			1 (1)		7 A^L	33 (26)	4	3 (2)	22 (20)	1 (1)	2 (2)	1 (1)[c]
1 B	30	8		21			1	1 B^L	8	2		4		2	
2 B	14	4	1	9				2 B^L	101 (12*)	17	2	61	16 (12*)	5	
3 B	34	6		24			4	3 B^L	272 (1)	20	1	224	4	22	1 (1)[a]
4 B	9	5		4				4 B^L	19	2		13		4	
5 B	11	4	1	5			1	5 B^L	30	21	1	6	2		
								6 B^S	29	10	2	15	1	1	
								7 B^L	38	11	3	16	3	5	
								1 D^L	22	1		15	1	5	
								2 D^S	132 (5 + 4*)	30		94 (1)	4 (4*)	4 (4)	
3 D	25	5		14			6	3 D^L	83	7		64	3	9	
4 D	18	6		10			2								
								5 D^L	37	3		30		4	
6 D	18	3		12		1	2	6 D^S	10	3		7			
7 D	19 (14)	3	14 (13)	1	1 (1)			7 D^S	27 (22)	5	1 (1)	17 (17)	1 (1)	3 (3)	

[a] 1 III + 1 IIIt; [b] 2 III + 1 IV; [c] 2 IV + 1 IVt

Table 4. Number of PMCs with multivalents in monotelodisomic (2n=42t) F_1 hybrids between ditelosomics of 'Chinese Spring' and euploid 'Cappelle Desprez', as well as two monsomic types (2n=41) of the latter variety. In brackets, the number of critical cells (for monotelodisomics: IIIt or IVt; for monosomics: III without I)

Telosomic or monosomic	No. of cells	Multivalents per cell					
		None	1 III	1 IV	2 III	1 III +1 IV	2 IV
2 B^L	34 (1)	5	7	21		1 (1)	
3 B^L	65	1	4	56		1	3
2 $D^{S\text{ or }L}$	23 (3)	4	2	15 (1)			2 (2)
3 D^L	53	2	6	30	1	3	11
2 B	220 (3)	217	3 (3)				
2 D	282 (10)	271	11 (10)				

translocation to be present in 'Hybride du Joncquois', one of the parents of 'Cappelle Desprez'. However, Bourgeois et al. (1978) could not find this translocation in two descendants of 'Cappelle Desprez'.

Considering the previous thorough studies (Riley et al. 1967; Law and Worland 1973), and in view of both the discrepancy mentioned (Bourgeois et al. 1978) and the not yet explained pseudocritical cells involving chromosomes 2B and 2D (Table 3), the present study of the structural rearrangements between 'Chinese Spring' and 'Cappelle Desprez' was carried through with chromosomes 2B, 3B, 2D, and 3D only. In addition, meiosis in mono 2B and mono 2D of 'Cappelle Desprez' was studied. The results of the analyses are summarized in Table 4. Low frequencies of critical cells occurred in all types of 2B and 2D studied. No critical cells were found in monotelodisomic hybrids for chromosomes 3B and 3D.

Double-monotelodisomic F_1 hybrids

The final proof whether two chromosomes are involved in the same or in different translocations was given by studying meiosis in double-monotelodisomic F_1 hybrids. Several double-monotelodisomics of 'Chinese Spring' were constructed by crossing ditelosomic stocks of this variety (cf. Linde-Laursen and Larsen 1974). These constructs were crossed with euploids of both 'Starke' and 'Cappelle Desprez', and among the offspring double-monotelodisomic F_1 hybrids were selected. The results of studying meiosis in such hybrids are summarized in Table 5. In general, they confirm the earlier tentative conclusions.

Between 'Chinese Spring' and 'Starke' there is a structural rearrangement between chromosomes 7A and 7D. In the same way there is a structural rearrangement between chromosomes 5B and 7B which differentiates 'Cappelle Desprez' from 'Chinese Spring'. There are no indications that these rearrangements are anything but reciprocal translocations. The results also clearly confirm that the translocation 5B–7B does not differentiate 'Chinese Spring' and 'Starke', and likewise that translocation 7A–7D does not differentiate 'Chinese Spring' and 'Cappelle Desprez'. This leads to the situation that both translocations will show up in hybrids between 'Starke' and 'Cappelle Desprez', which was previously shown (Table 2).

Critical cells that occurred in double-monotelodisomics of CS×ST: 2B+7D and 3B+7A could be attributed to the chromosomes 2B, 7D or 7A individually. No cells were found in which the telosomes belonged to the same multivalent. In the same way it could be concluded from double-monotelodisomics of CS×CD: 7A+7B and 7B+7D that the critical cells always were critical for one telosome only: this must have been chromosome 7B. In both hybrids with telosomes 3B+3D a very low frequency of critical cells occurred. This phenomenon will be discussed later.

The analyses with the double-monotelodisomics made clear that in both crosses chromosomes 2B and 2D are involved in the same structural rearrangement. However, the occurrence of a considerable proportion of pseudocritical cells, as well as the fact that both chromosomes showed critical cells in mono CD×ST (Table 2) and in mono CD (Table 4) indicate that the rearrangement is different from just a reciprocal translocation.

Conclusion and explanatory hypothesis

The whole set of data leads to the conclusion depicted in Fig. 2. 'Chinese Spring' differs from 'Starke' by a reciprocal translocation between chromosomes 7A and 7D and by another structural rearrangement between chromosomes 2B and 2D. 'Chinese Spring' differs from 'Cappelle Desprez' by a reciprocal translocation between chromosomes 5B and 7B and by another structural rearrangement between chromosomes 2B and 2D. 'Starke' differs from 'Cappelle Desprez' by reciprocal

Table 5. Number of PMCs with multivalents in double-monotelodisomic F_1 hybrids (2n = 42tt) between aneuploid constructs of 'Chinese Spring' and euploids of both 'Starke' and 'Cappelle Desprez'. In brackets two numbers of critical cells. First figure: cells are critical or pseudocritical (*) for one telosome only (IIIt or IVt, if *: III + It without I). Second figure: cells are critical or pseudocritical (*) for both telosomes (IIItt or IVtt, if *: IIIt + It without I; some other types are mentioned in footnotes). Part of the data is from Linde-Laursen and Larsen (1974)

Double telosomic	No. of cells	Multivalents per cell						
		None	1 III	1 IV	2 III	1 III + 1 IV	2 IV	Others
'Chinese Spring' × 'Starke'								
$2B^L + 2D^S$	149 (14/26*)	12	6 (2/3*)	94		32 (10/22*)	4 (2/0)[6]	1 (0/1)[a]**
$2B^L + 7D^S$	119 (91 + 2*/1 + 9*)	14	4 (4*/0)[2]	90 (88/0)	1 (0/1)[3]	10 (1/9*)[4]		
$3B^L + 3D^S$	265 (0/1)	42	1	181		15	25	1 (0/1)[c]
$3B^L + 7A^L$	93 (81 + 1*/0)	10	4 (4*/0)[1]	72 (71/0)		4 (4/0)	3 (3/0)	
$5B^L + 7B^L$	37	7		24		1	5	
$7A^L + 7D^S$	77 (2/68)	5	55 (1/53)	12 (0/11)	1 (0/1)	4 (1/3)		
'Chinese Spring' × 'Cappelle Desprez'								
$2B^L + 2D^S$	105 (6/9*)	7	4 (1/0)[7]	78 (1/0)[7]	1	10 (2/8*)	5 (2/1*)[5,6]	
$3B^L + 3D^S$	106 (5 + 1*/1)	9	10	72	2 (1/0)	4 (1/0)	7 (2/1)	2 (2/0)[b,d]**
$5B^L + 7B^L$	47 (0/41)	6	33 (0/33)		1 (0/1)	6 (0/6)		1 (0/1)[e]
$7A^L + 7B^L$	24 (21 + 1*/0)	2	6 (6/0)	14 (14/0)		1 (1*/0)	1 (1/0)	
$7A^L + 7D^S$	90	18	9	59			4	
$7B^L + 7D^S$	7 (6/0)		2 (2/0)	5 (4/0)				

[a] 1 IIIt + 2 IV + 1 It; [b] 1 III + 1 IVt + 1 IV; [c] IVtt + 2 IV; [d] 1 III + 1 VI + 1 It; [e] 1 IIItt + 1 VI

[1] Only one of the critical cells is pseudocritical; [2] only two of the critical cells are pseudocritical; [3] critical cell has 2 IIIt; [4] pseudocritical cells have 1 IVt + 1 III + 1 It; [5] pseudocritical cell has 2 IV + 2 It without I; [6] cells with 2 IV + 2 IIt or with 1 IV + 1 IVt + 1 IIt; [7] critical cells have 1 IVt + 1 IIt and 1 IIIt + 1 IIt

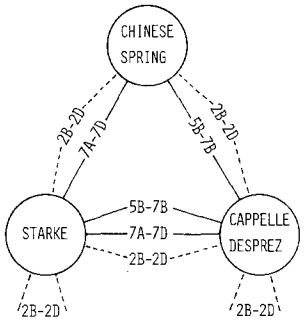

Fig. 2. Diagram representing the reciprocal translocations (———) and a postulated duplication-deficiency (– – – –) that differentiate the three varieties of common wheat: 'Chinese Spring', 'Starke' and 'Cappelle Desprez'

translocations between chromosomes 7A and 7D, between chromosomes 5B and 7B, and by another structural rearrangement between chromosomes 2B and 2D. The latter chromosomes are also involved in the formation of multivalents in euploid 'Cappelle Desprez'. Therefore, it seems highly probable that also the multivalents in euploid 'Starke' are the result of a rearrangement in chromosomes 2B and 2D (Table 1).

Most results concerning chromosomes 2B and 2D would fit the following hypothesis: part of the long arm of chromosome 2B is missing and has been replaced by a duplicated part of the long arm of chromosome 2D. The consequences of such a structural rearrangement in the various cytotypes of the present analyses are depicted in Fig. 3. For the sake of simplicity only one chiasma per chromosome arm is drawn, with preference for a distal location; it is also postulated that negative chiasma interference occurs around the breakpoint in the long arm of chromosome 2B.

Such a duplication-deficiency chromosome could have originated through a reciprocal translocation. Parallel co-orientation of the centromeres in a translocation multivalent gives rise to duplication-deficiency gametes, which, if not lethal, could give rise to individuals that are homozygous for this structural rearrangement.

One might question how both 'Starke' and 'Cappelle Desprez' carry the same duplication-deficiency. This might be explained by the fact that both varieties have the English landrace Squarehead in their pedigree.

One last conclusion of the present study concerns chromosomes 3B and 3D. Despite the extra attention given to several aneuploid types involving these chromosomes, the analysis did not yield sufficient evidence for the confirmation of a structural rearrangement involving chromosomes 3B and 3D of 'Cappelle Desprez' (Riley et al. 1967; and others). This conclusion is supported by the fact that Bourgeois et al. (1978) could not detect a 3B–3D translocation in either of the wheat varieties 'Moisson' and 'Roazon', which are direct descendants of 'Cappelle Desprez'. The discrepancy between authors could be related to heterogeneity of 'Cappelle Desprez', since of its parents ('Hybride du Joncquois' and 'Vilmorin 27') only the first one carries the 3B–3D translocation (Law 1971).

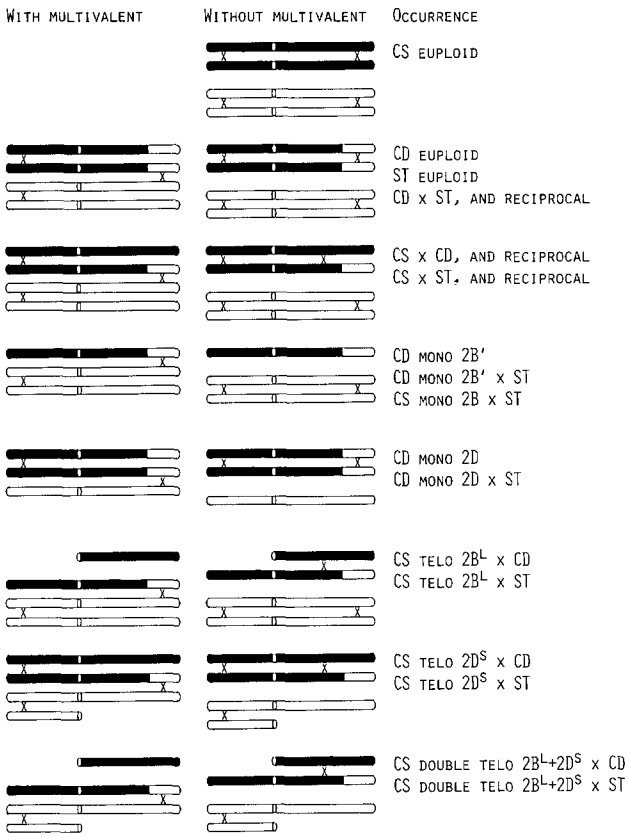

Fig. 3. Schematic drawings of meiotic configurations (with or without multivalent realisation) as a result of a postulated duplication–deficiency involving chromosomes 2B (▬) and 2D (▭) of common wheat. Only one chiasma (×) per chromosome arm is drawn. 'Cappelle Desprez' = CD, 'Starke' = ST, and 'Chinese Spring' = CS; 2B′ = incomplete chromosome 2B with duplicated segment of chromosome 2D

Discussion

Multivalents are a common phenomenon in F_1 hybrids between wheat varieties. Generally, reciprocal translocations are considered to be the cause of these configurations. In the early work on aneuploidy in wheat (Sears 1953), the possible disturbing effect of multivalents was recognised, especially the increase in the incidence of 'univalent shift'. In an earlier report on the production of monosomic and telosomic series in 'Starke' (Lange et al. 1981) from crosses with monosomics of 'Cappelle Desprez' and ditelosomics of 'Chinese Spring', followed by repeated backcrossing, it was shown that shifts had occurred for eight chromosomes. Four of them (7A, 7D, 2B and 2D) are involved in structural rearrangements. With respect to chromosomes 5B and 7B difficulties were expected, so for these chromosomes other parental material was chosen to circumvent the irregularities. This indicates the potential of structural rearrangements as a disturbing factor. Thus, detailed cytogenetic knowledge on the problem is needed. Therefore, the following discussion will deal with multivalent realisation, the presence of various not yet explained critical cells and of multivalents with more than four chromosomes, and some considerations on the evolutionary aspects of chromosome rearrangements.

Multivalent realisation

Completeness of multivalents. The multivalents which are the result of structural rearrangements can be complete, incomplete or not realised at all. In general, this phenomenon will be influenced by gross chiasma frequency and is fully comparable with the situation where sometimes two univalents appear instead of a bivalent.

The structural rearrangements mentioned in Figs. 2 and 3 will give rise in non-critical cells to only one type of complete multivalent: the quadrivalent, and consequently also to only one type of incomplete multivalent: the trivalent. The rarely occurring multivalents with more than four chromosomes will be discussed later.

Considering the euploid F_1 hybrids and those aneuploid F_1 hybrids, in which the aneuploid chromosomes obviously do not interfere with a structural rearrangement, the percentages of incomplete multivalents can be calculated. These are 9% for CD×ST (1,328 multivalents in 782 cells; Tables 1 and 2), 6% for CS×ST (1,266 multivalents in 1,338 cells; Tables 1, 3 and 5), and 12% for CS×CD (757 multivalents in 761 cells; Tables 1, 4 and 5). This shows that there is considerable variation among the hybrids for the proportion of incomplete multivalents. However, within the hybrids there is also such variation: for instance, between the percentages observed in euploid cells and the total of aneuploid cells (4% vs. 10% for CD×CS, 19% vs. 4% for CS×ST, and 11% vs. 14% for CS×CD; also from Tables 1–5). The figures do not show a consistent pattern. Therefore, the variation is considered to be brought about by factors outside the scope of the present study, e.g., by the influence of the environment on chiasma frequency. Thus, for the following part of this discussion, incomplete and complete multivalents will be considered together, keeping in mind that the observed variation probably also occurs in relation to the frequency of multivalent realisation.

Frequency of multivalent realisation. Next to the question of whether a multivalent is complete or not comes the question of whether the multivalent is realised at all. In general, this phenomenon is considered to be influenced by both the gross chiasma frequency and the size of the chromosome parts that are involved in the

Table 6. Calculated estimates of coefficients of multivalent realisation in PMCs of three varieties of common wheat, 'Starke' (ST), 'Cappelle Desprez' (CD), and 'Chinese Spring' (CS), and their euploid or aneuploid F_1 hybrids. T1 = translocation 5B–7B, T2 = translocation 7A–7D, and DD = duplication-deficiency 2B–2D. Figures in brackets are calculated from the other two values for the same material. All data from Tables 1–5, excluding the few PMCs with too many multivalents

Variety or hybrid	Critical chromosomes	No. of cells	Coefficients of multivalent realisation						
			T1	T2	DD	T1+T2	T1+DD	T2+DD	T1+T2+DD
Varieties									
ST+CD	none	455			0.05				
CD mono	2B	220			0.01				
CD mono	2D	281			0.04[b]				
Hybrid CD×ST									
CD×ST	none	782							1.70
mono	$5B^S$–$7B^S$	71	0.65[a]						
			0.76[b]					(0.80)	1.56
mono	7A+7D	56		0.64[a]					
				0.88[b]			(1.00)		1.88
mono	2B	91			0.04	(1.69)			1.73
mono	2D	82			0.09	(1.59)			1.68
Hybrid CS×ST									
CS×ST	none	1,338						0.95	
mono	7A+7D	36		0.58[a]					
				0.75[b]	(0.08)			0.83	
(d-)telo	$7A^L+7D^S$	136		0.86	(0.13)			0.99	
telo	$2B^L$	101		(0.92)	0.12			1.04	
telo	$2D^S$	132		(0.76)	0.07			0.83	
d-telo	$2B^L+2D^S$	144[c]		(0.88)	0.26			1.14	
Hybrid CS×CD									
CS×CD	none	761					0.99		
d-telo	$5B^L+7B^L$	46	0.87		(0.15)		1.02		
telo	$2B^L$	34	(0.85)		0.03		0.88		
telo	$2D^{S\text{ or }L}$	23	(0.78)		0.13		0.91		
d-telo	$2B^L+2D^S$	98[c]	(0.94)		0.10		1.04		

[a] Based on critical cells; [b] based on cells with trivalent; [c] excluding also the cells mentioned in footnotes 5–7 of Table 5

structural rearrangement. Therefore, for the three structural rearrangements, estimates for the coefficients of realisation were calculated. The data of Tables 1–5 were used in various ways. The euploid and monosomic stocks of varieties were suitable for a direct estimate of the coefficient of multivalent realisation, as were the critical cells with telosomic marker(s). The critical cells in monosomic F_1 hybrids appeared to lead to an underestimate of the realisation of the multivalents because the presence of a pair of univalents, most probably originating from a bivalent, in many cells also harbouring a trivalent, rendered the cell non-critical. Therefore, an estimate was calculated, based on the trivalent frequency. However, this figure may be slightly too high.

In all other cases the data of Tables 1–5 could only be used to calculate sums of coefficients of realisation of two or three multivalents together. To do so the following formula was used. If, in case of a maximum of three multivalents, the frequencies of PMCs with no, one, two, or three multivalents are called p, q, r, and s, and if the three coefficients of realisation of the multivalents are called x, y, and z, it can be said that:

$$p=(1-x)(1-y)(1-z)$$
$$q=(1-x)(1-y)z+(1-x)(1-z)y+(1-y)(1-z)x$$
$$r=(1-x)yz+(1-y)xz+(1-z)xy$$
$$s=xyz$$

From these equations it can be calculated that:

$$x+y+z=q+2r+3s=1-p+r+2s.$$

In case of a maximum of two multivalents the same formula can be applied, but here both z and s are zero.

The direct estimates and the calculated sums of estimates of coefficients of multivalent realisation are summarized in Table 6. In general, the figures agree relatively well with each other. The translocations 5B–7B and 7A–7D each show a high coefficient of multivalent realisation, about 0.84, with relatively little variation. The coefficient of realisation of the 2B–2D multivalent is much lower, about 0.09, and shows a wider range.

Riley et al. (1967), Law (1971) and others reported a high frequency of multivalents as a result of the 5B–7B translocation. In the present study this could be confirmed together with the discovery of the 7A–7D translocation, which also has a strong tendency for multivalent realisation. In the light of the preceding remarks about complete and incomplete multivalents it may be assumed that both these translocations in principle always give rise to a multivalent pairing association and that the realisation is being regulated by chiasma frequency only. In case of random chiasma distribution such an assumption would lead to the conclusion that the translocation breakpoints are located in or very near to the centromere. However, as there is growing evidence that in wheat the distribution of the chiasmata is far from random, because they are probably restricted to the distal halves of each chromosome arm (Law, pers. commun.; Dvořák and Chen 1984; Snape et al. 1985), it can only be concluded that the translocation breakpoints are in the proximal half of one of the chromosome arms of each chromosome involved.

The estimated coefficients of multivalent realisation for the structural rearrangement between chromosomes 2B and 2D are low and rather variable. It is tempting to try to relate the various values to the types of multivalents, to which they belong, in terms of distribution of chiasmata, etc., but the risk for inadmissible speculation seems too high. The hypothesis presents a model in which most data can be fitted in. The size of the duplication must be such that also interstitial chiasmata can occur, because some of the hypothesized associations can only be explained by assuming the occurrence of such chiasmata, e.g., between the telosome $2B^L$ and the duplication-deficiency chromosome. However, in those cases an interstitial chiasma nearly always seems to prevent the occurrence of a chiasma in the duplicated segment.

Unexplained multivalent configurations

Not yet explained multivalent configurations were observed in three groups of PMCs: (1) cells with multivalents with more than four chromosomes (mostly hexavalents, 18 PMCs, most of them occurring in CD×ST; Tables 1, 2, and 5), (2) cells with more multivalents than explained in Fig. 2 (23 PMCs, mostly occurring in CS×ST and CS×CD, often in combinations comprising the telosomes 2B or 2D; Tables 1, 2, 3, and 5, including the footnotes 5–7 of Table 5), and (3) cells that are critical for other chromosomes as mentioned in Fig. 2 (10 PMCs, most of them critical for chromosomes 3B or 3D; Tables 2, 3 and 5). On a total of 5,363 analysed cells the number of aberrant cells is too low to disturb the analysis and too high to be neglected.

It appears unsatisfactory to explain all these aberrant configurations by assuming illegitimate non-homologous chromosome association, or perhaps homoeologous chromosome association, which could have been brought about by a rare failure of the 5B system (Riley, pers. commun.). Other mechanisms may probably occur as well. In haploid wheat some bivalent association has been reported (Kimber and Riley 1963), and even a trivalent has been observed (Linde-Laursen and Larsen, unpubl. result). Bivalents also occurred in reconstituted amphihaploid wheat from crosses between *T. dicoccoides* and *T. tauschii* (Lange 1986). As it is widely assumed that chromosome association in haploids is the result of smaller homologous chromosome segments, part of the aberrant configurations in the present study could also be the result of homoeologous or non-homologous associations which are legitimate on the basis of smaller homologous segments. As both the aneuploid structure of most of the material studied and the occurrence of multivalents might disturb the spatial arrangements of the chromosomes, this could create an environment in which these smaller homologous segments do associate more readily than in balanced euploid plants.

Evolutionary significance

As mentioned before, there is growing evidence that in wheat the chiasmata are restricted to the distal halves of each chromosome arm (Law, pers. commun.; Dvořák and Chen 1984; Snape et al. 1985). This suggests that at least one half of the chromosome would be excluded from the recombination process. This might be an evolutionary strategy to keep large blocks of genes together, but it also could result in the linkage of less favourable genes to such blocks. In all cases, translocations are perhaps the only tool for the plant to change the linkage situations in the proximal parts of the chromosomes. Such thinking gives an extra dimension to the occurrence of translocations in wheat.

Another aspect of translocations in relation to the evolution of wheat comes from the presented hypothesis regarding chromosomes 2B and 2D. As said before, the postulated duplication-deficiency chromosome could have resulted from a translocation multivalent. This leads to a cyclic reasoning in which homologous segments give rise to translocations that may result in duplicated segments again. Such systems might have played a role in the evolution of wheat.

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