Meiotic expression of modified chromosome constitution and structure in $\times$ *Triticosecale* Wittmack

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The chromosome constitution and the meiotic behaviour of plants in the F3, F4 and F6 progenies of one cross between 6x-triticale (female) and *Triticum aestivum* (male) were analysed. C-banding of meiosis proved to be a good method to score the individual levels of pairing, to verify the chromosome constitution, and to detect structural variations.

Amongst the plants examined, the chromosome constitution varied in the third genome (0–7" D and 0–6" R), and all plants had the whole A and B genomes in common. Rye chromosomes presented some modifications in distribution of heterochromatin. Other karyological variations such as D/R centric fusions or telocentrics were also occasionally observed. Segregation for missing heterochromatin in the telomeres of the arm 3RS was found amongst the plants. Chromosome pair 3R showed significantly more chiasmata in plants in which heterochromatin is deleted (– –) or present (++) in both telomeres than in heterozygous (– +). Both heterochromatin and chromosome constitution are discussed in relation to factors affecting meiotic pairing and interest in setting out new hybridizations.

INTRODUCTION

After introduction of Giemsa staining for differential chromosome analysis in triticale it became evident that heterochromatin is located at the telomeres of 11 out of the 14 chromosome arms of the rye chromosomes, and at the centromeres and interstitial regions of the wheat chromosomes.

The telomeric heterochromatin of rye chromosomes has been correlated with certain morphological and cytological undesirable characters. Kaltsikes *et al.* (1975) noticed that the presence of rye heterochromatin in triticale causes aberrant nuclei in a coenocytic endosperm. The production of such aberrant nuclei leads to the formation of cavities in the endosperm and shrivelling grain at maturity.

The capacity of C-heterochromatin to affect univalency and aneuploidy in triticale has been discussed previously (Roupakias and Kaltsikes, 1977; reviews of Gupta and Priyadarshan, 1982, and Lukaszewski and Gustafson, 1986). Accordingly, a series of studies have been carried out to analyse the chromosome constitution and the amount of telomeric heterochromatin of rye chromosomes in secondary triticale lines (Lukaszewski and Apolinarska, 1981; Ziauddin

and Kasha, 1982; Varghese and Lelley, 1983; Gustafson *et al.*, 1985; Lukaszewski, 1986).

Giemsa banding could be very informative to investigate the influence of structural and/or numerical differences of chromosomes on the meiotic pairing in genetically well defined lines of triticale. In this paper, we applied this technique to study the influence of both chromosome constitution and telomeric C-heterochromatin on the meiotic association of chromosomes, using a sample of karyotypically unstabilized plants belonging to the early progenies of a cross between a primary 6x-triticale line and a common wheat. The pairing affinity of wheat chromosomes in comparison with rye chromosomes in triticale is also discussed.

MATERIALS AND METHODS

The plant material studied derived from the cross between the triticale line "P-60" and the common wheat cultivar "Chaimite". "P-60" is a hexaploid primary line which was obtained at the Department of Cereals and Legumes by one of the coauthors (C. Soler) at I.N.I.A. This line showed homogeneity for many biochemical and morpho-

logical characters after application of different electrophoretical and agronomic analyses. "Chaimite" is a Portuguese wheat variety commonly used in wheat improvement in Spain.

Seven F3, seventeen F4 and twenty-four F6 plants were utilized in this study. The plants were selected at random within the progenies of each generation of self-pollination. This plant material formed a part of an ongoing program designed to obtain secondary triticales lines.

Karyological analysis was carried out in all plants analysed. The criteria defined in the Workshop on Wheat Chromosome Nomenclature held during the 7th International Wheat Genetic Symposium (Cambridge, 1988) were adopted to identify and designate the wheat chromosomes. The amount and distribution of heterochromatin and the size and external morphology for the rye chromosomes were used as identifying features, using the C-banding patterns for the somatic chromosomes according to the International Workshop on Rye Chromosome Nomenclature and Homoeology Relationships (Sybenga, 1983).

To identify individual wheat chromosomes at first metaphase in meiosis, the pattern of C-banding for nine chromosomes (4A, 7A and the seven of the B genome) described earlier (Ferrer *et al.*, 1984) was used. In addition, wheat chromosomes 2A, 5A and 6A were recognized using the somatic heterochromatin descriptions as a reference.

Seminal roots of about $\frac{1}{2}$ cm in length were excised, pretreated in cool water for 28 hours and fixed in 45 per cent acetic acid for 24 hours. Anthers for meiotic analysis of pollen mother cells (PMCs) were fixed in acetic acid-alcohol 1:3. Preparations and staining of both somatic and meiotic chromosomes were carried out by the Giemsa C-binding technique as described earlier (Jouve *et al.*, 1980).

RESULTS

Chromosome constitution and modifications

The chromosome constitutions of the segregant plants (F3 to F6) were studied (table 1). The plants

Table 1 Variation of somatic chromosome constitution of the plant material analyzed. " = chromosome pair; ' = monosomic; t = telosomic; d = telomeric duplication; ++, +- and -- = homozygous normal, heterozygous and homozygous deficient bivalent for a telomeric deletion in 3RS, respectively; * = plants with $2n = 42$ and similar chromosome constitutions used to analyse the influence of telomeric heterochromatin of 3RS on pairing; 7RL.2DS = centric fusion

Progeny	No. of plants	Fixed karyotype		Variable karyotype		
		A + B genomes	R genomes	D genome	R genome	2n
F ₃	1	14"	1R" 5R"	3" 1'	2R' 3R ⁺⁻ 4R" 6R" 7R'	47
	1	14"	1R" 5R"	3" 1'	3R ⁺⁻ 4R" 6R" 7R'	46
	1	14"	1R" 5R"	1" 3'	2R' 3R ⁺⁻ 4R" 6R" 7R' 45	
	1	14"	1R" 5R"	1" 2'	3R ⁺⁻ 4R" 6R" 7R'	43
	1	14"	1R" 5R"	1" 2' 1'	3R ⁺⁻ 4R" 7R"	43
	1	14"	1R" 5R"	3"	3R ⁺⁻ 7R"	42
	1	14"	1R" 5R"	2"	3R ⁺⁻ 4R" 6R"	42
F ₄	2	14"	1R" 4R" 6R"	1" 2'	3R ⁺⁻ 5R" 7R/2D'-7R'	44
	1	14"	1R" 4R" 6R"	1" 2'	3R ⁺⁻ 5R" 7R'	44
	1	14"	1R" 4R" 6R"	1" 2'	3R ⁺⁺ 5R" 7R"	44
	1	14"	1R" 4R" 6R"	1" 2R'	3R ⁺⁻ 5R" 7R"	44
	2	14"	1R" 4R" 6R"	3" 1'	5R" 7R'	43
	1	14"	1R" 4R" 6R"	1" 1'	3R ⁺⁺ 5R" 7R"	43
	2	14"	1R" 4R" 6R"	1" 1'	3R ⁺⁺ 5R' 7R"	43
	1	14"	1R" 4R" 6R"	1" 1	3R ⁺⁺ 5R" 7R'	42
	2*	14"	1R" 4R" 6R"	1" 1'	3R ⁺⁻ 5R" 7R'	42
	1	14"	1R" 4R" 6R"	2" 1'	3R ⁺⁻ 7R'	42
	1	14"	1R" 4R" 6R"	1" 1' 1'	3R ⁺⁻ 5R"	42
	1	14"	1R" 4R" 6R"	1" 1'	3R ⁺⁺ 5R"	41
	1*	14"	1R" 4R" 6R"	2'	3R ⁺⁺ 5R" 7R"	42
F ₆	2	14"	1R" 4R" 6R" 7R"	1"	3R ⁺⁻ 5R ^d	42
	1	14"	1R" 4R" 5R" 6R"	1"	3R ⁺⁺ 7R/2D'-7R'	42
	6*	14"	1R" 4R' 5R" 6R" 7R"	1"	3R ⁺⁺	42
	6*	14"	1R" 4R" 5R" 6R" 7R"	1"	3R ⁺⁻	42
	5*	14"	1R" 4R" 5R" 6R" 7R"	1"	3R ⁺⁻	42
	1	14"	1R" 4R" 5R" 6R" 7R"		3R ⁺⁻	40
	1	14"	1R" 4R" 5R" 6R" 7R"	1" 1'	3R ⁺⁻	42
	2	14"	1R" 4R" 5R" 6R" 7R"	7"		42

showed a uniform karyotype for the A and B genomes ($7''$ AA + $7''$ BB) and a unstabilized constitution for the third genome (0–17 D and 0–13 R). The total chromosome number (40 to 47) and the range of variable karyotypes showed a tendency to regularize over generation time. Only two out of the 48 plants analysed showed the common wheat chromosome constitution, incorporating the seven chromosomes of the D genome instead of the rye chromosomes. Chromosome 2R was absent in all plants analysed, with the exception of two plants in the F3 in which it was present as a monosomic addition. The chromosomes 3R, 4R, 5R, 6R and 7R were sometimes either absent or present in monosomic condition. On the average, 18.3 and 80.4 per cent, respectively, for the D and R genomes, were fixed in disomic condition in 44 out of the 46 karyotyped triticales plants.

Two plants showed heterozygosity for a pair composed by the chromosome 7R and the centric fusion product 7RL.2DS, and two plants showed the arm 2DL as a mono-telocentric addition. This was probably produced by misdivision in meiosis during an earlier generation. The presence of chromosome 2D in many plants lacking in chromosome 2R was confirmed by C-banding.

Modifications affecting both C-banding pattern and size of the telomeric heterochromatin in rye chromosomes were found amongst the segregant plants (fig. 1). The modifications consisted of duplication, reduction or loss of heterochromatin. Thus, chromosomes 1R, 3R, 4R, 5R, and 7R were found as more or less modified chromosomes in some plants as compared to the R chromosomes of the parental triticales "P-60". Missing heterochromatin in the telomeres of the short arm of chromosome 3R was the most evident modification and emerged segregating among the plants on each successive generation. Plants were classified as homozygous deficient when heterochromatin was deleted from both telomeres of 3RS (—), heterozygous (+—) and homozygous normal in which 3RS exhibited in both telomeres a C-heterochromatin band (++) . The telomeric heterochromatin on the arm 4RL occasionally appeared as a deletion. A duplication of the telomeric heterochromatin of arm 5RL was observed in some plants.

Meiotic pairing behaviour

The meiotic pairing was individually analysed per each identified chromosome at first meiotic metaphase (fig. 2). Data on chiasma frequencies per chromosome arm and genomes are registered for

Figure 1 Magnification of rye chromosomes in segregant plants showing some modifications in heterochromatic blocks (arrows).

the plants grouped according to their generation (table 2).

It was observed that; (i) the maximum chromosome association coincided successfully with expectations of 14 AA + BB bivalents plus a variable number of bivalents, equal to D + R pairs, in each plant; (ii) the wheat chromosome pairs showed a higher mean number of chiasmata per bivalent (1.61–2.13) than the rye ones (0.85–1.47), regardless of the chromosome constitution; (iii) a certain variation for both wheat and rye pairing values was observed amongst the plants. However, the total mean number of chiasmata in rye and wheat bivalents per plant followed similar tendencies and a relatively close correlation between chiasma frequency of wheat and rye chromosomes was observed ($r = 0.7138$; $t = 6.0305$; $df = 44$; $P < 0.001$) amongst the plants (fig. 3); (iv) long arms paired more than short arms regardless their chromosome nature; and (v) rye-wheat bivalents (2DS.7RL-7R) and trivalents (2D-2DS.7RL-7R) with unambiguous chiasmatic associations and cooriented centromeres were observed in two plants carrying the 7RL.2DS centric fusion.

The influence of telomeric heterochromatin of the short arm of chromosome 3R on the meiotic pairing was comparatively analyzed. Plants having $2n = 42$ and similar chromosome constitution (marked with asteriks in table 1) were grouped according to the telomeric structure of chromosome 3R. Chromosome pair 3R showed moder-

Figure 2 Micrographs on chromosome pairing in different plants from segregating progenies: (a) $2n = 41$ ($3R^{--}$), and (b) $2n = 44$ ($3R^{+-}$).

ately more chiasmata in short arm in homozygous normal ($++$) than in homozygous deficient ($--$) bivalents. However, when comparisons of the mean number of chiasmata in $3RS--$ and $3RS++$ among the different groups of plants were performed by t -tests the deviations were not significant (table 3).

A significant reduction in pairing level was noted in heterozygous deficient $3R+-$ bivalents, regardless of the chromosome number and structure of each plant. The chromosome pair $3R$ formed more univalents or open rod bivalents

in the short arm in heterozygous than in both homozygous normal and homozygous deficient plants.

DISCUSSION

The variation in chromosome composition of the third genome in plants of F3 and following generations of the cross between $6x$ -triticale and *T. aestivum* could be conditioned by chromosome constitution of the F2 plant from which they were

Figure 3 Relationship between mean chiasmata number in wheat and rye chromosomes of 44 segregant plants analysed.

Table 2 The mean number of chiasmata per chromosome arm (2AS to 7RL) and per bivalent in the A-, B- and R-genome chromosomes, of the F3, F5 and F6 plants analyzed. Contingency χ^2 tests concern the relative contribution to the meiotic configurations (univalents, rod bivalents and ring bivalents) of each chromosome pair among the plants in each generation. * = Significant at the level of 5 per cent

	F ₃	F ₄	F ₆
2AS	0.77	0.79	0.87
2AL	1.13	1.22	1.30
4AS	0.59	0.67	0.65
4AL	0.98	1.07	1.08
5AS	0.78	0.73	0.71
5AL	1.16	1.17	1.20
6AS	0.76	0.79	0.82
6AL	1.05	1.13	1.22
7AS	1.00	0.96	1.05
7AL	1.12	1.06	1.14
1BS	0.67	0.64	0.68
1BL	1.17	1.15	1.10
2BS	0.93	0.96	1.05
2BL	1.06	1.12	1.12
3BS	0.77	0.79	0.87
3BL	1.14	1.12	1.25
4BS	0.76	0.80	0.82
4BL	1.18	1.15	1.24
5BS	0.63	0.53	0.44
5BL	1.25	1.22	1.22
6BS	0.72	0.64	0.71
6BL	1.03	1.03	1.09
7BS	0.69	0.78	0.73
7BL	1.07	1.09	1.16
1RS	0.34	0.32*	0.27*
1RL	0.83	0.79	0.84
3RS	0.13*	0.39*	0.53*
3RL	0.75	0.79	0.79
4RS	0.48*	0.65	0.57*
4RL	0.78	0.79	0.78
5RS	0.36	0.50	0.55
5RL	0.85	0.93	0.95
6RS	0.19*	0.17*	0.25*
6RL	0.69	0.92	0.95
7RS	0.26*	0.25*	0.26*
7RL	0.96	0.85	0.87
A-bivalents	1.87	1.91	1.99
B-bivalents	1.85	1.85	1.93
R-bivalents	1.12	1.21	1.21
No. Plants	7	17	22
No. Cells	688	1100	1150

derived. Moreover, the composition depends on the meiotic behaviour and chromosome transmission within F1 gametes. The meiotic behaviour of F1 hybrids with a genome formula AABBDR have been previously investigated (Tarkowski, 1969; Sánchez-Monge and Sánchez-Monge, 1977; Bernard and Bernard, 1978; Soler *et al.*, 1980; Schlegel *et al.*, 1980; Jouve *et al.*, 1982, 1985). Cells with 7 A-genome bivalents + 7 B-genome

bivalents + 7 D-genome univalents + 7 R-genome univalents were recorded as the most frequent chromosome association in these hybrids. This meiotic behaviour corresponds well to that expected on the assumption of homologous pairing only, and opens the possibility of elimination or reciprocal substitution of some R or D homoeologous chromosomes in the F2 and following generations. Our results on the chromosome composition of plants in F3 to F6 seem to confirm the assumption of D/R substitutions. This is clear in the plants with $2n = 42$ chromosomes (29 out of 48 plants studied).

The substitution of chromosome 2R by 2D into hexaploid triticale has been found in a considerable number of secondary triticale lines (Zillinsky, 1973; Gustafson and Zillinsky, 1973, 1978; Merker, 1975; Gustafson and Bennett, 1976; Rogalska, 1978; Pilch, 1981a, b; Sandha *et al.*, 1984; Armstrong and Fedak, 1985; Jouve *et al.*, 1989). Most studies attribute this substitution to a series of desirable characteristics of segregant plants (Zillinsky, 1980; Lukaszewski and Gustafson, 1984; Varughese *et al.*, 1986).

The variation in the level of meiotic pairing observed amongst different plants could be dependent upon some of the following causes: (i) genotype of each plant; (ii) chromosome constitution of the third genome of each plant; (iii) heterochromatin constitution of rye chromosomes of each plant. Firstly, the homozygosity or heterozygosity in the wheat genotype component, the only one coming from two different sources, could have a minor importance. Jung and Lelley (1985a, b) and Jung *et al.* (1985) studied the cytological and morphological expression of interactions between wheat and rye genomes in hexaploid triticale lines, that were developed using genetically pure lines of both parental species. They demonstrated that interactions between the rye and wheat genomes in triticale, rather than their genotypic constitution are responsible for the reduction in chiasma number in hybrids heterozygous for the wheat, rye or both components. In a previous study, we used C-banding in meiosis as an approach to the analysis of wheat and rye genome interactions in triticale, and observed that pairing intensity in this amphiploid is more dependent upon the inter-genomic interaction between the rye and wheat genomes than upon their genotypic composition (Galindo and Jouve, 1989).

Secondly, the variation in the level of meiotic pairing observed amongst the different plants could be more influenced by the chromosome constitution of the third genome than for their

Table 3 Mean number of chiasmata per chromosome arm in homozygous normal (++), heterozygous (+-) and homozygous deficient (--) plants. *t*-tests concern the comparison of mean number of chiasmata per homologous arm among the three groups of plants. * = Significant at the level of 5 per cent. ** = Significant at the level of 1 per cent

Chromosome arm	Mean number of chiasmata in plants with			<i>t</i> test		
	3R ⁻⁻	3R ⁺⁺	3R ⁺⁻	3R ⁻⁻ = 3R ⁺⁺	3R ⁻⁻ = 3R ⁺⁻	3R ⁺⁺ = 3R ⁺⁻
2AS	0.84	0.81	0.77	0.385	0.644	0.373
2AL	1.31	1.23	1.21	0.743	0.807	0.155
4AS	0.80	0.60	0.50	1.294	1.322	0.357
4AL	1.17	1.06	0.99	0.915	1.242	0.462
5AS	0.77	0.73	0.63	0.353	1.226	0.704
5AL	1.21	1.19	1.13	0.262	0.872	0.681
6AS	0.83	0.81	0.81	0.152	0.127	0.002
6AL	1.17	1.16	0.95	0.007	1.055	1.086
7AS	1.07	1.01	0.96	0.770	1.092	0.450
7AL	1.08	1.13	1.12	0.337	0.302	0.007
1BS	0.72	0.67	0.61	0.415	0.619	0.304
1BL	1.15	1.01	1.13	0.287	0.179	0.649
2BS	1.04	1.01	0.93	0.408	0.844	0.522
2BL	1.13	1.07	1.15	0.501	1.345	0.555
3BS	0.89	0.85	0.75	0.617	0.780	0.520
3BL	1.23	1.19	1.15	0.369	0.542	0.212
4BS	0.85	0.79	0.87	0.529	0.193	1.032
4BL	1.24	1.20	1.15	0.314	0.859	0.483
5BS	0.49	0.48	0.54	0.004	0.298	0.220
5BL	1.25	1.17	1.23	0.562	0.174	0.291
6BS	0.77	0.72	0.61	0.319	0.733	0.475
6BL	1.08	1.08	1.04	0.000	0.363	0.318
7BS	0.83	0.71	0.72	0.813	0.783	0.055
7BL	1.16	1.02	1.08	0.499	0.922	0.212
1RS	0.34	0.31	0.32	0.147	0.121	0.121
1RL	0.88	0.82	0.84	0.492	0.296	0.149
3RS	0.58	0.58	0.13	0.056	3.402**	2.422*
3RL	0.81	0.86	0.70	0.336	0.543	0.751
4RS	0.59	0.61	0.64	0.103	0.283	0.145
4RL	0.84	0.78	0.68	0.478	0.900	0.422
5RS	0.55	0.48	0.52	0.462	0.187	0.252
5RL	0.95	0.93	0.93	0.249	0.130	0.000
6RS	0.29	0.18	0.18	0.847	0.705	0.000
6RL	0.95	0.94	0.92	0.144	0.168	0.235
7RS	0.30	0.20	0.32	0.690	0.104	0.582
7RL	0.90	0.88	0.81	0.247	0.866	0.639
No. plants	7	7	6			
No. PMCs	400	350	400			

genotype. A negative and significant correlation between the D/R ratio (number of chromosomes of D-genome/number of chromosomes of R-genome) and the mean number of chiasmata in rye chromosomes was observed ($r = -0.3785$; $t = 2.4189$; $df = 44$; $0.01 < P < 0.05$). This result seems to imply that a positive interference between D chromosomes and meiotic pairing of rye chromosomes exists. Rees (1955) and Rees and Thompson (1956) suggested that in rye, chiasma frequency and terminalization are polygenically controlled, and Lelley (1975a), Weimarck (1975), Jung and

Lelley (1985a, b) and Jung *et al.* (1985) demonstrated that the polygenic balance can break down when rye is placed in a wheat background. In conclusion, variations in the number of D chromosomes relative to R chromosomes present in the triticales background could affect with different intensity the meiotic stability of rye chromosomes. In hexaploid triticales (Thomas and Kaltsikes, 1974; Lelley, 1975b; Schlegel, 1978a; Jung and Lelley, 1985a, b; Jung *et al.*, 1985; Galindo and Jouve, 1989) and in wheat-rye addition lines (Schlegel, 1978b; Orellana *et al.*, 1984), rye

chromosomes always show reduced pairing at metaphase I, as an expression of their interaction with the wheat chromosomes. Recently, Fominaya and Orellana (1988) demonstrated a phenomenon of interference between wheat and rye chromosomes as a cause of the decrease of rye-rye and wheat-wheat homologous pairing observed at metaphase I in triticale with respect to their corresponding rye and wheat parents.

Finally, regarding the relationship between heterochromatin and chiasmata in both wheat and rye homomorphic bivalents it seems clear that chromosomes having C-bands in either the telomeres (rye) or pericentromeric regions (1B and 4B in wheat) had the lowest mean number of chiasmata. Moreover, arms having subtelomeric or intercalary blocks of heterochromatin (4AL, 2BS and 5BL) show increased levels of pairing relative to arms having similar or higher size. This agrees with the previous assumption of Dvorak and McGuire (1981) who suggested that differentiation at the level of pairing among genomes in *T. aestivum* could be related to the amount of DNA and heterochromatin present in chromosomes.

It was very interesting to note that chiasma number in chromosome arm 3RS in plants of constitution 3R+— was reduced by almost to a quarter in comparison with the equivalent homozygous condition, whether 3R++ or 3R—-. Although allelic differences between plants 3R++, 3R+— and 3R—- cannot be excluded, there was not a significant different behaviour of the remaining arms, not even 3RL (table 3), and these results led us to assume a local influence of the structure of C-heterochromatin on the pairing behaviour of each specific telomeric region. The present results on pairing behaviour of chromosome 3R suggest that the structural configuration of telomeric regions influences the pairing intensity, and this could be related with the interference between the DNA late replication of C-heterochromatin and cryptic structural requirements of the telomeric pairing initiation sites.

Previous studies of isogenic lines of triticale with or without telomeric heterochromatin in specific rye chromosome arms have indicated that the absence of C-heterochromatin increases chromosome pairing (Thomas and Kaltsikes, 1976; Merker, 1976; Schlegel, 1982; Schlegel and Huelgenhof, 1985). However, analysis of the 3RS chromosome arm in the present study suggests that there is no correlation between the presence or absence of C-heterochromatin and chromosome pairing in homozygous condition. This implies that heterochromatin content does not necessarily

affect meiotic pairing as much as its distribution. As a consequence, it could be perhaps suggested that the removal of telomeric heterochromatin in specific rye chromosomes is not as important as their homozygous (deficient or normal) structure which is reached early in the amphiploid triticale. Our results support the view of Bennett (1974) who pointed out that heterochromatin plays a major role in meiotic pairing failure and cytological stability in triticale. We suggest that both the heterochromatin structure and the chromosome constitution play an important role in meiotic stability in secondary lines of triticale, and that in consequence both factors are to be into account in reducing meiotic instability in triticale.

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